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Immature Stages and Reproductive Ecology of *Copelatus parallelus* Zimmermann, 1920 (Coleoptera, Dytiscidae)

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Abstract A *Copelatus parallelus* female collected in Kyoto Prefecture laid at least 115 eggs during a period of 108 days. The developmental period for each stage was as follows: egg, within 7 days; 1st instar larva, 2–43 days; 2nd instar larva, 3–23 days; 3rd instar larva, 5–56 days; pupation after transition on the soil, 3–8 days; emergence from pupation, 4–6 days. Egg and larval stages were spent in the water. Then, after transition on the soil, each larva formed a pupal chamber in the soil. The 3rd instar larvae survived on land for up to 46 days, even when the soil was dry. The surface of pupae was covered with many setae, causing it to float on the water. Newly emerged adults remained in the pupal chambers for up to 68 days, and their bodies did not change color while they remained in the soil. When water was poured over the soil, adults emarged from the pupal chambers and floated on the water surface. The longer it took for an adult to escape from the pupal chamber, the longer it took for the body color to change. Based on these observations, we concluded that *Copelatus parallelus* has a specialized ecology for growth and life in unstable environments where the waters dry up periodically.
Key words: *Copelatus parallelus*, description, Dytiscidae, endangered species, larva, pupa, reproductive ecology.

Introduction

The dytiscid beetle *Copelatus parallelus* Zimmermann, 1920 (Fig. 1) is a small aquatic beetle (ca. 3.8–4.0 mm in body length) (Mori & Kitayama, 2002). The species has been known as one of the rarest Dytiscidae species in Japan (Mori & Kitayama, 2002), with only two records to date: the original description from Settsu (northern part of Osaka Prefecture and southeastern part of Hyôgo Prefecture) (Zimmermann, 1920) and a record of a female in Osaka Prefecture (Ohkura, 1957). Saijo and Shiyake (2004) rediscovered the species in Shiga Prefecture, and Murakami (2012, 2013) and Watanabe and Kato (2017) reported additional observations in Kyoto and Shiga Prefectures. This species is probably endemic to the Yodo River (Yodo-gawa) system in central Japan, and is listed as "Critically Endangered" in the current national red data book of Japan (Ministry of the Environment of Japan, 2015). The ecology of this species is poorly known. Adults are found in areas of shallow water less than 20 cm in depth (Saijo & Shiyake, 2004; Murakami, 2012, 2013). Their habitats are small water bodies that are unstable and easily dry out (Saijo & Shiyake, 2004; Murakami, 2012). At present, there is no information about its reproductive ecology or larval morphology. Elucidating the larval morphology of this species will contribute to the detection of new habitats. Moreover, although ex situ conservation of endangered species is conducted in Japan (e.g., Kitano & Watanabe, 2016), findings on each species' ecology are often unreported (Kitano & Watanabe, 2016).

It is essential to clarify the life history and reproductive environments of *C. parallelus*, since the information will contribute to enact the appropriate conservation measures, environmental maintenance for conservation, and future ex situ conservation. It is urgently necessary to determine the im-

pacts of such actions on *C. parallelus* habitats.

In this study, we attempted laboratory rearing of *C. parallelus* to reveal its reproductive ecology and morphology of immature stages. Additionally, we proposed a novel method for rearing *C. parallelus*.

Materials and Methods

Adults and rearing methods. The first author collected three *C. parallelus* adults (two males and one female) at Uji-gawa, Fushimi-ku, Kyoto City, Kyoto Prefecture in central Japan on November 6, 2016. These three individuals were brought to the rearing room of the Ishikawa Insect Museum (Hakusan, Ishikawa Prefecture) on November 7, 2016. The rearing room was maintained at 26℃ and lit up from 8:15 to 17:15 (Japan Standard Time: JST) during the daytime. We installed dead leaves from emergent *Typha latifolia* plants and Java moss (Hypnaceae) in a rearing container for adults (16 × 27 × 20 cm) to provide sites for hiding and oviposition (Fig. 2). The third author collected a female adult at the same location on November 12, 2016. This individual was reared at the Laboratory of Forest Biology (Kyoto City, Kyoto Prefecture) from November 13, 2016, to determine whether this female had already mated. The rearing room was maintained at 25℃ and lit up from 10:00 to 19:30 (JST). We installed dead leaves from emergent plants and Java moss in a rearing container for adults (10 cm in diameter, 4 cm in height). Quantities of chironomid larvae (live and frozen) were provided to adults as prey every two days. Both rearing experiments were terminated on March 31, 2017.

Recovery, recording, and rearing method for eggs and larvae. Eggs and larvae found in the rearing container were checked every 1–3 days. We carefully checked crevices and surfaces of the substrate to detect eggs. Eggs obviously being delayed in recovering were also counted for the number of days without being excluded.

