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Competitive exclusion of a burying beetle by mongoose

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Abstract

Competitive exclusion, a mechanism for local extinction of organisms, has been well established among taxonomically related species, including those within the same genus, family, or class in animal communities. This study, however, focuses on competitive exclusion that occurs across phyla, exemplified by the exclusion of a native insect by an invading exotic mammal, where food resources overlap. The hypothesis proposed in this study is that the small Indian mongoose (*Urva auropunctata*) has caused the local extinction of a burying beetle (*Nicrophorus nepalensis*) on Okinawa Is., Japan due to competition for carcasses of small vertebrates. To test this hypothesis, a comparison of beetle abundance was conducted between the area intensively controlled for mongoose and the area where mongoose control was weak or nonexistent. The former situated north of the boundary to prevent mongoose from crossing, and the latter located south of the boundary. To determine the user of carcasses on the forest floor, mouse carcasses were laid and their consumers were observed in each area. The results showed that the beetle abundance was clearly higher in the former than in the latter, and no beetles were collected where mongoose have never been controlled. The beetles often buried the mouse carcasses for their reproduction in the former, whereas in the latter, mongoose frequently consumed the

35 mouse carcasses. These results provide evidence of competitive exclusion of the burying
36 beetle by mongoose. This conclusion represents the first demonstration of competitive
37 exclusion across phyla in an animal community.
38
39 **Introduction**
40 There are various causes for local extinction of organisms (e.g., Branch et al. 2013). In
41 the case of physical and chemical factors, for example, habitat losses due to climate change
42 (e.g., Parmesan, 1996), volcanic eruption and fire (e.g., Williams et al. 2006), logging and
43 land reclamation (e.g., Grogan et al. 2010), abandonment of villages (e.g., Mauerhofer et al.
44 2018), and increase pollution and pesticide usage (e.g., Russell et al. 1995) have caused local
45 extinctions. In the case of biological factors, predation (e.g., Barun et al. 2010), hunting (e.g.,
46 Branch et al. 2013), parasitism (e.g., Schloegel et al. 2006), and hybridization (e.g., Rymer
47 and Simberloff 1996) have also caused local extinctions. In some cases, physical and
48 chemical factors have indirectly caused the local extinction of predators or parasites through
49 the reduction of their prey or hosts (e.g., Wood et al. 2010).
50 Competitive exclusion is a biological process whereby a species drives another species
51 to extinction through competition for resources, which may include food and habitat (e.g.,

52 Hardin 1960). In plant communities, competitive exclusion often occurs among
53 taxonomically distinct species such as the competition between conifers and broadleaved
54 trees during ecological successions (e.g., Vayreda et al. 2016). In animal communities,
55 however, laboratory studies have traditionally been used to assess competitive exclusion
56 among closely related species (e.g., Gause 1936). Recent field studies have also found
57 evidence of competitive exclusion through observations of exclusions of native species by
58 exotic invading species. In most instances, however, investigations have been conducted
59 among related taxonomic species that were within the same genus (e.g., Bøhn et al. 2008),
60 family (e.g., Porter and Savignano 1990), or class (Karatayev et al. 2009). Although
61 intensive competition across phyla has been reported in many cases (e.g., Brown and
62 Davidson 1976), all previous studies have been conducted among coexisting animals in the
63 field and have not confirmed local extinctions. In this study, I will demonstrate the first
64 example of competitive exclusion across animal phyla under field conditions.
65 As of 2021, UNESCO has added dense subtropical forests on four islands in
66 Southwest Japan to its list of natural World Heritages Sites. This included the "Yambaru"
67 region located in the northern part of Okinawa Is. (Fig. 1), where several endemic species
68 occur. However, the small Indian mongoose (*Urva auropunctata*; formerly *Herpestes*

69 *auropunctatus*), hereafter referred to as “mongoose”, is an exotic invading mammal that has
70 threatened the existences of some endemic small vertebrates in the region. Historically,
71 there were no mammal predators in the region, thus making the endemic vertebrates
72 potentially vulnerable to predation by introduced predators, such as mongoose. Mongoose
73 were introduced in the southern part of the island in 1910 to reduce rodent damage to sugar
74 cane plantations and to control vipers (Yagihashi et al. 2021). Since then, mongoose have
75 spread and reached the Yambaru region around 1990 (Yagihashi et al. 2021). Mongoose is
76 named in the IUCN list of 100 of the World’s Worst Invasive Alien Species (Lowe et al.
77 2000), and has caused various extinctions of numerous snakes, reptiles, amphibians,
78 shrews, and ground-nesting birds on some islands of the Caribbean and Hawaii (Hays and
79 Conant 2007). In the Yambaru region, Ozaki et al. (2002) reported that the distribution of
80 an endemic flightless bird, the Okinawa rail (*Gallirallus okinawae*), had been reduced,
81 potentially as a result of mongoose predation and competition.
82 To halt the negative impacts of mongoose, the national and local governments
83 launched mongoose eradication programs in the Yambaru region in 2000. An east–west
84 boundary (the SF line or Shioya Bay–Fukuji line; Fig. 1) was established in 2006 using
85 fences and dam lakes to prevent mongoose from crossing, and an intensive mongoose

86 culling program was conducted to the north of the boundary. The number of mongoose
87 collected in this area has decreased year by year, with only 33 collected in 2020, which is
88 one nineteenth of the number collected in 2000 (Okinawa-Amami Natural Environment
89 Office 2021). Three endemic bird species have since been observed to have returned to the
90 area (Yagihashi et al. 2021). Two additional boundaries, the ST line (Shioya Bay–Taira
91 line) and the line along Road No. 14 (the R14 line; Fig. 1), were established in the southern
92 area in 2013 and 2017, respectively. Currently, intensive mongoose culling occurs in the
93 area to the north of the R14 line.
94 To study relationships between necrophagous beetle assemblages and forest
95 environments, I used carrion-baited pitfall traps from the Yambaru region to the central
96 area of Okinawa Is. in 2013 and 2014. A burying beetle species (*Nicrophorus nepalensis*)
97 was frequently observed in the Yambaru region but was not detected in the central area,
98 despite similar forest environmental conditions prevailing in both areas (Ueda et al. 2016).
99 A pair of burying beetles of the genus *Nicrophorus* typically buries a small vertebrate
100 carcass such as that of a rodent, bird, amphibian, or reptile, which are then used as
101 nourishment for their broods (Pukowski 1933). Mongoose are also known to scavenge
102 intensively on small vertebrates (e.g., Abernethy et al. 2016). Therefore, I hypothesized that

mongoose may be locally excluding the burying beetle from accessing a small vertebrate carcass as a reproductive resource. To test this hypothesis, I collected *N. nepalensis* using traps in areas both located north and south areas of the SF line, and compared the beetle abundances between them. Next, I observed the consumers of mouse carcasses laid on the forest floor using an infrared sensor camera, to determine whether the reproductive resource of *N. nepalensis* was being stolen by mongoose. Based on my results, I discussed evidence for the competitive exclusion of the native burying beetle by the exotic mongoose.

