LIFE HISTORY TRAITS OF FIVE GROUND BEETLE (COLEOPTERA: CARABIDAE) SPECIES COMMON IN HONSHU ISLAND, JAPAN

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Ground beetles have been used as bioindicators for monitoring environmental changes. However, to interpret monitoring results, we need further information on their life-history traits. We selected Harpalus griseus, H. eous, H. tridens, Synuchus cycloderus and Carabus procerulus, species common in Honshu Island, Japan. We examined their hind wings, flight muscles, gut contents and ovarian eggs to understand their flight activity, feeding traits and reproductive strategies. The three Harpalus species showed wing length / body length ratios (W/B) of 0.88–0.99. In H. tridens, the proportion of individuals with flight muscles and caught in aerial traps was lower than in the other two. S. cycloderus was macropterous with a W/B ratio of 0.75, but no individual was caught in aerial traps, and none possessed flight muscles. Carabus procerulus was brachypterous. The three Harpalus species fed mainly on seeds and partly on arthropods. S. cycloderus was a generalist predator. Gut contents of C. procerulus consisted of amorphous fluid, suggesting extra-oral digestion. Egg type was categorized by the number and size of ovarian eggs. Synuchus cycloderus had many-small eggs, while the other four had few but large eggs.

Keywords: Coleoptera, Carabidae, life-history, bioindicator, fecundity, feeding traits, flight activity, reproductive strategy.

INTRODUCTION

At least 40,000 species of ground beetles (Coleoptera: Carabidae) have been described in the world (Thiele 1977). Because ground beetles are sensitive to environmental changes in their habitat, they are frequently used for monitoring these changes (Brooks et al. 2012). For example, field surveys on ground beetles exhibit chronological changes in abundance and species composition in response to environmental changes (Lövei & Sunderland 1996). However, we cannot fully understand the reason their response because of the shortage of basic information on life-history traits of each species. To overcome this shortage, we intend to incorporate various data obtained through the dissection of ground beetles with field surveys.

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In Japan, at least 1,500 carabid species have been identified (Hori 2006). The Biodiversity Center of Japan selected ground beetles as one of the bioindicator groups for environmental changes since 2003 through “Monitoring Sites 1,000 Project” (Ministry of the Environment of Japan 2003). They have focused on species believed to be sensitive to environmental changes. Although ground beetles are not habitual fliers (e.g. Thiele 1977), the response to environmental changes is expected to be different between flying species and non-flying species (Magura & Lövei 2020). Consequently, we employed aerial traps to capture flying individuals.

Ground beetles can be short- or long-winged (brachypterous and macropterous, respectively). The information on their wings is indispensable for understanding flight activity (Shibuya et al. 2018) because only macropterous adults are capable of flying. However, under natural conditions, the wings are folded and hidden beneath the elytrae, so databases usually do not provide enough information about the wing type of a given species.

Furthermore, the development of flight muscles is essential for flying (van Huizen 1977, Nelemans 1987, Fujisaki 1994, Desender 2000, Matalin 2003, Kotze 2008, Kotze et al. 2011). However, flight muscles of ground beetles have been less studied (but see van Huizen 1977, Nelemans 1987, Desender 2000, Matalin 2003).

Flight activity is related to feeding traits and reproductive strategy (e.g. Fujisaki 1994, Ikeda et al. 2008). However, the information on the food of many ground beetles have not yet been clarified, and even syntheses (Larochelle 1990) are lists of often observations in the field and laboratory, because recent analytic techniques, such as DNA analysis and stable isotope method, are not always omnipotent and easily applicable. Nevertheless, since species with various feeding habits may respond differently to environmental changes (Magura et al. 2019), detailed research on this trait is inevitable. In the light of previous studies that revealed the food of ground beetles by examining gut contents (Ishitani 1996, Sunderland et al. 1995), we also tried to clarify the feeding traits based on gut contents. Several insects have flight ability before reproduction but often lose it later (Fujisaki 1994). Similarly, some species of ground beetles develop flight muscles in the early adult stage, and their muscles degenerate later (Matalin 2003). We tried to confirm if this phenomenon exists among the species studied.