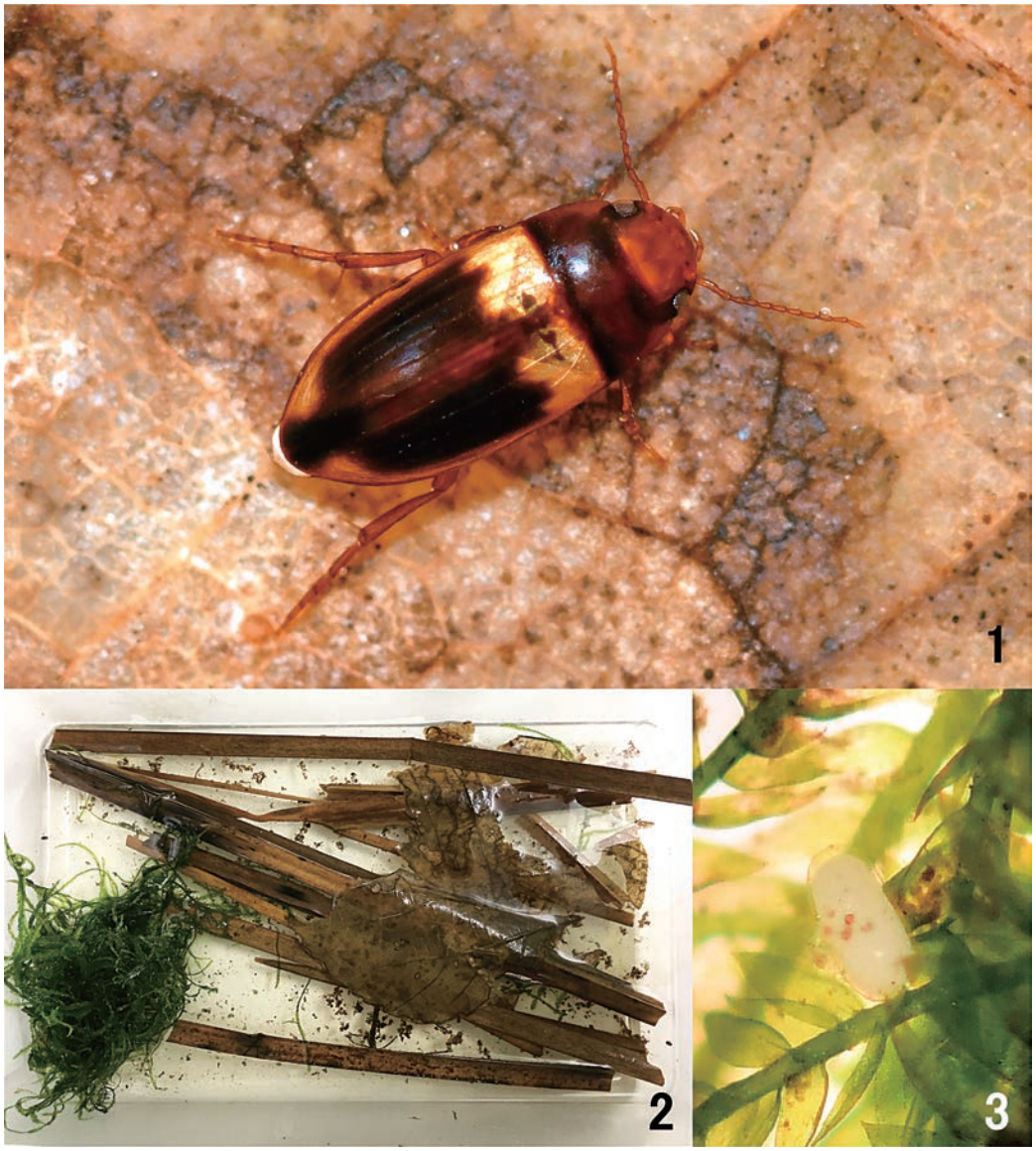
When eggs and larvae were found, we recorded the date of confirmation and the developmental stage. The eggs and larvae obtained were reared individually in plastic cups (‘larval cups’; 8 cm in diameter, 4 cm in height, ca. 5 mm in water depth) containing Java moss and maintained below 26℃. The larvae were fed frozen chironomid larvae and fresh daphnia and chironomid larvae collected from the field.

We prepared plastic cups (‘pupation cups’; the same size as larval cups) with crushed and moistened peat moss (1 cm in depth) for the pupation soil. We forcibly placed 3rd instar larvae, on the peat moss in the pupation cups if they did not eat prey items and walked without stopping for up to a day.

For each individual, dates of hatching, molting, transition on the soil, pupation and emergence were recorded in detail, as well as the environment in the larval and/or pupation cups.

Newly emerged adults were maintained individually and fed frozen chironomid larvae in the larval cups; they were checked periodically until their body color matured. Maturity was judged by comparing the individual with the parental generation. The day on which the body color became the same as that of females in parental generation was regarded as the ‘coloring’ day.

Estimation of coloring conditions in new adults. To investigate the conditions under which new adults changed in color, we used Pearson’s correlation coefficient (Excel software) to examine the relationship between the number of days from transition on the soil to entering the water (i.e., the number of days from emergence to the start of mature feeding) and the number of days from entering the water to becoming colored (i.e., the number of days from the start of mature feeding to becoming colored).



Figs. 1–3. *Copelatus parallelus* (1 & 3) and its rearing container. —— 1, A *Copelatus parallelus* adult from Kyoto Prefecture; 2, a rearing container for adults; 3, an egg laid on Java moss.

Observation of immature stages. The external morphology of larvae was observed and photographed under a stereoscopic microscope (Nikon SMZ) with a charge-coupled device (CCD) camera and control unit (Nikon Digital Sight DS-L2). We prepared 2–3 digital photographs by focus stacking, using the digital image processing software Adobe Photoshop CS4 for Macintosh.

To examine external morphology, a 3rd instar larva was dried using a vacuum freeze-drying equipment and given an ultrathin gold coating by high-vacuum evaporation. Fine structures on the body surface were photographed under a scanning electron microscope (SEM; JEOL JCM-6000 Neoscope Scanning Electron).