Materials and methods

Study site

In 2017, I established 24 sites in the evergreen broad-leaved forests spanning the north to central regions on Okinawa Is. (Fig. 1a). Each site was located more than 200 m apart from one another. Among these sites, 14 were positioned to the north of the SF line, two sites were located between the SF line and the R14 line (an area known as the "buffer zone"), and eight sites were situated south of the R14 line (Fig. 1a). In the area north of the SF line, the intensive mongoose control (more than 4,000 trap days per year) has been continuously conducted from the year 2000 around the sites (within a 500 m radius from

each site). Around the two sites in the buffer zone, mongoose has continuously been controlled since 2000, with the exception of two-year intermittent lapse around the southern site (refer to detailed data provided in the repository). The intensive control began in 2015 around the northern site. For six of the eight sites located to the south of the R14 line, mongoose control activities had been implemented for a period ranging from one to six years prior to 2010 (Fig. 1a) (refer to detailed data provided in the repository). Furthermore, mongoose control measures were initiated in 2017 around the northernmost site. Notably, mongoose control has never been conducted around the two sites positioned to the south of the R14 line (Fig. 1a). In 2019, I established 27 sites with 21 of these sites coinciding with those set up in 2017 (Fig. 1b). Fifteen sites were placed north of the SF line, two sites were placed within the buffer zone, and 10 sites were placed south of the R14 line (Fig. 1b). Mongoose has never been controlled in the two additional sites located south of the R14 line (Fig. 1b).

Field trapping of *N. nepalensis*

Field trapping of *N. nepalensis* was conducted using hanging traps (see details in Appendix 1). Two fish-baited hanging traps were deployed at each site with a distance of

137 more than 100 m between them. It is known that *N. nepalensis* are active from autumn to
138 spring (Ueda 2019). In 2017, the traps were set on 14–17 Nov., and beetle collection and
139 replacements of propylene glycol and bait were carried out on 18–20 Jan., 15–16 March,
140 and 9–12 April, 2018. Trapping was concluded on 16–17 May 2018. In 2019, the traps
141 were set on 25–28 Oct., and beetle collection and replacements of propylene glycol and bait
142 were performed on 11–13 Dec. 2019 and 7–8 Feb. 2020. The beetle collection was planned
143 to be conducted every two months, but due to COVID-19, I was unable to visit Okinawa,
144 and trapping had to be terminated on 10–12 July 2020, with an interval of five months.
145
146 Observation of consumers of mouse carcasses
147 During the 2017–2018 collection period, I conducted observations of consumers of
148 mouse carcasses on the forest floor at one of the two beetle-trapping locations within each
149 site. Mouse carcasses were sourced in pet shops where they are commercially sold as food
150 for carnivorous pet. I selected a white mouse weighing approximately 35 g (mean: 33.9 g,
151 range: 30.1–39.6 g) due to its conspicuousness and appropriate size for burying by *N.*
152 *nepalensis*. Two mice were used for the observation, with one covered with a steel rack and
153 a concrete block to prevent interference from animal scavengers (Appendix 2). The hind leg

154 of the mouse was tied to the steel rack with dental floss to track the position of the buried
155 mouse (Appendix 2). An infrared sensor camera (Ltl-6210MC, Ltl Acorn®) was placed
156 near the mice (Appendix 2). Photographs were also taken every hour with the interval
157 function of the camera. Details of the setup for the observation are provided in Appendix 2.
158 The first observation session was conducted from 9–12 to 12–15 April 2018, for a
159 duration of 3–4 days. Subsequently, the mice were replaced, and the second observation
160 session was conducted from 12–15 to 23–25 April 2018, for a duration of 10–11 days.
161 After completing each observation session, I checked for the presence and condition of the
162 mouse. If the mouse was found unchanged, it was considered “not used”. If any residues
163 (such as hair, bones, tail, and/or skin) were found on the ground, it was regarded as
164 “consumed on the ground by invertebrates”, and I attempted to identify the consumers
165 (such as maggots, *N. nepalensis*, necrophagous dung beetles (*Onthophagus itoi*), a hermit
166 crabs (*Coenobita cavipes*) and/or another species of land crab), either within and/or beneath
167 the residue or through interval photography. If a mouse was found buried and one or two
168 adults of *N. nepalensis* were present inside or near a carcass (Appendix 3), it was
169 categorized as being "buried by *N. nepalensis*" for the purpose of reproduction. If the
170 mouse was not found, and the tied dental floss was cut, it was considered as “disappeared”.

If the mouse without the cover disappeared shortly after photographs of mongoose were taken, it was considered to have been “consumed by mongoose” (Appendix 4a). Similarly, if the mouse with the cover disappeared and several photographs of mongoose were taken around the concrete block after the mouse without the cover had disappeared, it was considered to have been “consumed by mongoose” (Appendix 4b). While I could not confirm from photographs that the mouse with the cover was consumed by mongoose, it is likely that mongooseucceeded in pulling the floss with its forelegs and/or mouth and fed upon it. When the mouse carcass disappeared after photographs of other vertebrates (such as crows (*Corvus macrorhynchos*), domestic cats, rats, or boars (*Sus scrofa*)) were taken, it was considered to have been “taken away or consumed by other vertebrates”. If the mouse disappeared without any photographs of vertebrates, it was regarded as “disappeared due to unknown factors”.

