Acta Zoologica Academiae Scientiarum Hungaricae 66(Suppl.), pp. 185–198, 2020
DOI: 10.17109/AZH.66.Suppl.185.2020

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

Sonomi Shibuya[1], Keizi Kiritani[2†] and Kenji Fukuda[1]

[1]*Graduate School of Agricultural and Life Sciences, The University of Tokyo*
Yayoi, Bunkyo-ku, Tokyo 113-8657, Japan
E-mails: sshibuya@g.ecc.u-tokyo.ac.jp, https://orcid.org/0000-0003-3951-1505
Fukudakenji@g.ecc.u-tokyo.ac.jp, https://orcid.org/0000-0002-9980-3107
[2]*Ito, Shizuoka, Japan*

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.

†Dr. Keizi Kiritani died on February 2, 2020.

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* Tschitschérine 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. 1*a–d*). The oblongum of *S. cycloderus* was relatively indistinct (Fig. 1*d*) compared to that of the three *Harpalus* species (Fig. 1*a–c*). The hind wings of *C. procerulus* were short, and most wing veins including the oblongum were degenerate except the radius vein (Fig. 1*e*).

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).

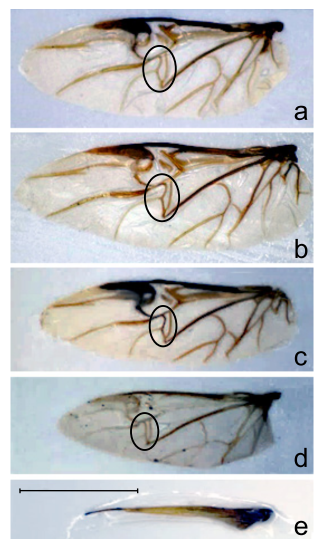

Fig. 1. Morphology of hind wings. *Harpalus griseus* (a), *H. eous* (b), *H. tridens* (c) and *Synuchus cycloderus* (d) were macropterous. They all have oblongum (black circle) with wing veins and membrane. *Carabus procerulus* (e) was brachypterous. Most wing veins including oblongum and membrane were degenerate and only their radius vein remained. Scale for all: 5 mm

Flight muscles

The three *Harpalus* species have developed dorsal longitudinal and dorsal-ventral indirect muscles (see *H. griseus,* Fig. 2*a* 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. 2*b*) nor *C. procerulus* had flight muscles throughout their entire adult life (Table 1).