Results: Description of Immature Stages and Reproductive Ecology

Copelatus parallelus ZIMMERMANN, 1920

(Figs. 4–6)

Material examined. All specimens were reared by the first author: three eggs, three 1st instar larvae, two 2nd instar larvae, four 3rd instar larvae, and three pupae fixed in 70 % ethanol. The adults were collected in the field in Uji-gawa, Fushimi-ku, Kyoto City, Kyoto Prefecture, Honshu, Japan, 6. XI.2016, K. WATANABE leg.

Egg. Length ca. 1.0 mm, general shape: oval, entirely cream colored.

First instar larva. Body length ca. 2.3 mm, entirely cream colored.

Second instar larva. Body length ca. 3.2 mm, entirely cream colored, with light colored patterns on thorax and abdominal segments.

Third instar larva. Body length ca. 6.0 mm in expanded specimen preserved in 70 % ethanol.

Body elongate, more or less robust, thorax slightly wider than head; entirely brown but partly brightly colored in thorax and abdomen.

Head subquadrate, length same as width. Surface of frons and vertex reticulate. Frontal margin of front clypeus gently rounded but both sides dentate. Posterolateral corner with spine-like setae. Maxillary stipes robust. Antenna 4-segmented, last antennal segment with short sensorial appendage. Mandible simple, inner margin with fine serrations.

Thorax. Prothorax with short keel and coarse spines on front–lateral area. Meso- and metathorax shorter than prothorax. Legs slender, without swimming setae.

Abdomen 8-segmented, bearing coarse spines on dorsal and lateral surface; 7th and 8th segments without lateral fringe of swimming setae. Last segment triangular, urogomphi shorter to subequal relative to length of the last segment.

Pupa. Body length ca. 3.6 mm, entirely cream colored, dorsum of thorax and abdomen with dense setae.

Remarks. The larva of the *Copelatus* is characterized by the unique form of body, such as dentate mandibles, legs without swimming setae and short urogomphi (EPLER, 2010), though the larvae of most species of the genus is still unknown. MICHAT and TORRES (2009) described an Argentine species, *C. longicornis* SHARP including the chaetotaxy of 1st and 3rd instars. Five *Copelatus* species have been known from Japan, except for *C. parallelus*: *C. weymarni* BALFOUR-BROWNE, *C. oblitus* SHARP, *C. teranishii* KAMIYA, *C. kammuriensis* TAMU et TSUKAMOTO and *C. nakamurai* GUEORGUIEV (TAJIMA & YANAGIDA, 2010; HAYASHI, 2015; MITAMURA *et al.*, 2017). However, the five species have not been described morphologically. The habitus of these species shows that the form of the head is important for their identification. For example, the outline of head is rounded in *C. oblitus* but quadrate in the others (see MITAMURA *et al.*, 2017). If examination including chaetotaxy is carried out, identification based on larvae may become possible for *Copelatus*.

Reproductive ecology. The 1st instar larva was obtained on November 26, 19 days after starting adult rearing; an egg was found on the surface of Java moss in the water (Fig. 3). The female continued to lay eggs for 108 days until March 14, 2017, and in total 89 eggs and 26 larvae were obtained within the days. Eggs were laid singly on Java moss during this period. The eggs were covered with a viscous substance, enabling them to adhere to the surface of substrates. No fertilized eggs were obtained from the female collected on November 12, 2016 and reared alone. Only two infertile eggs