Data analysis

To demonstrate the impact of mongoose on *N. nepalinsis*, illustrations of the relationships between the number of collected beetles per trap at each site and the average distance to the two trapping locations from the SF line in north or south direction were

188 presented. The comparison of the number of beetles collected per trap was conducted
189 between sites positioned to the north and south of the SF line using the Kruskal-Wallis test.
190 For this analysis, JMP 8 (SAS Institute 2009) was employed. Additionally, the correlation
191 analysis assessing the relationships between the number of beetles collected per trap and
192 the distance from the SF line was performed utilizing the Pearson product-moment
193 correlation coefficient. This analytical procedure was executed independently for the
194 northern and southern regions of the SF line due to the substantial disparity in beetle
195 abundance between these areas. Microsoft Excel for Mac ver. 16.51 (Microsoft 2019) was
196 used for this analysis.
197 Additionally, the relationships between mongoose density and beetle abundance were
198 displayed. To obtain mongoose density data, I utilized the number of mongoose captured
199 by the cylinder trap (Yambaru Wildlife Conservation Center 2023) in 2016 - 2018. The
200 Ministry of the Environment has had extensive use of this type of traps in the area north of
201 the SF line since 2007, and the government of Okinawa Prefecture has been using these
202 traps within the buffer zone since 2013. The mongoose home range is estimated to be from
203 1.0 to over 50 ha in the Caribbean Isls. and range from 6.0 to over 70 ha in Hawaii
204 (Berentsen et al. 2017). Therefore, I used the number of mongoose caught per day per

205 cylinder trap set within a 500 m radius (c.a. 78.5 ha) of the beetle trapping location as the
206 data for mongoose density. Mongoose densities differed between traps in the same site
207 because pairs of traps in the same site were more than 100 m apart, while the cylinder traps
208 were often set within 10–40 m distances; thus, all beetle trap data were treated
209 independently. Since no cylinder traps for mongoose were set within a 500 m radius of the
210 beetle trap location in the area south of the R14 line in 2016 - 2018, the relation data
211 between the mongoose density and the beetle abundance was not indicated except for a data
212 for the beetle trap set nearest to the road (Trap No. Gen 2-1 shown in the repository).
213 It is known that *N. nepalensis* is a species that inhabits forested areas (Ueda 2019).
214 The abundance of other forest *Nicrophorus* species, such as *N. quadripunctatus,* which is
215 present in Japan (with exception of the southern islands), is known to significantly increase
216 with incresing canopy cover (Ueda and Sato 2020). In order to identify the environmental
217 factors that affect the abundance of *N. nepalensis*, the relationship between the beetle
218 abundance and canopy cover percentage was illustrated. The correlations of these
219 relationships were further analyzed using the Pearson product-moment correlation
220 coefficient. Microsoft Excel for Mac ver. 16.51 (Microsoft 2019) was used for this analysis.
221 In order to determine the canopy cover percentage at the trapping location, hemispherical

222 photographs were taken using a digital camera (Nikon Coolpix 4500) equipped with a
223 fisheye lens (Nikon FC-E8) at a height of 1.2 m directly adjacent to the traps on 12–15
224 April 2018 and 9–11 July 2020. The LIA32 software ver. 0.378 (Yamamoto 2008) was
225 utilized to compute the canopy cover percentage from the hemispherical photographs. Since
226 the canopy cover percentages differed between traps in the same site, all beetle trap data
227 were treated independently.

228 To demonstrate whether the mongoose is appropriating the reproductive resource of
229 *N. nepalensis* in the area south of the SF line, the utilization proportion of classified
230 consumers on mouse carcasses with or without covers was illustrated through observations
231 conducted in the area south of the R14 line, within the buffer zone, and in the area north of
232 the SF line, respectively. The comparison of category frequencies, specifically categorized
233 as carcasses buried by *N. nepalensis*, those consumed by mongoose, and other categories
234 was subjected chi-square tests between the areas situated north and south of the SF line.
235 This comparative analysis was independently carried out for observation sessions with and
236 without cover. JMP 8 (SAS Institute 2009) was utilized for this analysis.

237

238 **Results**

239 The abundance of *N. nepalensis* was notably higher in the northern area of the SF line
240 compared to the southern area for both sampling periods (Fig. 2). The abundances were
241 significantly differed between the northern and southern areas of the SF line by Kruskal-
242 Wallis test for both periods ($Z = -4.07$, $P < 0.0001$ for the 2017–2018 period, and $Z = -4.37$,
243 $P < 0.0001$ for the 2019–2020 period). During the 2017–2018 period, the abundance was
244 moderate within the buffer zone when compared to the areas north of the SF line and south
245 of the R14 line (Fig. 2a). No beetles were captured at the sites where mongoose has never
246 been controlled (Fig. 2a). However, even in the area south of the R14 line, a limited number
247 of individuals (0.5–4.5 per trap) were collected at the sites where mongoose has/had been
248 controlled (Fig. 2a). In the 2019–2020, there was no difference between the traps within the
249 buffer zone (2.0–12.5 per trap) and those where mongoose has/had been controlled in the
250 area south of the R14 line (4.0-9.0 per trap) (Fig. 2b). No beetles were captured at the sites
251 where mongoose has never been controlled (Fig. 2b). The abundance exhibited a negative
252 correlation with distance from the SF line in both the northern and southern directions
253 (Table 1). This correlation attained statistical significance in the northern direction during
254 the period of 2017–2018 and in the southern direction during the period of 2019–2020
255 (Table 1).

No mongoose was caught in the area north of the SF line, while a few were caught in the area south of the line (Fig. 3). The presence and absence of mongoose affected the beetle abundance during both sampling periods but the mongoose density did not affect the beetle abundance in the area where mongoose were present (Fig. 3).

In the area north of the SF line, there was a significant increase in beetle abundance in conjunction with an increase in the canopy cover percentage during both sampling periods ($r = 0.46$, $P = 0.023$ for 2017–2018 period, and $r = 0.40$, $P = 0.042$ for 2019–2020 period), despite the narrow range of canopy cover percentages: 92.5–99.3 % for 2017–2018 period and 93.1 - 99.0 % for 2019–20 period, respectively (Fig. 4). Conversely, in the area south of the SF line, there was no significant relationship observed between the beetle abundance and the canopy cover percentage for both collections ($r = 0.20$, $P = 0.397$ for 2017–2018 period, and $r = 0.19$, $P = 0.389$ for 2019–2020 period) (Fig. 4).