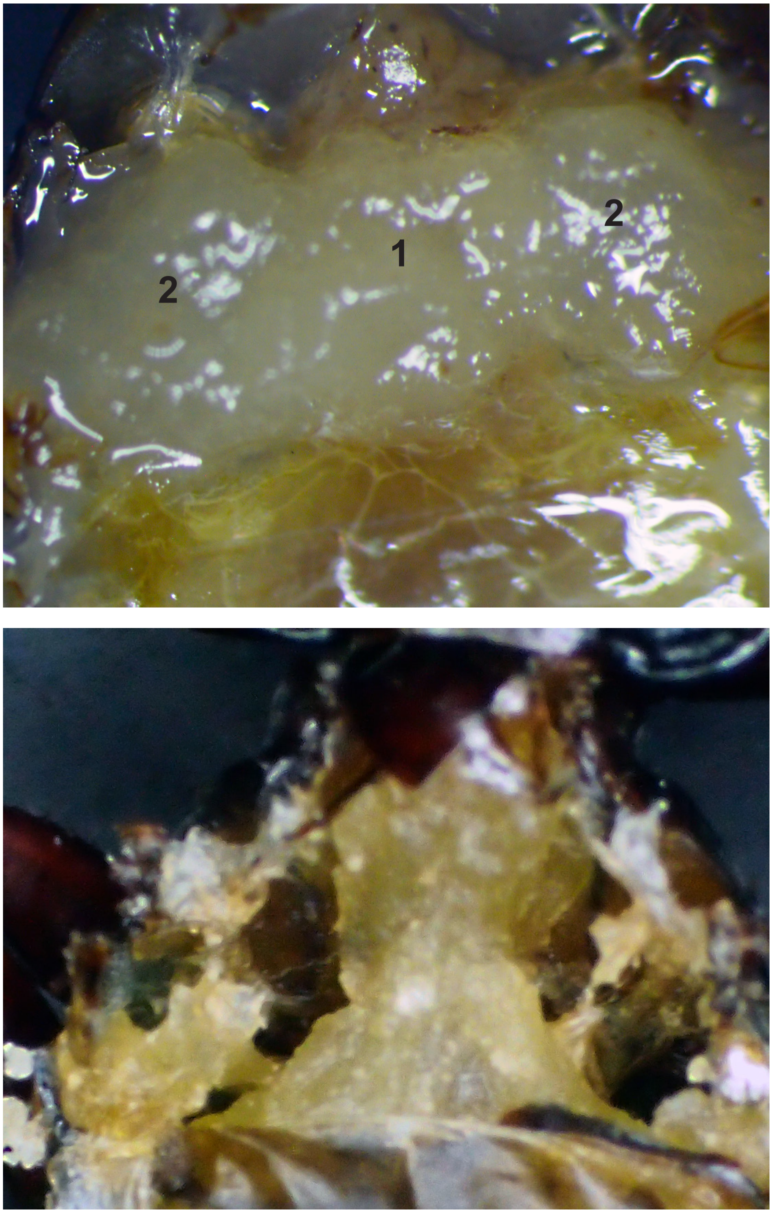

Fig. 2. Flight muscles in *Harpalus griseus* and their absence in *S cycloderus*. (a) Flight muscles in *H. griseus*. 1 = dorsal longitudinal indirect muscles, 2 = dorsal-ventral indirect muscles. (b) Showing the vacant flight muscles in *S. cycloderus*. Both 1 (absent) and 2 (holes) were missing. The gut is visible at position 1

Table 1. Life history traits of five species common on Honshu Island, Japan.

Characteristic	Species				
	Harpalus griseus	*Harpalus eous*	*Harpalus tridens*	*Synuchus cycloderus*	*Carabus procerulus*
Flight activity	High	High	Low	None	None
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	Granivorous/ partially carnivorous	Granivorous / partially carnivorous	Granivorous / carnivorous	Generalist carnivorous	Less generalist carnivorous
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.* (2017*b*); ** from Shibuya *et al.* (2017*a*); *** 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*. 2017*b*), 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*. 2017*a*). 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.* 2017*b*). 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.* 2017*a*), 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, Sasakawa 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.* 2017*b*). 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.* 2017*b*), 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).

*

Acknowledgements – This work was supported by JSPS KAKENHI Grant Number JP18K05740. We thank Junichi Yukawa for valuable comments on an early draft of this paper, Zaal Kikvidze for linguistic advice and Nobuko Morihiro for her assistance in dissection work.

REFERENCES

Brooks, D. R., Bater, J. E., Clark, S. J., Monteith, D. T., Andrews, C., Corbett, S. J., Beaumont, D. A. & Chapman, J. W. (2012): Large carabid beetle declines in a United Kingdom monitoring network increases evidence for a widespread loss in insect biodiversity. – *Journal of Applied Ecology* **49:** 1009–1019. https://doi.org/10.1111/j.1365-2664.2012.02194.x

Desender, K. (2000): Flight muscle development and dispersal in the life cycle of carabid beetles: patterns and processes. – *Entomologie* **70:** 13–31.

Fujisaki, K. (1994): Adaptive significance and evolution of dispersal polymorphisms in insects. – *Scientific Reports of the Faculty of Agriculture, Okayama University* **83:** 113–132. [in Japanese with English summary]

Habu, A. & Sadanaga, K. (1965): Illustrations for identification of larvae of the Carabidae found in cultivated fields and paddy-fields (III). – *Bulletin of the National Institute of Agricultural Sciences. Ser. C, Plant Pathology and Entomology* **C19:** 81–216. [in Japanese with an English summary]

Holling, C. S. (1959): The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. – *Canadian Entomologist* **91**: 293–320. https://doi.org/10.4039/Ent91293-5

Hori, S. (2006): Carabidae. *In*: Maruyama, M. (ed.): *Essays on beetles in forest and waterside*. – Tokai University Press, Kanagawa, 326 pp. [in Japanese]

Ikeda, H., Kagaya, T., Kubota, K. & Abe, T. (2008): Evolutionary relationships among food habit, loss of flight, and reproductive traits: Life history evolution in the Silphinae (Coleoptera: Silphidae). – *Evolution* **62:** 2065–2079. https://doi.org/10.1111/j.1558-5646.2008.00432.x