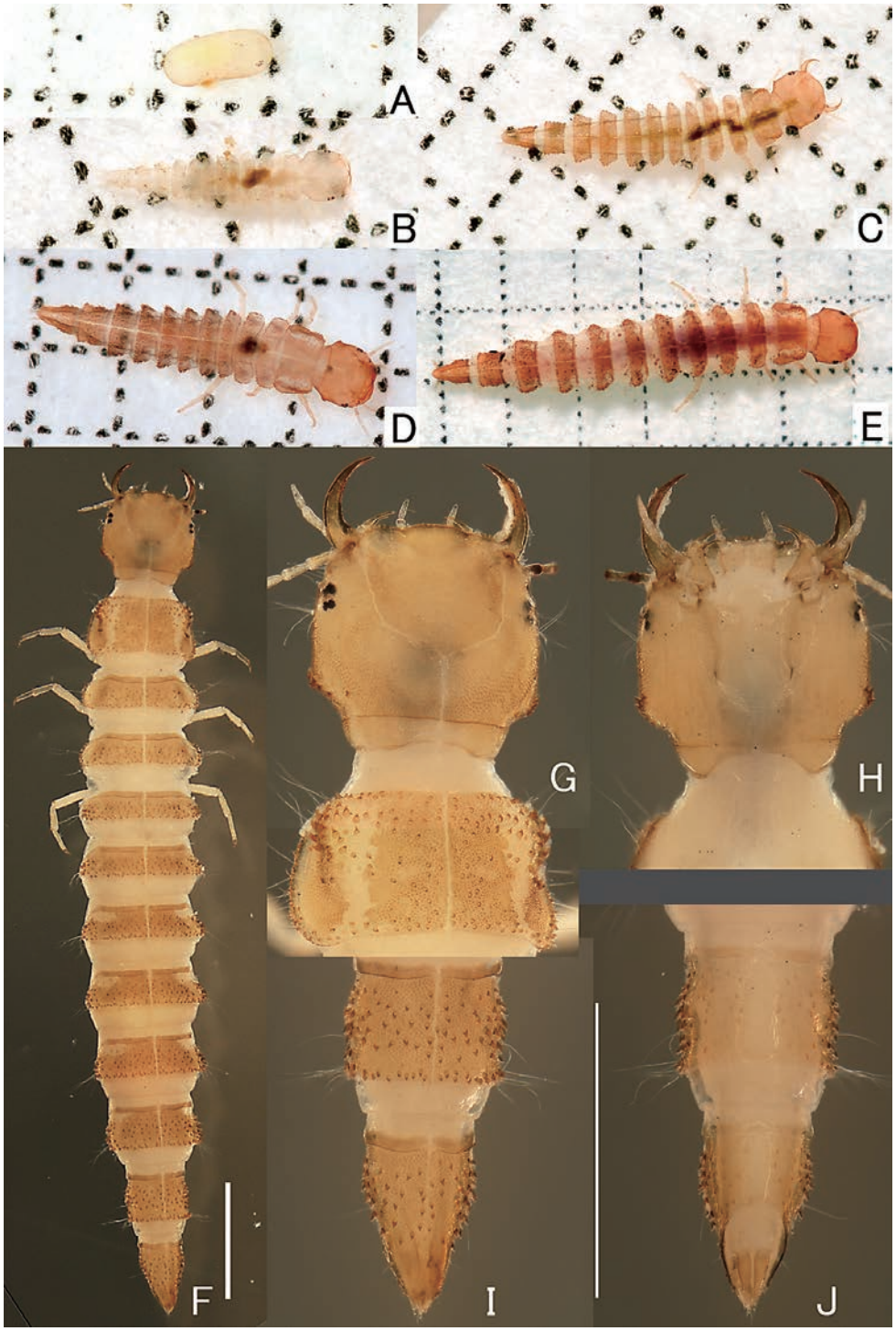


Fig. 4. Egg and larva. —— A, A living egg; B–E, living larvae (B, 1st instar; C, 2nd instar; D, 3rd instar; E, fully grown 3rd instar); F–I, a 3rd instar larva. —— F, Habitus; G & H, head and prothorax; I & J, last two segments of abdomen. —— F, G & I, Dorsal view; H & J, ventral view. Scale bars: 1.0 mm.