During observations of consumers of mouse carcasses, as expected mongoose were only observed to the area south of the R14 line (Fig. 5). More than half of the carcasses were consumed by mongoose in this area, and the proportion of mice consumed did not differ between the first and second observation sessions (Fig. 5). The mice that were buried by *N. nepalensis* were observed only to the area north of the SF line (Fig. 5). The

proportion of buried mice was lower during the first observation session than during the second, in which more than half of the mice were buried (Fig. 5). Within the buffer zone, all the mice were consumed on the ground by invertebrates except for one mouse carcass that was taken away by a domestic cat (Fig. 5). The frequency of the three categories exhibited significant differences between the areas situated north and south of the SF line across all observations (Table 2). During the first observation session, all the mice were buried by the adults to a depth of several centimeters and had not been processed into spherical shape, whereas during the second observation session all the buried mice were already spherical, and some had their bodies collapsed by larval feeding.

Discussion

In the area north of the SF line, where no mongoose were captured near the study sites due to the intensive mongoose control, the abundance of *N. nepalensis* was high, and the beetle abundance increased with an increase in canopy cover percentage. Many mouse carcasses were buried by *N. nepalensis* for their reproduction. Conversely, in the area south of the SF line, where a few mongooses were captured near the study sites or where no mongoose control had been conducted during 2016–2018, the beetle abundance was low

where mongoose has/had been controlled for one year or longer, and zero where mongoose has never been controlled. A considerable number of mouse carcasses were consumed by mongoose, and the correlation between the beetle abundance and canopy cover percentage was not observed, likely due to the pressure exerted by mongoose. Based on these results, I conclude that this exotic mammal has locally excluded the native insect through competition for small vertebrate carcasses on the ground in the forests of Okinawa Is. This conclusion represents the first demonstration of competitive exclusion across phyla in the animal community.

The competitive exclusion of *N. nepalensis* by mongoose probably did not occur solely through the consumption of carcasses but also through predation on small vertebrates. On Amami-Oshima Is. (Fig. 1), which is another heritage island invaded by mongoose, mongoose predation pressure resulted in reduced abundances of endemic rabbits, woodcocks, two reptile species, and three frog species (Watari et al. 2008). Such mongoose predation pressure could have indirectly contributed to the local extinction of *N. nepalensis* by reducing the abundance of vertebrates of sizes suitable for *N. nepalensis* reproduction on Okinawa Is. Although incidental predation of *N. nepalensis* that are feeding, processing, or nurturing their broods on carrion may happen, predation of burying

beetles by mongoose has never been documented worldwide (Young, 2014). In Japan, while numerous insects have been observed in the gut of mongoose, no remains of burying beetle have been reported (Abe, 1992; Ogura et al., 2002; Funakoshi et al., 2012), implying that the direct pressure of mongoose predation on *N. nepalensis* is minimal and likely incidental if it occurs.

The low numbers of buried carcasses observed during the first session may be attributed to its relatively short duration compared to the second session. Beetles of the genus *Nicrophorus* are capable of reproducing on decayed carcasses that have already been oviposited by flies (e.g., Springett 1968), thus increasing the proportion of buried carcasses over time in the second session. Within the buffer zone, neither carcasses buried by the beetle nor those consumed by mongoose were observed, possibly due to the low densities of both beetles and mongoose.

The intensive control of mongoose has been carried out within the buffer zone since 2013, leading to the expansion of *N. nepalensis* distribution through competitive release from mongoose. This, in turn, could have resulted in an increase in the number of beetles flying into the area south of the R14 line between the 2017–2018 and 2019–2020 sampling periods, leading the significant negative relationship between the beetle abundance and the

distance from the SF line in the latter period. The expansion of the distributions of three endemic birds, which were released from the mongoose predation and competition pressure, has been also observed in the buffer zone (Yagihashi et al. 2021). The competitive release of *N. nepalensis* from mongoose may rapidly expand because *Nicrophorus* spp. are good flyers (Creighton and Schnell 1988, Attisano and Kilner 2015). The first record of *N. nepalensis* in Japan was documented by Kurowasa (1980) based on a specimen collected in 1964 at Yona, Kunigami, situated to the north of the SF line. The introduction of mongoose to the island in 1910 might have potentially led to the extirpation of *N. nepalensis* in the southern and central regions of Okinawa Is. before the first record. Nevertheless, future research concerning the competitive release of *N. nepalensis* within such regions must seek to reaffirm the historical evidence of competitive exclusion.

I attempted to analyze the relationships between the abundance of *N. nepalensis* in the area north of the SF line and various environmental metrics that I measured, including tree density, mean diameter of trees at breast height (DBH), maximum DBH, basal area of trunks, and canopy cover percentage (refer to detailed data provided in the repository). Unfortunately, no statistically significant relationships were discerned except for canopy cover percentage. Ueda and Kanetani (in prep.) observed correlations between the

341 abundances of three diurnal necrophagous dung beetles and canopy cover percentages
342 ranging from 95.6% to 99.4% within a conifer plantation forest. This finding demonstrates
343 the capacity of necrophagous beetles to respond to the relatively narrow range of canopy
344 cover. However, it is worth noting that *N. nepalensis* was primarily observed to be
345 nocturnal, as evidenced by the burial of mouse carcasses occurring during nighttime based
346 on photographs captured hourly by the sensor camera deployed in this study. Further study
347 is needed to clear the mechanism underlying *N. nepalensis*' response to canopy cover. The
348 negative correlation between beetle abundance in the northern area of the SF line and
349 distance from the SF line is likely attributed to the differences in canopy cover.
350 Specifically, the six trap positions within the three north-western coastal sites exhibited low
351 canopy cover (mean: 96.7%, range: 92.5% – 99.2% in 2017–2018 and 96.5%, 93.2% –
352 98.1% in 2019–2020), resulting in reduced beetle captures by these traps (mean: 44.6,
353 range: 12 – 70 in 2017–2018 and 38.5, 20 – 52 in 2019–2020). This phenomenon
354 accounted for the negative relationships between abundance and distance.
355 In the future, mongoose eradication program may be extended into the area south of
356 the R14 line. This expansion was initiated in 2022 on Yagachi Island, located
357 approximately 3 km southwest of the R14 line and is connected to Okinawa Is. by bridges.