Ishitani, M. (1996): Ecological studies on ground beetles (Coleoptera: Carabidae, Brachinidae) as environmental indicators. – *Miscellaneous Reports of the Hiwa Museum for Natural History* **34**: 1–110. [in Japanese with an English summary]

Ito, Y. (1959): *Comparative ecology. 1st ed*. – Iwanami Shoten, Tokyo, 366 pp. [in Japanese]

Johnson, C. G. (1969): *Migration and dispersal of insects by flight*. – Methuen, London, 700 pp. https://doi.org/10.1126/science.166.3905.592

Kawanabe, H. & Yahiro, K. (eds) (2008): *Carabidae.* – Yasaka Shobo, Tokyo, 222 pp. [in Japanese]

Kotze, D. J. (2008): The occurrence and distribution of carabid beetles (Carabidae) on islands in the Baltic Sea: a review. – *Journal of Insect Conservation* **12**: 265–276. https://doi.org/10.1007/s10841-008-9147-4

Kotze, D. J., Brandmayr, P., Casale, A., Dauffy-Richard, E., Dekoninck, W., Koivula, M. J., Lövei, G. L., Mossakowski, D., Noordijk, J., Paarmann, W., Pizzolotto, R., Saska, P., Schwerk, A., Serrano, J., Szyszko, J., Taboada, A., Turin, H., Venn, S., Vermeulen, R. & Zetto, T. (2011): Forty years of carabid beetle research in Europe – from taxonomy, biology, ecology and population studies to bioindication, habitat assessment and conservation. – *Zookeys* **100:** 55–148. https://doi.org/10.3897/zookeys.100.1523

Kubota, K., Lee, C. Y. & Kim, J. K. (2000): Invertebrates on the forest floor in Kangwon Province, Republic of Korea, with special reference to Japanese red pine forest infested with the pine needle gall-midge (Thecodiplosis japonensis). – *Sinrin-bunka-kenkyu* **21:** 137–146. [in Japanese with an English summary]

Larochelle, A. (1990): *The food of the carabid beetles (Coleoptera: Carabidae, including Cicindelinae)*. – Association des Entomologistes Amateurs du Québec, Québec, 132 pp.

Lövei, G. L. & Sunderland K. D. (1996): Ecology and behavior of ground beetles (Coleoptera: Carabidae). – *Annual Review of Entomology* **41**: 231–256. https://doi.org/10.1146/annurev.en.41.010196.001311

Magura, T., Lövei, G. L. & Tóthmérész, B. (2019): Various edge response of ground beetles in edges under natural versus anthropogenic influence: a meta-analysis using life-history traits. – *Acta Zoologica Academiae Scientiarum Hungaricae* **65**(Suppl.): 3–20. https://doi.org/10.17109/AZH.65.Suppl.3.2019

Magura, T. & Lövei, G. L. (2020): The permeability of natural versus anthropogenic forest edges modulates the abundance of ground beetles of different dispersal power and habitat affinity. – *Diversity* **12**: 320. https://doi.org/10.3390/d12090320

Matalin, A. V. (2003): Variations in flight ability with sex and age in ground beetles (Coleoptera, Carabidae) of south-western Moldova. – *Pedobiologia* **47:** 311–319. https://doi.org/10.1078/0031-4056-00195

Ministry of the Environment of Japan (2003): Monitoring Sites 1000 Project. http://www.biodic.go.jp/moni1000/index.html

Mori, M. (2015): Harpalinae in Hyogo Prefecture (1). – *Kiberihamushi* **38:** 13–19. [in Japanese]

Nelemans, M. N. E. (1987): Possibilities for flight in the carabid beetle Nebria brevicollis (F.) The importance of food during larval growth. – *Oecologia* **72:** 502–509. https://doi.org/10.1007/BF00378974

Osawa, N., Terai, A., Hirata, K., Nakanishi, A., Makino, A., Sakai, S. & Sibata, S. (2005): Logging impacts on forest carabid assemblages in Japan. – *Canadian Journal of Forest Research* **35:** 2698–2708. https://doi.org/10.1139/x05-188