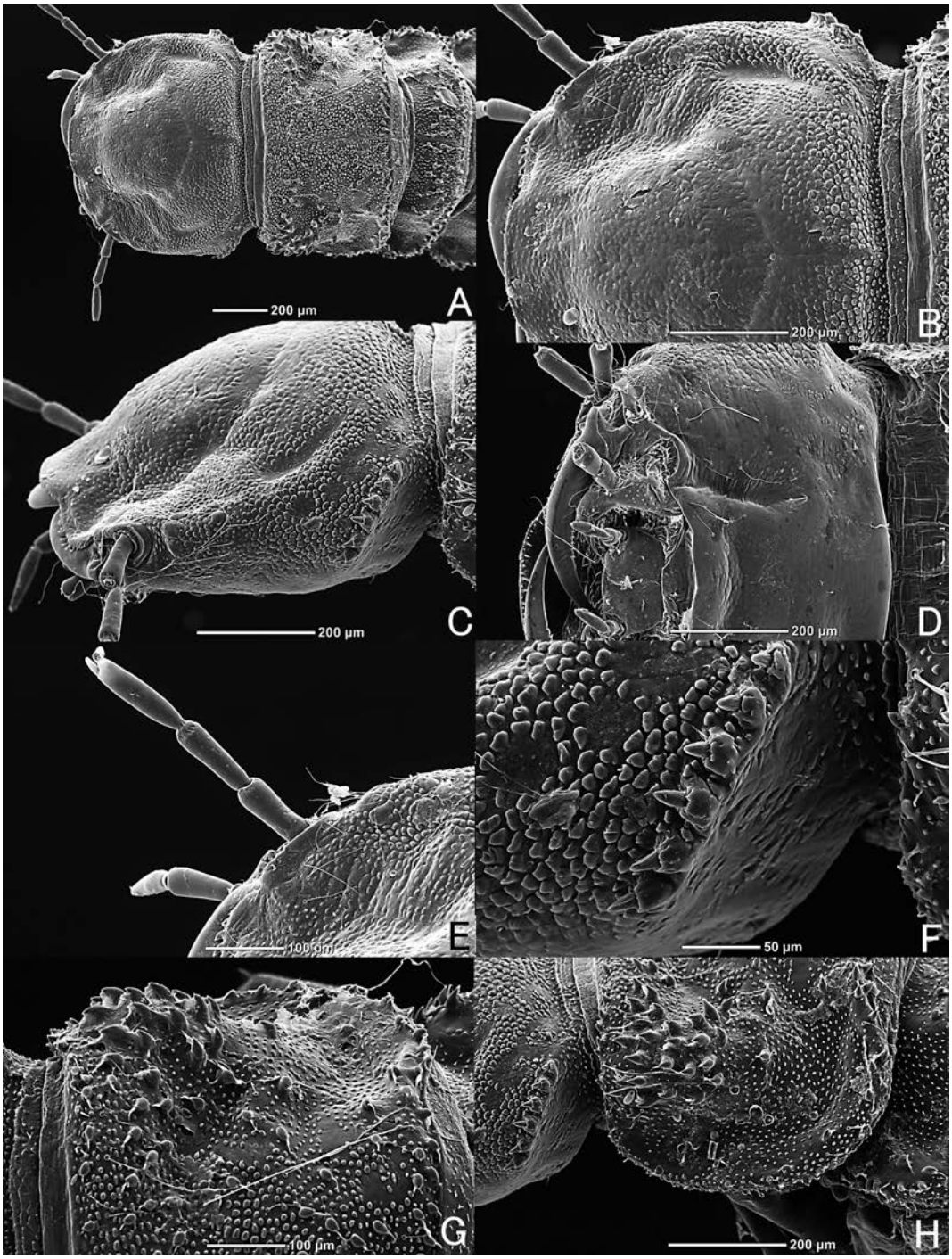


Fig. 5. Scanning electron microscope (SEM) photographs of a 3rd instar larva of *Copelatus parallelus*. —— A & H, Head and prothorax; B–F, head (E, antenna; F, spine-like setae); G, prothorax. —— A, B, E & G, dorsal view; C, F & H, lateral view; D, ventral view. Scale bars: 50 µm for F; 100 µm for E & G; 200 µm for A–D & H.

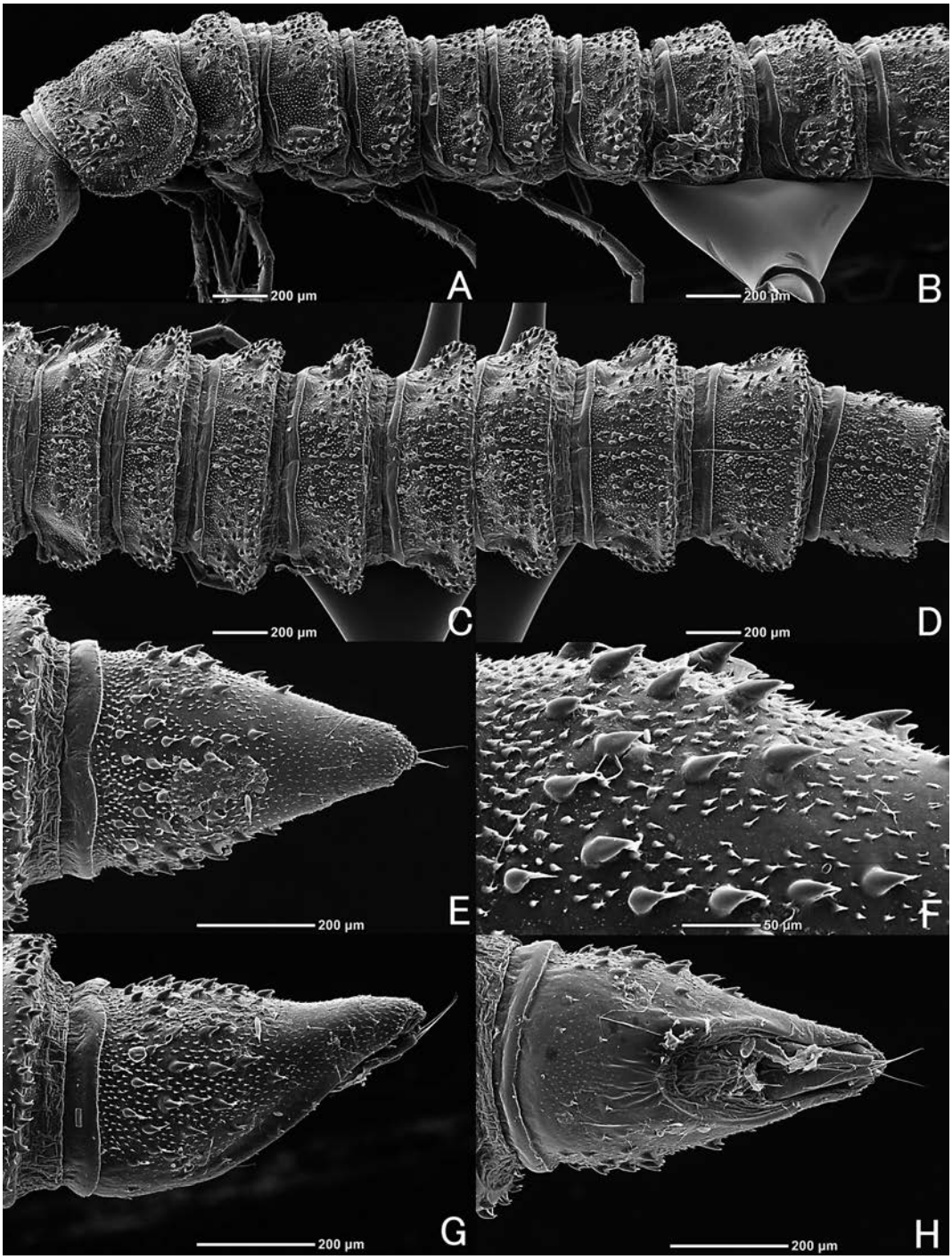


Fig. 6. SEM photographs of a 3rd instar larva of *Copelatus parallelus*. —— A & C, Thorax and abdominal segments; B & D, abdominal segments; E–H, last segments. —— A, B & G, Lateral view; C–F, dorsal view; H, ventral view. Scale bars: 50 µm for F; 200 µm for all others.