Future research concerning the competitive release of *N. nepalensis* should not only seek to reaffirm the historical evidence of competitive exclusion as previously mentioned, but also has the potential to develop a mathematical model for estimating mongoose density using beetle collection data. Canopy cover percentage could be incorporated as an environment variable into the formula. This formula would likely be a useful and important tool for monitoring mongoose density in mongoose eradication programs. Presently, mongoose density is monitored using the cylinder traps with limited capture efficiency, necessitating daily checks to mitigate the risk of inadvertent capture leading to the mortality of domestic vertebrates. In contrast, beetle traps are sufficient to set them sparsely and only require monthly or less frequent check-ups.

Conclusion

The abundance of the burying beetle (*Nicrophorus nepalensis*) was high in the area north of the SF line, the first boundary preventing the small Indian mongoose (*Urva auropunctata*) from crossing. Intensive control of this alien small carnivore began in this area from 2000 onwards, and no mongoose were caught near the beetle trapping locations in these years. Conversely, beetle abundance was either zero or low in the area south of the

SF line, where a few mongoose were caught near the beetle trapping locations or where no mongoose control has been conducted in these years. In the area north of the SF line, many mouse carcasses on the forest floor were buried by *N. nepalensis* as food for their broods. In contrast, in the area south of the SF line, many mouse carcasses on the forest floor were consumed by mongoose. The variance in beetle abundance in the area north of the SF line was likely due to the variance in forest conditions, as beetle abundance increased with an increase in canopy cover percentage. However, this relationship was not observed in the area south of the SF line due to mongoose pressure. From these results, I concluded that this exotic mammal had locally excluded the native insect through competition for small vertebrate carcasses on the ground of forests of Okinawa Is. forests.

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Conflict of interest statement

The author declares no conflict of interest.

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504 **Legend of Figure**

505 **Fig. 1** Study sites during the 2017–2018 (a) and in 2019–2020 (b) sampling periods on
506 Okinawa Is., Japan
507 SF line: the first boundary established to prevent mongoose from passing through in 2006.
508 Line along Road No. 14: an additional boundary established in 2017. Closed circle: a site
509 subject to ongoing, rigorous mongoose control since the year 2000 in its vicinity. Grey
510 circle: a site where mongoose control has/had been conducted for a duration of one year or

longer in its vicinity. Open circle: a site lacking historical mongoose control in its vicinity.

Fig. 2 Relationships between the abundance of *Nicrophorus nepalensis* at each site and the distance from the first boundary established to prevent mongoose from passing through in 2006 (the SF line shown in Fig. 1)

a: 2017–2018 collection, b: 2019–2020 collection. The line along Road No. 14 is an additional boundary established in 2017 (shown in Fig. 1). Closed, grey, and open circles are ditto with Fig. 1.

Fig. 3 Relationships between the number of *Nicrophorus nepalensis* collected by each beetle trap and the number of mongoose caught per day per cylinder trap set within a 500 m radius of the beetle trap location in 2016 - 2018

a: 2017–2018 collection, b: 2019–2020 collection. Closed circle: data in the area north of the SF line, open circle: data in the area south of the SF line. The beetle trap data that did not have corresponding cylinder traps set within a 500 m radius of the beetle trap were removed.

Fig. 4 Relationships between the number of *Nicrophorus nepalensis* collected by each beetle trap and the canopy cover percentage

a: 2017–2018 collection, b: 2019–2020 collection. Closed and open circles are ditto with

528 Fig. 3.

529 **Fig. 5** Utilization percentage of classified consumers of mouse carcasses

530 a: first observation session conducted for a duration of 3–4 days from 9–12 to 12–15 April,

531 2018, b: second observation session conducted for a duration of 10–11 days from 12–15 to

532 23–25 April, 2018. S: data in the area south of the line along Road No. 14, B: data within

533 the buffer zone (between the line along Road No. 14 and the SF line), N: data in the area

534 north of the SF line.

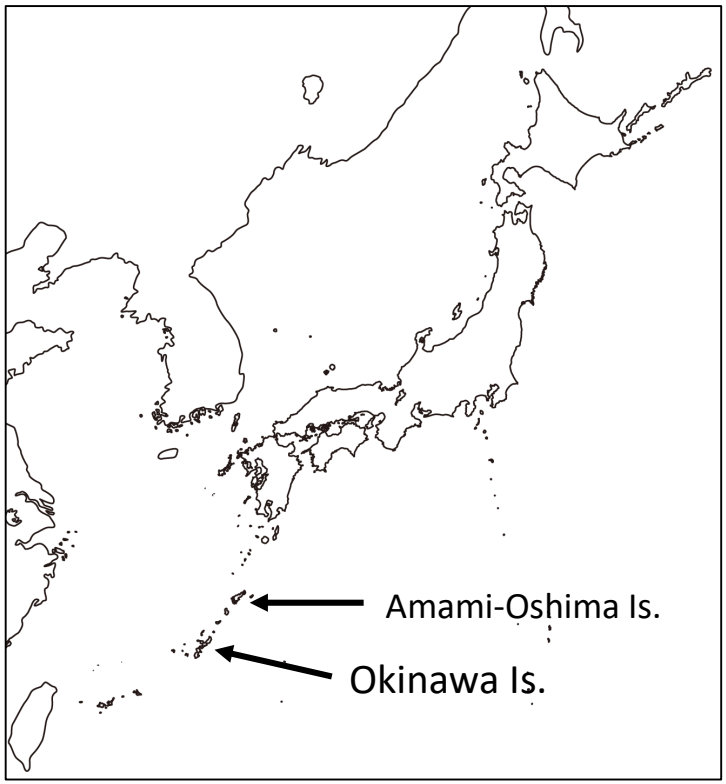
Table 1 Results of the Pearson product-moment correlation coefficient between the number of beetles collected per trap and the distance from the SF line