Sasakawa, K. (2010): Field observations of climbing behavior and seed predation by adult ground beetles (Coleoptera: Carabidae) in a lowland area of the temperate zone. – *Environmental Entomology* **39:** 1554–1560. https://doi.org/10.1603/EN10097

Shibuya, S. (2005): *Vegetation regeneration and ground beetle responding to forest cutting in abandoned coppice forest.* – Master Thesis, The University of Tokyo, 40 pp. [in Japanese with an English summary] http://hdl.handle.net/2261/19895

Shibuya, S., Kikvidze, Z., Toki, W., Kanazawa, Y., Suizu, T., Yajima, T., Fujimori, T., Mansournia, M. R., Sule, Z., Kubota, K. & Fukuda, K. (2014): Ground beetle community in suburban Satoyama – A case study on wing type and body size under small scale management. – *Journal of Asia-Pacific Entomology* **17:** 775–780. https://doi.org/10.1016/j.aspen.2014.07.013

Shibuya, S., Kiritani, K., Murakami, T., Fukaya, M., Morihiro, N., Yajima, T. & Fukuda, K. (2015): Studies on the feeding habits of Synuchus cycloderus (Bates) (Coleoptera: Carabidae) by means of gut dissection method. – *Japanese Journal of Entomology (New Series)* **18:** 95–103. [in Japanese with an English summary] https://doi.org/10.20848/kontyu.18.4_95

Shibuya, S., Kiritani, K. & Fukuda, K. (2017*a*): Biology of Synuchus cycloderus (Coleoptera: Carabidae) – The seasonal activity, reproductive phenology and flight ability of adult populations. – *Japanese Journal of Entomology (New Series)* **20:** 19–31. [in Japanese with an English summary] https://doi.org/10.20848/kontyu.20.1_19

Shibuya, S., Kiritani, K., Morihiro, N. & Fukuda, K. (2017*b*): Biology of three Harpalus species (Coleoptera: Carabidae) – Flight muscle polymorphism, feeding habits and reproductive phenology. – *Japanese Journal of Entomology (New Series)* **20:** 167–182. [in Japanese with an English summary] https://doi.org/10.20848/kontyu.20.4_167

Shibuya, S., Kiritani, K. & Fukuda, K. (2018): Hind wings in ground beetles (Coleoptera: Carabidae and Brachinidae) – morphology, length, and characteristics of each subfamily. – *Japanese Journal of Ecology (New Series)* **68**: 19-41. [in Japanese with an English summary] https://doi.org/10.18960/seitai.68.1_19

Solbreck, C., Anderson, D. B. & Förare, J. (1990): Migration and the coordination of life-cycles as exemplified by Lygaeinae bugs. *In*: Gilbert, F. (ed.): *Insect life cycles: Genetics, evolution and co-ordination*. – Springer-Verlag, London, 258 pp. https://doi.org/10.1007/978-1-4471-3464-0_14

Solomon, M. E. (1949): The natural control of animal populations. – *Journal of Animal Ecology* **19:** 1–35. https://doi.org/10.2307/1578

Sota, T. (2000): *Carabus in four seasons: Life history evolution and species diversity*. – Kyoto University Press, Kyoto, 247 pp. [in Japanese]

Sunderland, K. D., Lövei, G. L. & Fenlon, J. (1995): Diets and reproductive phenologies of the introduced ground beetles Harpalus affinis and Clivina australasiae (Coleoptera: Carabidae) in New Zealand. – *Australian Journal of Zoology* **43:** 39–50. https://doi.org/10.1071/ZO9950039

Thiele, H.-U. (1977): *Carabid beetles in their environments*. – Springer-Verlag, Berlin, 369 pp. https://doi.org/10.1007/978-3-642-81154-8

van Huizen, T. H. P. (1977): The significance of flight activity in the life cycle of Amara plebeja Gyll. (Coleoptera, Carabidae). – *Oecologia* **29:** 27–41. https://doi.org/10.1007/BF00345360

Zhang, J., Drummond, F. A., Liebman, M. & Hartke, A. (1997): Phenology and dispersal of Harpalus rufipes DeGeer (Coleoptera: Carabidae) in agroecosystems in Maine. – *Journal of Agricultural Entomology* **14:** 171–186.

Received February 29, 2020, accepted September 7, 2020, published December 28, 2020