In this study, we selected five species of ground beetles for comparative study. Two of them, Harpalus griseus (Panzer) and Harpalus eous Tschitschéréine were captured most frequently in aerial traps (Malaise and flight interception traps). The remaining three species, Synuchus cycloderus (Bates), Harpalus tridens Morawitz and Carabus procerulus procerulus (Chaudoir) responded sensitively to vegetation cutting (Shibuya et al. 2014). The purpose of this study was to clarify the flight activity, feeding traits, and reproductive strategy of
the five species through the dissection of individuals captured in pitfall and flight traps.

**MATERIAL AND METHODS**

**Collection methods**

We collected adults of the five selected species from Oaota-no-Mori Satoyama landscape, Kasiwa City, Chiba Prefecture, Honshu Island in central Japan (100 ha, 35°54’N, 139°55’E, 18–25 m a.s.l.). The landscape consists of grassland, broad-leaved forest, coniferous forest and bamboo stand.

Pitfall traps: We used unbaited pitfall traps (plastic cups with 102 mm in top diameter, 123 mm in depth with five 1–2 mm holes for drainage at the bottom). A total of 196 traps were set once a month in June, July, September and November 2011 and in June, July, September and October 2012 and October 2013, 9 times in total. We also collected ground beetles once a week from 32 out of the 196 traps, 44 times in total, from April 2012 to April 2013.

Aerial traps (Malaise and flight interception traps): We set three Malaise traps, and 10 flight interception traps to capture flying individuals from October to December 2012 and April to December 2013. We collected ground beetles weekly, 54 times in total.

**Examination of flight potential**

Hind wing – We examined the morphological features of hind wings of 54, 70, 157, 924 and 32 individuals of *H. griseus*, *H. eous*, *H. tridens*, *S. cycloderus* and *C. procerulus*, respectively. The elytrae and the right hind wing were removed from the body, and that hind wing was glued on a slip of drafting paper. We observed morphological features of the hind wing and measured its length from the base to the tip with digital callipers (measurable up to 0.01mm precision) under a binocular microscope (Olympus SZX10) at a magnification of 10× (zoom ratio is 0.63 to 6.3×). The body length was measured from the front margin of the labrum to the apex of elytra using digital callipers. We calculated the hind wing length to body length (W/B) ratio for all five species.

Flight muscles – We dissected the thorax of the individuals mentioned above and examined the existence of flight muscles beneath the thorax under a binocular microscope.

The ratio of aerial trap catch: In addition to the information on flight muscles, we evaluated the flight activity using the relative abundance of individuals captured in aerial traps to the total number of individuals captured: Aerial activity ratio = the numbers captured in aerial traps / (the numbers captured in aerial traps + pitfall traps).

**Dissection methods – gut contents**

To clarify feeding habits, we removed the guts of dissected individuals and examined their contents under a binocular microscope. When the contents consisted of fluid or amorphous material without animal fragments, we designated them as amorphous fluid. Next, we performed a paper strip test (Uri Ace BT Terumo, Japan) for detecting protein and glucose and used iodine for detecting starch. Subsequently, we mounted the gut contents on a slide to examine animal fragments and starch particles under an optical microscope (Nikon ECLIPSE E800, 40–400× magnification).
**Dissection of the ovaries**

We removed the ovaries to examine their maturity and counted the number of ripe eggs separated from the ovaries. We measured the size of ripe eggs along their major axis using the photo taken under a binocular microscope, and we expressed the ratio of this major axis to body length as the relative egg size (egg length / body length). Egg types were subsequently categorized according to the number and size of ovarian eggs.

**RESULTS**

**Hind wing morphology and length**

All individuals of *Harpalus griseus*, *H. eous* and *H. tridens*, and *Synuchus cycloderus* were macropterous with the oblongum surrounded by wing veins (Fig. 1a–d). The oblongum of *S. cycloderus* was relatively indistinct (Fig. 1d) compared to that of the three *Harpalus* species (Fig. 1a–c). The hind wings of *C. procerulus* were short, and most wing veins including the oblongum were degenerate except the radius vein (Fig. 1e). The ratios of the wing to body length (W/B) ranged between a low of 0.23 in *C. procerulus* to a high of 0.99 in *H. griseus* (Table 1).