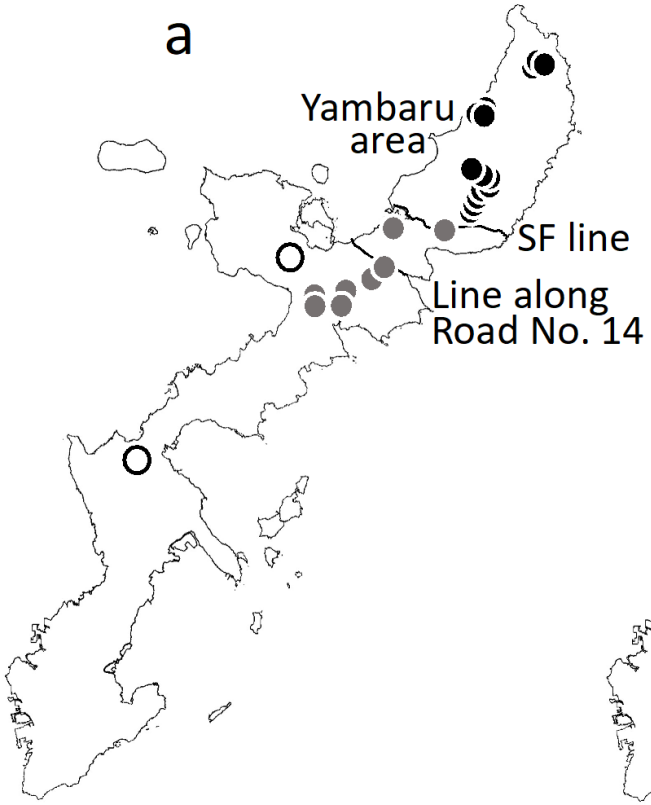
Sampling period	2017–2018		2019–2020	
	r	*P*	r	*P*
North of the SF line	**-0.58**	**0.030**	-0.36	-0.186
South of the SF line	-0.58	0.081	**-0.66**	**0.019**

Table 2 Results of chi-square test for the frequency of three categories of mouse carcass utilization (carcasses buried by *Nicrophorus nepalensis* , those consumed by mongoose, and other categories) between the areas situated north and south of the SF line

	1st observation session		2nd observation session	
	Likelihood ratio	*P*	Likelihood ratio	*P*
Without cover	**12.0**	**0.0025**	**18.2**	**0.0001**
With cover	**12.4**	**0.0020**	**24.2**	**< 0.0001**

Fig. 1


Amami-Oshima Is.
Okinawa Is.