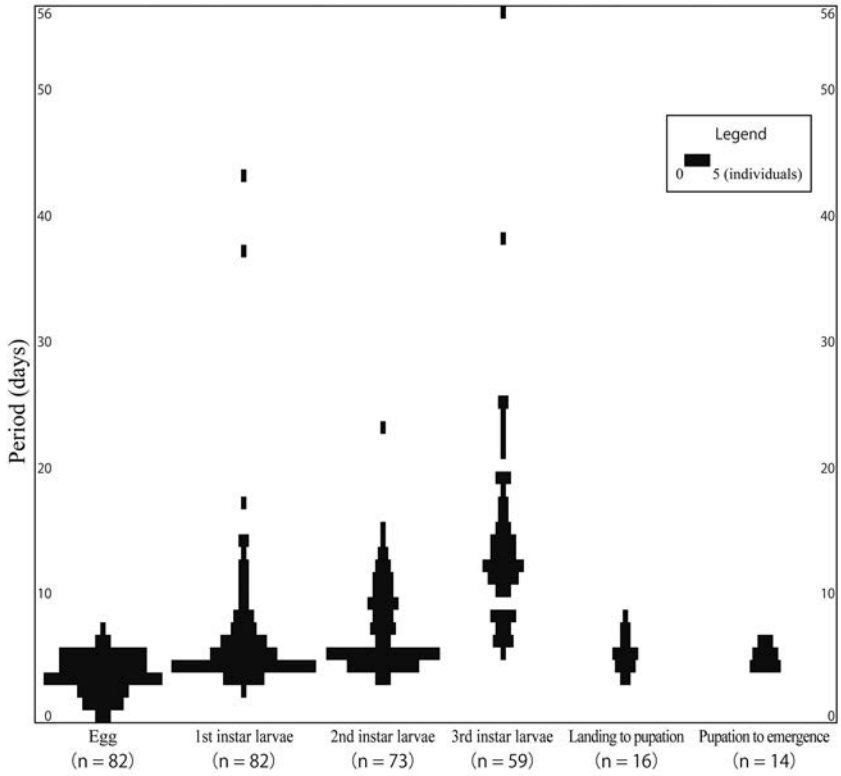


Fig. 7. Histogram of each developmental stage from egg to emergence.

were obtained during the 138 days between November 13, 2016 and March 31, 2017. These eggs died from fungi four days after discovery.

Fig. 7 shows the number of days in each developmental stage from egg to emergence. Of the 89 eggs, 82 eggs were fertile; the remaining seven eggs did not hatch. The unhatched eggs became moldy and died. The egg period was 0–7 days (mean 3.4 days, n = 82). As shown in Fig. 7, most eggs (ca. 70 %) hatched within 3–5 days. However, our most realistic estimate of the egg period is approximately seven days, because we could not count eggs every day.

The larvae started eating from the day of hatching with living chironomid larvae and living Tubificina as prey (Fig. 8A). However, the larvae did not eat much living daphnia and frozen chironomid larvae. The larvae were able to capture living chironomid larvae and living Tubificina when the prey size was within approximately three times the body length of the hatched larvae. When larvae encountered a larger prey, they did not engage their mandibles when preys moved aggressively. However, the larvae attacked preys repeatedly and finally succeeded in subduing them. After the start of feeding, larvae stopped eating once they became satiety. They fed again on the same prey after several hours, repeating this process several times until the body color of the preys became transparent from their sucking. When frozen chironomid larvae were offered, the larvae frequently tried to eat, but many larvae stopped eating after repeated attempts at predation.

The period of each developmental stages was as follows: 1st instar, 2–43 days (mean 6.7 days, n = 82); 2nd instar, 3–23 days (mean 7.0 days, n = 73); 3rd instar, 5–56 days (mean 14.2 days, n = 59). There was a large individual variation in the developmental period of each larval instar (Fig. 7). His-

tograms of the developmental stages (Fig. 7) showed the highest frequency of developmental periods as follows: 1st instar, 4–5 days; 2nd instar, 4–5 days; 3rd instar, 6–14 days.

Only one case of molting from a 2nd to 3rd instar larva was observed (Fig. 8B). Molting started when the larva was not secured to the plant and finished after approximately one minute. Immediately after molting, the whole body color of the larva was white and transparent, and it moved around freely without feeding. When a prey approached, the larva walked away quickly and did not exhibit predation behavior. After several hours, when the body began to color, the larva started to feed.

After transition to land, the larvae dug into the soil and made a pupal chamber ca. 4 mm in diameter and pupated at 3–8 days (mean 5.1 days, n = 16) (Fig. 8C). We observed several occasions when pupae floating to the water surface when the soil was immersed in water. We recorded two caces of premature transition on the soil of 3rd instar larvae. These larvae were discovered in the soil as they were after days 9 and 46. They started feeding after being returned to larval cups.

Emergence was observed at 4–6 days (mean 4.8 days, n = 14) after pupation (Fig. 8D). Most newly emerged adults did not emarged from the pupal chambers by themselves. Newly emerged adults remained in the pupal chambers for 12–68 days (mean 35.4 days, n = 35), until we manually removed them from the pupal chambers or the soil; during their stay in the soil, the body did not color. Of the 14 newly emerged adults whose pupal chambers could be observed from outside, two individuals escaped from the pupal chambers on days two and four after emergence, but remained in the soil. The remaining 12 individuals stayed in the pupal chambers until we poured water over the soil in the containers (Fig. 8E). There were 21 individuals that we could not observe within the pupal chambers and that did not escape from the soil. However, they floated to the water surface immediately after we poured water onto the soil (Fig. 8F). Although the floating new adults had not yet changed color, their color changed 1–26 days (mean 4.8 days, n = 35) after entering the water. These adults began feeding from the day they escaped from the pupal chambers.