**Flight muscles**

The three *Harpalus* species have developed dorsal longitudinal and dorsal-ventral indirect muscles (see *H. griseus*, Fig. 2a as an illustration). The average percentages of individuals with flight muscles ranged from 29.1% in *H. tridens* to 76.8% in *H. griseus* (Table 1). The percentages decreased with ageing: from 100%, 90% and 67% in July to 67%, 50% and 17% in November for *H. griseus*, *H. eous* and *H. tridens*, respectively.

Neither *S. cycloderus* (Fig. 2b) nor *C. procerulus* had flight muscles throughout their entire adult life (Table 1).

*Fig. 1. Morphology of hind wings. Harpalus griseus* (a), *H. eous* (b), *H. tridens* (c) and *Synuchus cycloderus* (d) were macropterous. They all have oblongum (black circle) with wing veins and membrane. *Carabus procerulus* (e) was brachypterous. Most wing veins including oblongum and membrane were degenerate and only their radius vein remained. Scale for all: 5 mm*
Fig. 2. Flight muscles in *Harpalus griseus* and their absence in *S cycloderus*. (a) Flight muscles in *H. griseus*. 1 = dorsal longitudinal indirect muscles, 2 = dorsal-ventral indirect muscles. (b) Showing the vacant flight muscles in *S. cycloderus*. Both 1 (absent) and 2 (holes) were missing. The gut is visible at position 1.
Table 1. Life history traits of five species common on Honshu Island, Japan.

| Characteristic       | Harpalus griseus | Harpalus eous | Harpalus tridens | Synuchus cycloderus | Carabus procerulus |
|----------------------|------------------|---------------|------------------|--------------------|-------------------|
| **Flight activity**  |                  |               |                  |                    |                   |
| Wing morphology      | Macropterous     | Macropterous  | Macropterous     | Macropterous       | Brachypterous     |
| Wing/body length ratio | 0.99            | 0.95          | 0.88             | 0.75               | 0.23              |
| Flight muscle %      | 76.8*            | 71.2*         | 29.1*            | 0**                | 0                 |
| Aerial activity %    | 76.0*            | 72.2*         | 16.0*            | 0**                | 0                 |
| **Feeding habit**    |                  |               |                  |                    |                   |
| Starch grains %      | 75.9*            | 64.0*         | 60.5*            | 0                  | 0                 |
| Animal fragments %   | 27.6*            | 12.0*         | 55.3*            | 74.1***            | 0                 |
| Amorphous fluid %   | NA               | NA            | NA               | 8.9***             | 100               |
| **Egg number & size**| Few-Large        | Few-Large     | Few-Large        | Many-Small         | Few-Large         |
| Av. no. of ovarian eggs | 9.0*            | 4.0*          | 8.7*             | 75.9               | 3.2               |
| Egg/body length ratio | 0.19*           | 0.17*         | 0.20*            | 0.08               | 0.20              |

* From SHIBUYA et al. (2017b); ** from SHIBUYA et al. (2017a); *** from SHIBUYA et al. (2015)

# See details in Material and methods
Capture in aerial traps

The aerial activity ratios ranged from 16.0% in *H. tridens* to 76.0% in *H. griseus*. No individual of *S. cycloderus* or *C. procerulus* was captured in aerial traps (Table 1).

Gut contents

Most individuals of the *Harpalus* spp. contained starch grains in their guts (Table 1), while plant tissue fragments were found at a low rate. Individuals with animal fragments in the guts were 27.6–55.3% (Table 1).

Most adults of *S. cycloderus* had animal fragments detected in their guts (Table 1) and most fragments were about 0.1 mm in diameter. Frequently, multiple prey species were detected in the gut of the same individual. Some species of Collembola, including *Hypogastrura gracilis* (Folsom) with a body size of about 1 mm, were detected in the guts of 11 individuals. We also found compound eyes and legs with a pair of claws. Amorphous fluid was detected while starch grains were not detected (Table 1).

Amorphous fluid was found in all individuals of *C. procerulus*, while neither starch grains nor cuticles were found (Table 1). Glucose was detected in the guts of nearly half of the individuals examined (Table 1).

Reproductive characteristics

In the three *Harpalus* species, individuals captured from June to August had immature ovaries and had mature eggs from September onwards but in low numbers (Table 1). The size of the eggs was 2.1–2.4 mm, and the ratio of the egg to body length were 0.17–0.20 (Table 1).