a
Yambaru area
SF line
Line along Road No. 14

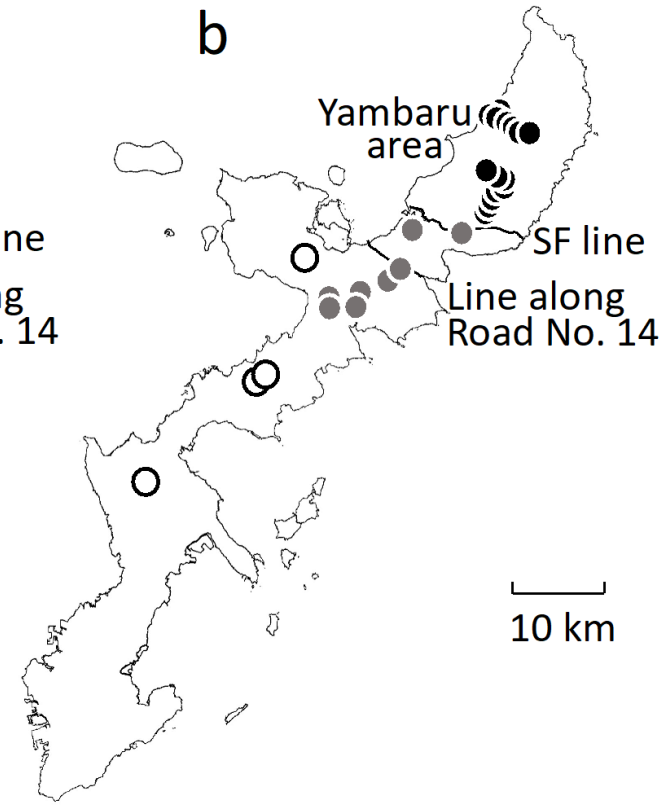

b
Yambaru area
SF line
Line along Road No. 14
10 km

Fig. 2

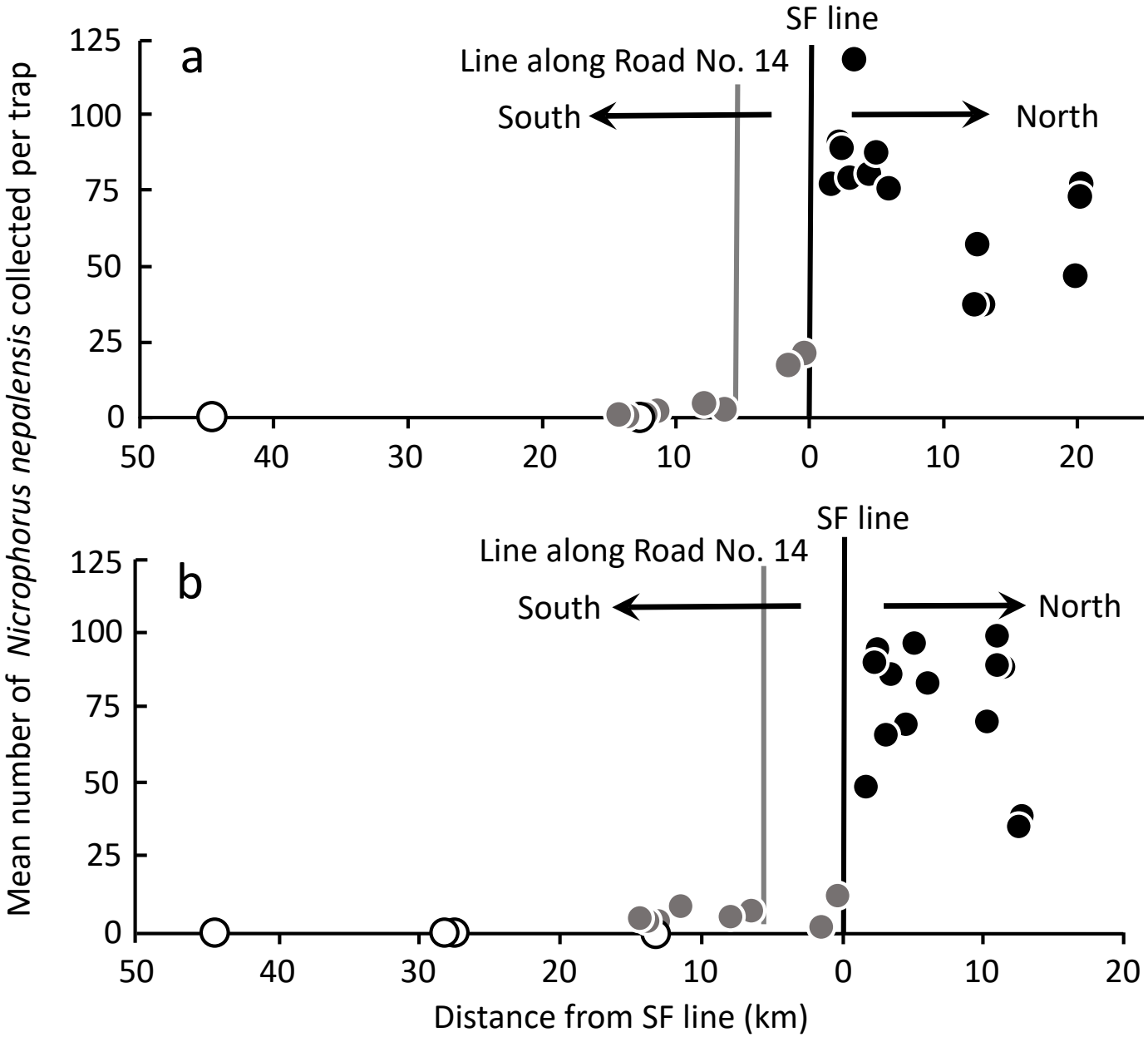

a
b
SF line
Line along Road No. 14
South
North
Mean number of Nicrophorus nepalensis collected per trap
Distance from SF line (km)
125
100
75
50
25
0
50
40
30
20
10
0
10
20

Fig. 3

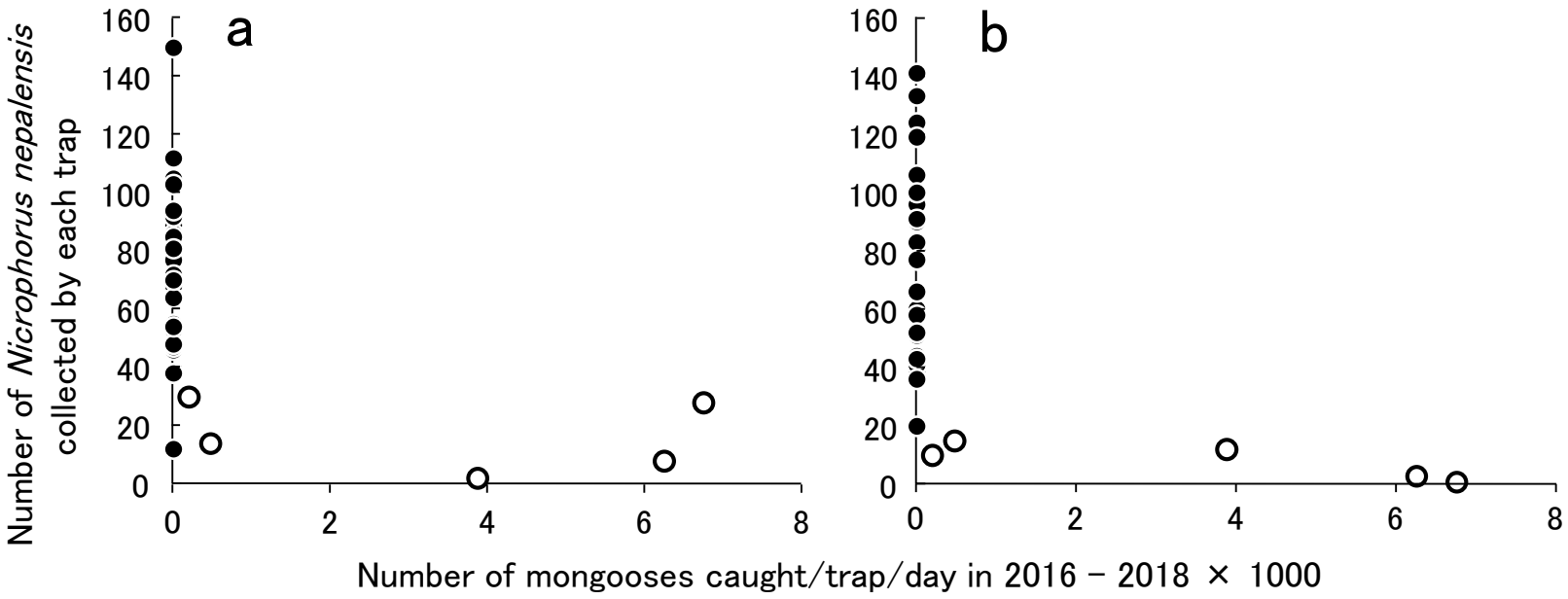

a
b
Number of *Nicrophorus nepalensis* collected by each trap
0
20
40
60
80
100
120
140
160
0
2
4
6
8
Number of mongooses caught/trap/day in 2016 – 2018 × 1000