Fig. 9 shows the relationship between the number of days between transition on the soil and entering the water (i.e., the number of days from emergence to the start of mature feeding) and the number of days from entering the water to becoming colored (i.e., the number of days from the start of mature feeding to becoming colored). The body color of one of the 35 new adults did not change until 26 days after it entered the water. Therefore, the data for this individual were excluded from the analysis. A statistically significant correlation ($r = 0.642$, $P < 0.001$) was detected between the number of days from transition on the soil to entering the water and the number of days from entering the water to becoming colored.

Discussion

Estimation of ovipositional season and the egg and larval periods. After collecting adults from the riverbed (in soil or sediment) during winter, they started mating in the rearing rooms at 26℃. As a result, 1st instar larvae were obtained after 19 days. The egg period confirmed in this experiment was from 0 to 7 days; however, all eggs were not found on the day of oviposition, and some eggs were collected during development. Based on Fig. 7, a more reliable estimation of the egg period is 3–7 days, with a maximum of approximately seven days. We estimated that eggs were actually laid within approximately two weeks after their mating. The one female collected alone while the overwintering produced only two infertile eggs. It is highly possible that this female was unmated at the time of collection. In natural environments, the activity of adults would decline due to a decrease in temperature after the collection day (November 12). Therefore, in natural environments, reproductive activity and oviposition would occur the following spring, after overwintering.

Fig. 8. *Copelatus parallelus*. —— A, Larvae preying on living chironomid larvae (a, 1st instar; b, 3rd instar); B, 3rd instar larva just after molting; C, pupa in a pupal chamber; D, new adult just after emergence; E, new adult that remained in a pupal chamber for 53 days; F, new adult floating after pouring water on the soil.

Oviposition occurred on the surface of Java moss, and no eggs were found on the leaves of emergent plants or on the inside surface of the container. Eggs were laid by attaching them to the leaves of dense plants. In natural environments, it is presumed that eggs are laid among shoal roots and gaps in plant residues. *Copelatus nakamurai*, which is similar to *C. parallelus*, in body size and spawning environment, lays eggs on the surface of Java moss (TAJIMA & YANAGIDA, 2010).

The ovipositional period was 108 days. In natural environments, it is considered longer; however, the results of this study are based on small samples from one female. The female laid at least 115 eggs during this period (89 eggs, 26 larvae), indicating that it was very prolific. Indeed, it is presumed that the original number of eggs was greater, as some individuals died before hatching or through predation.

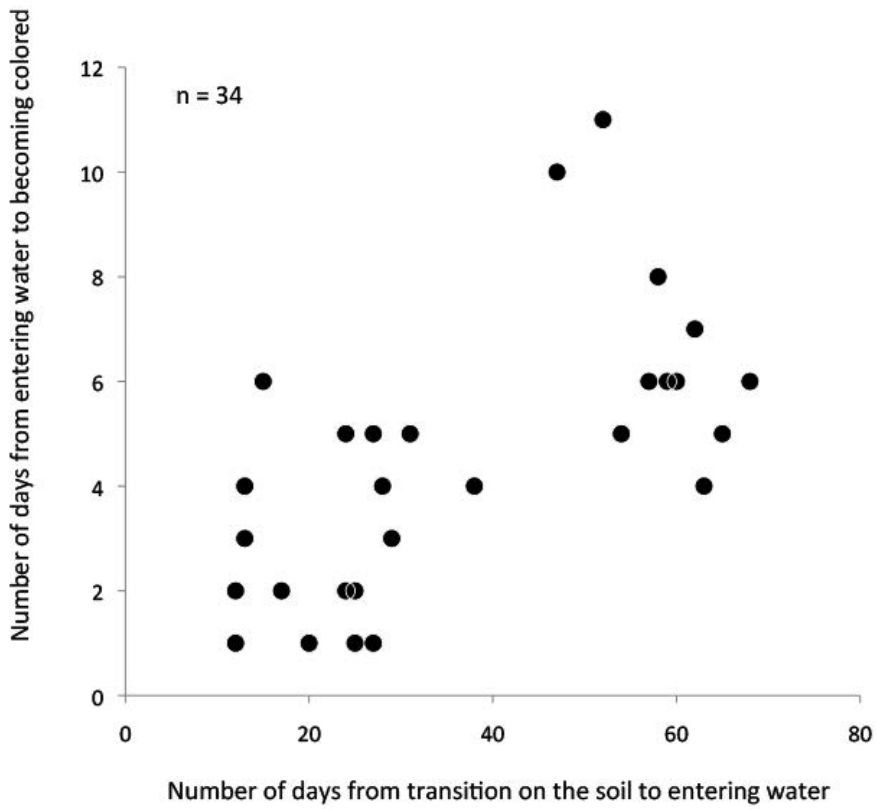


Fig. 9. The relationship between the number of days from transition on the soil to entering water (i.e., the number of days from emergence to the start of mature feeding) and the number of days from entering water to becoming colored (i.e., the number of days from the start of mature feeding to becoming colored).

As each of these larval periods was long, it may be more accurate to infer these periods from the histograms (Fig. 7) instead of using average values. Using this method, the larval period was 14–24 days, the sum of 4–5 days as 1st instar, 4–5 days as 2nd instar, and 6–14 days as 3rd instar. The larval period of *C. parallelus* is therefore much longer than that of *C. nakamurai* (mean 16.55 days at 24–28℃, TAJIMA & YANAGIDA, 2010). TAJIMA (2011) estimated that the short growth periods in *C. nakamurai* eggs and larvae allow this species to avoid drought risk. Given that the egg and larval periods of *C. parallelus* are longer than those of *C. nakamurai*, it is possible that the natural habitat of *C. parallelus* is in areas more resistant to drought compared with the habitat of *C. nakamurai*.