Ovaries of *S. cycloderus* were immature in the individuals captured between May and July, but mature eggs were found in those captured in the middle of October and thereafter. No individual was caught in August or September. The average number of mature eggs was 75.9 (Table 1). The eggs were smaller, both by size and in relation to body length (Table 1).

Ovaries of *C. procerulus* were immature from June to July, but eggs were found in individuals caught in September and thereafter. No individual was caught in August. The average number of ovarian eggs was low, but eggs were relatively big (Table 1).
DISCUSSION

Flight ability

The three species of Harpalus and Synuchus cycloderus were all identified to be mono-morphic macropterous. All individuals of C. procerulus had short wings with only radius vein remained, forming stick-shaped wings.

Flight activity is related to the ratio of the hind wing to body length (W/B) (Thiele 1977). Shibuya et al. (2018) proposed that species with W/B<0.75 are unlikely to fly. Considering this, it is not surprising that the three Harpalus spp. are all flyers, but S. cycloderus is on the border between flyer and non-flyer.

A fully formed hind wing is not sufficient for flight–developed functional flight muscles are also required (Fujisaki 1994). The percentage of individuals with flight muscles was lower in H. tridens than in the other two Harpalus spp. (Shibuya et al. 2017b), indicating H. tridens has the lowest flight activity.

Some ground beetles with monomorphic flight muscles have functional flight muscles during their entire adult life, while some species only temporarily (Matalin 2003). The three studied Harpalus species seemed to fall into this second group: we found decreasing trends in flight muscle possession from July to November. Some ground beetles that exhibit flight activity autolyze their muscles in association with reproductive activities (e.g. van Huizen 1977, Nelemans 1987, Fujisaki 1994, Desender 2000, Matalin 2003). We can assume a trade-off between flight and reproductive activities. Besides, some individuals of H. tridens may not develop flight muscles during their entire adult life.

No individual of Synuchus cycloderus, which showed the lowest W/B ratio among the four macropterous species, possessed flight muscles (Shibuya et al. 2017a). The fact that none of C. procerulus individuals has flight muscles can be easily understood by considering that all individuals possess short wings.

Flight activity

The three species of Harpalus that have flight muscles flew actively and were captured in aerial traps. The flight activity ratio was distinctly lower in H. tridens, than in H. eous or H. griseus (Shibuya et al. 2017b). Consistent with this, the W/B ratio of H. tridens was smaller, and the percentage of individuals with flight muscles was the lowest, indicating H. tridens has the lowest flight activity among the three Harpalus spp.

No S. cycloderus was captured in aerial traps (Shibuya et al. 2017a), suggesting this species does not fly. Thiele (1977) pointed out, however, that
macropterous species can be blown by the wind more than the brachypterous ones, since their unfolded wings offer a considerable area of resistance to the wind. *S. cycloderus* has much potential to manoeuvre by using its long wings as a hang glider when blown by the wind, even if it cannot actively fly. In contrast, the brachypterous *C. procerulus* possessing wings that lost their membrane has little chance to glide.

**Feeding habits**

The frequent presence of starch grains in the guts of the studied *Harpalus* spp. supports previous reports on their seed feeding in the genus (HABU & SADANAGA 1965, SAKAWA 2010, MORI 2015). Dissection revealed, however, that the degree of dependence on seeds varies between species. The ratio of seeds in the guts was the highest in *H. griseus* followed by *H. eous* and *H. tridens* (SHIBUYA et al. 2017b). Low rates of plant tissue fragments in their guts suggested that these could be taken accidentally when consuming seeds.

Remains of arthropod body were recognized in the guts of all three *Harpalus* species. Predation on arthropods was previously observed in *H. griseus* and *H. tridens* (HABU & SADANAGA 1965, MORI 2015). Our study shows that *H. eous* is carnivorous as well. The rate of arthropod fragments in *H. tridens*, however, was higher than that in *H. eous* and *H. griseus* (SHIBUYA et al. 2017b), indicating a higher dependency on animal prey compared to the other two.