Fig. 4

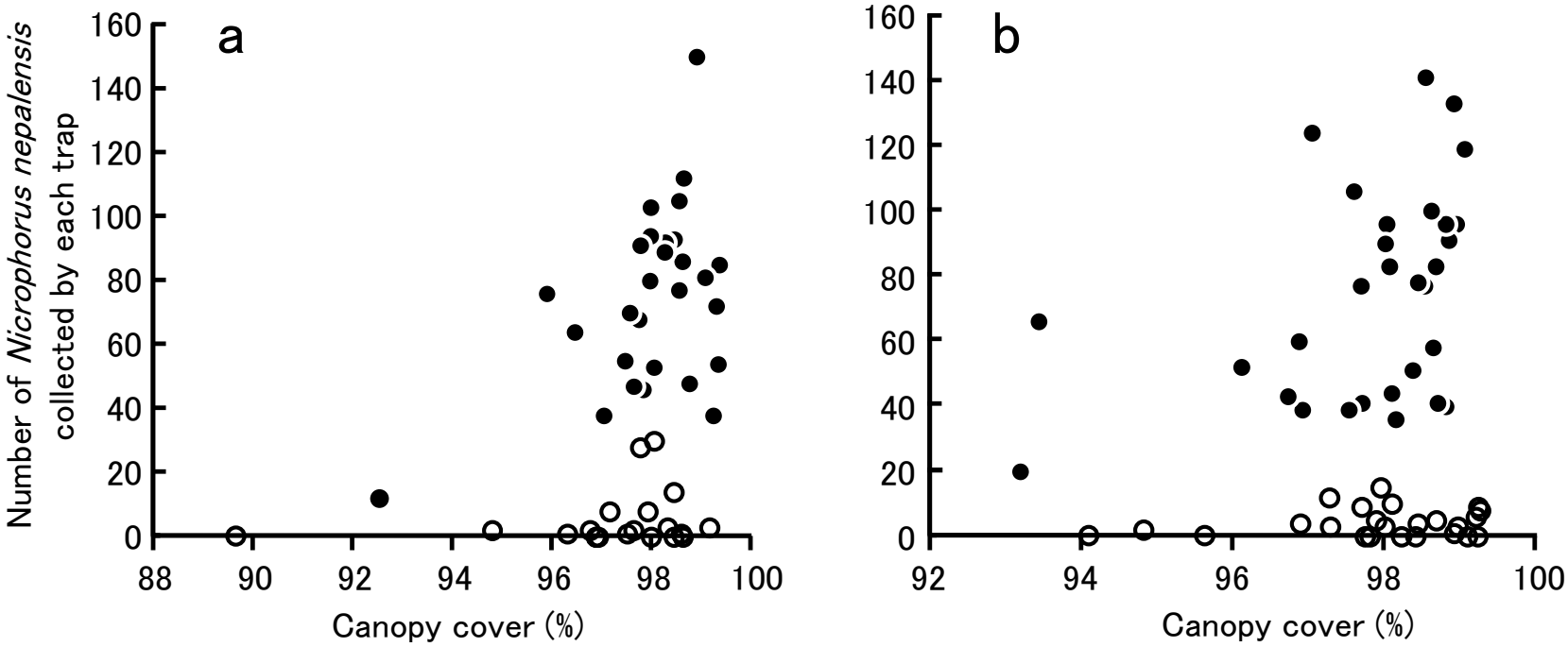
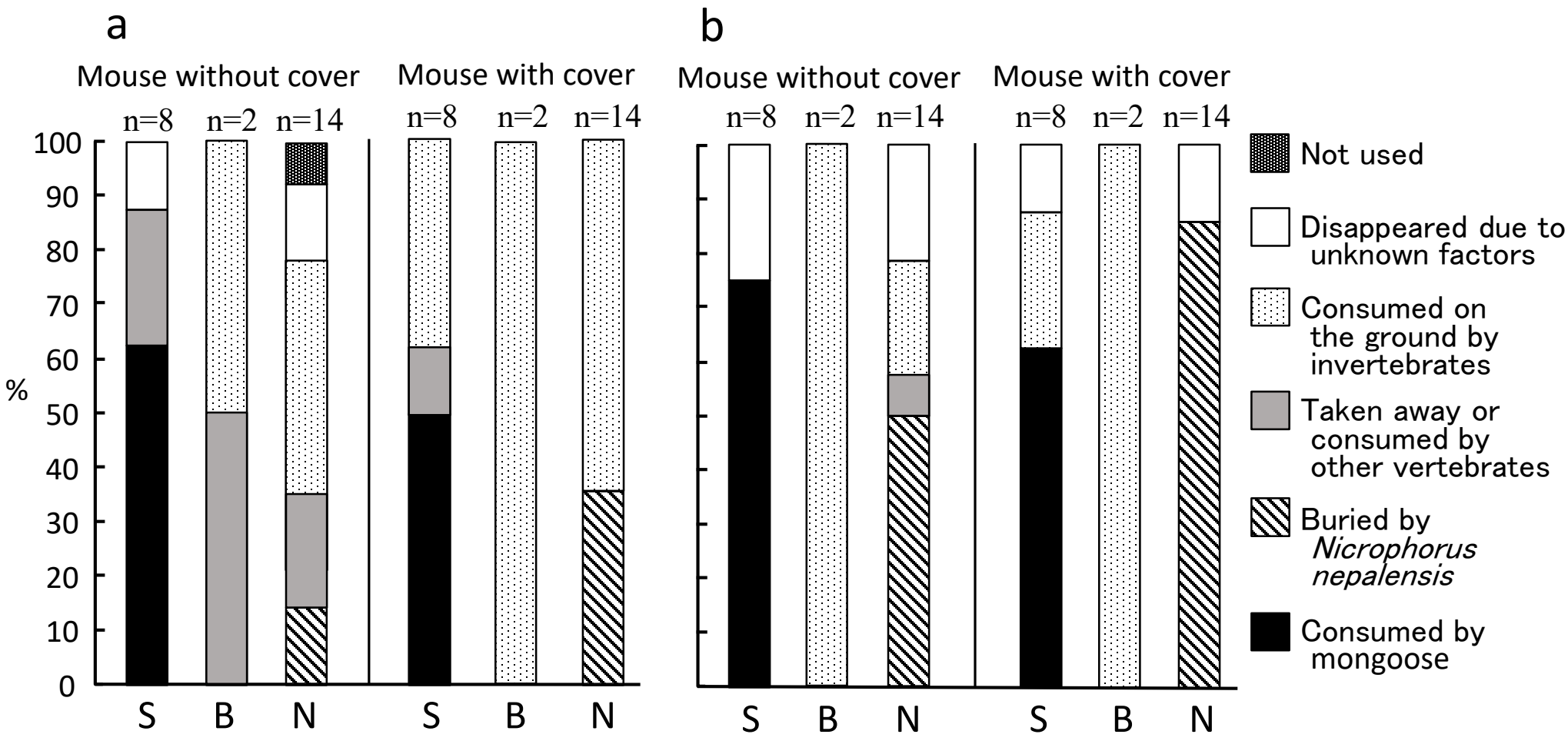

a
b
Number of *Nicrophorus nepalensis* collected by each trap
Canopy cover (%)
Canopy cover (%)
0
20
40
60
80
100
120
140
160
88
90
92
94
96
98
100

Fig. 5


a
b
Mouse without cover
Mouse with cover
n=8
n=2
n=14
100
90
80
70
60
50
40
30
20
10
0
%
S
B
N
Not used
Disappeared due to unknown factors
Consumed on the ground by invertebrates
Taken away or consumed by other vertebrates
Buried by Nicrophorus nepalensis
Consumed by mongoose