Various fragments of prey were detected in the guts of *S. cycloderus* (SHIBUYA et al. 2015), proving that it feeds on various arthropods. Multiple prey species were often detected in the gut of the same individual, indicating consumption of different sorts of prey during a short period. The prey body size was estimated to be nearly several millimetres based on the size of fragments. The find of a whole springtail indicated that *S. cycloderus* swallowed such a small arthropod without chewing. *Synuchus* spp. seemed to feed selectively on dipterous larvae (KUBOTA et al. 2000) but the finding of compound eyes and legs with claws suggests that they hunted not only larvae but also adults. *S. cycloderus* seemed to be a generalist carnivorous that preys voraciously and successively on various types of small arthropods often consuming them whole.

The gut contents of *C. procerulus* consisted of amorphous fluid; neither starch grains nor cuticles were detected. This suggested that the species feeds on relatively large prey, resorting to extra-oral digestion rather than chewing. *Carabus* spp. can feed on animal prey and also on fruit dropped to the ground (SOTA 2000). *C. procerulus* has also been reported to feed on tree sap (KAWANABE & YAHIRO 2008). Glucose was detected in the guts of nearly half of the
examined individuals of *C. procerulus*. This glucose might indicate feeding on fruit or plant sap.

Thus, we emphasize here that gut dissection, in which we combined using paper strip tests and observing both animal fragments and starch particles under a microscope, is an effective method for determining the diets.

**Feeding and flight activity**

Flight plays an essential role in the search for discontinuously distributed seeds in plant communities (Solbreck *et al.* 1990, Fujisaki 1994, Zhang *et al.* 1997). All three studied species of *Harpalus* showed flight activity, and were also predominantly granivorous, conforming to expectations.

*S. cycloderus*, which was presumed to be a non-flyer, was a carnivorous predator and did not eat seeds at all. Some species of *Carabus*, to which *C. procerulus* (brachyptery) belongs, eat larvae of Diptera and Lepidoptera on the ground (Sota 2000). *S. cycloderus* and *C. procerulus* crawl and search for their prey animals, and they may not need a flight to search for food. In fact, *H. tridens* showed the lowest flight activity among the three *Harpalus* species, and the rate of animal fragments in the guts exceeded that of *H. eous* or *H. griseus*. Our results indicate a close relationship between feeding habits and flight activity.

**Reproductive strategy**

The size of mature eggs of *S. cycloderus* was less than half, and the average number was more than 10 times than in the other four species. Thus, *S. cycloderus* may be called ‘many-small egg type’ and the other four species ‘few-large egg type’.

The degree of parental care of offspring affects the number of eggs and their sizes (Ito 1959). Parental brood care has also been reported for some ground beetles. For example, Pterostichini digs space for egg deposition and guard their eggs after oviposition (Thiele 1977). *C. procerulus* (few-large egg) deposits a single egg into a space produced by the tip of the abdomen (Sota 2000). Therefore, when considering the reproductive strategy of ground beetles, we have to take into account both egg types and parental care.

**Trade-off between reproductive activity and flight muscle development**

The oogenesis-flight syndrome hypothesis assumes that a trade-off exists between flight dispersal and egg development (Johnson 1969). The three *Harpalus* species were suggested to fly in their early adult stage. However,
later in their adult life, when they start to oviposit, they degenerate their flight muscles. In other words, they invest their energy in the development of flight muscles during the early stage of adult life, and in the reproductive activity later. This might be regarded as a temporal trade-off between dispersal and reproduction.

**Interpretation of ground beetle responses**

The examination of hind wings, flight muscles, gut contents and ovarian eggs enabled us to reveal important life-history traits of ground beetles concerning flight activity, feeding habits and reproductive strategy. We can apply this basic knowledge to interpret the various research results on ground beetles. Ground beetles have already been used as bioindicators worldwide, including Japan (Monitoring Site 1000 Project) (http://www.biodic.go.jp/moni1000/index.html) in addition to academic research. For example, we can explain the mechanism of a significant increase in the population of *S. cycloderus* (Shibuya et al. 2014) and its sensitive response to vegetation management reported elsewhere (Osawa et al. 2005, Shibuya 2005). We found *S. cycloderus* was a generalist predator preying on various small to large insects including springtails. If some of their prey decrease in abundance, they can consume alternative prey that has increased greatly after vegetation cutting. *S. cycloderus* has also a large number of ovarian eggs implying their great potential for population explosion through numerical response (Solomon 1949, Holling 1959).

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