Diet during the larval period. The larvae preyed upon living chironomid and Tubificina larvae. Although the larvae attempted predation several times, they could not prey upon daphnids due to their escape behavior. In natural environments, the habitat of *C. parallelus* is an unstable aquatic environment where the flooding period is limited. Therefore, the larvae find more abundant prey in animals whose populations rapidly increase following flooding. Under artificial rearing, they preyed on chironomid larvae, but could not prey on fast-moving daphnids, suggesting that fast-moving prey may not be suitable for larval feeding. It has been reported that the larvae of *C. nakamurai* that grow to adulthood under these rearing conditions also prey on mosquito larvae (TAJIMA & YANAGIDA, 2010).

We did not confirm this in the present study; however, *C. parallelus* larvae may eat mosquito larvae in natural environments like similar species *C. nakamurai*. Additionally, while *C. nakamurai* larvae prey on daphnids, smaller plankton (Kawaji, 2017), and frozen chironomid larvae (Tajima & Yanagida, 2010), *C. parallelus* larvae in the present study did not. Although some feeding habits are common between the two species, those of *C. parallelus* may be narrower than those of *C. nakamurai*.

Unique ecology during the larval period. During the larval period, we confirmed four ecologies. First, the larvae of *C. parallelus* prey upon immobile prey. In general, the larvae of most diving-beetle species perform predatory behavior in response to moving objects. There are some exceptions, as in *Cybister brevis* Aubé, 1838, which eats motionless Odonata nymphs (Ohba, 2009). The larvae of *C. parallelus* seem to use not only movement but also smell as clues in searching for prey. Because the *C. parallelus* habitat is an unstable environment, with intermittent flooding and drying, it is possible that larvae use smell to prey on the dead bodies of terrestrial small animals drowned during flooding. Second, the developmental periods of each instar exhibited large variation. At 24–28°C, the developmental periods of *C. nakamurai* were 2–4 days (3 days, n = 4) for 1st instar larvae, 3–5 days (3 days , n = 5) for 2nd instar larvae, and 7–15 days (9 days, n = 4) for 3rd instar larvae (Tajima & Yanagida, 2010). However, in *C. parallelus*, the same developmental periods took 2–43 days (42 days, n = 82), 3–23 days (21 days, n = 73), and 5–56 days (52 days, n = 59), respectively. In natural habitats of *C. parallelus*, the prey species and their densities vary depending on changes in the water level and flooding time and period; predation efficiency thus depends greatly on the environment. Therefore, opportunities to encounter prey are inevitably scarcer than in environments that are always flooded, and a wide range of growth periods per instar allows for the adjustment of growth rates according to food availability and environmental variation, increasing the probability of survival for the next instar. The third ecological topic examined in this study was tolerance to dry periods during drought. We twice underestimated the time of transitioned to land of the 3rd instar larvae. The first example was a larva that transitioned on February 13, 2017. When we checked on March 31 (46 days later), we discovered the larva in the soil. The second example was a larva that transitioned on Mach 2, 2017, and was also discovered in the soil, nine days later. Although in the first case, the soil in the rearing container was quite dry, both larvae were alive and began to feed as soon as they were placed in water and given prey. Although we observed only two examples, it is noteworthy that one larva survived on land for at least 46 days even when the soil was dry. Thus, it is likely that larvae can survive under detritus for approximately 1.5 months when their habitats dry up in natural environments. The fourth ecology-related observation had to do with the walking ability of the larvae. When reared in plastic cups, 3rd instar larvae reaching the timing of transition climbed the vertical surface of the cup, escaped from the water, and reached the lid. This behavior appears not to be accidental. It is presumed that the larva's short legs make it possible for them to emarge from water even on steep waterfront slopes. The surface tension generated between the lower surface of the body and the larval cup allowed the larvae to climb the inside of the cup.

Unique ecology after transition on the soil. Larvae spent 5–56 days (mean 14.2 days, n = 59) after molting, then landed and dug into the soil to create pupal chambers approximately 4 mm in diameter. Pupation occurred 3–8 days after transition on the soil (mean 5.1 days, n = 16). The surfaces of the pupae were covered with many setae, allowing them to float on water. We tried to forcibly sink a pupa using tweezers; however, it resurfaced even after it had been submerged many times. As mentioned above, the habitat of *C. parallelus* is an unstable environment with repeated flooding and drying. The pupae are therefore adapted through their surface structures to avoid drowning when the pu-

pal chamber is submerged due to rainfall or water level increase.

Most newly emerged adults remained in the pupal chamber; some escaped but remained in the soil. The new adults remained in the pupal chamber for up to 68 days; however, adults in the soil did not change color and did not escape to the soil surface. When new adults remained in the pupal chamber or within the soil, they floated to the surface immediately and became active when water was applied to reproduce a natural environment after rainfall. Therefore, it is highly possible that new adults escape the pupal chamber or start life in the water upon flooding caused by rainfall or water level increase. At the time of escape, all new adults did not become colored. In a study by TAJIMA and YANAGIDA (2010), individuals of *C. japonicus* SHARP, 1873 and *C. weymarni* that had soft wings and no body color had been collected in natural environments. The same observations were made by WATANABE (unpublished data). In natural environments, when the pupal chamber and its surroundings are inundated after emergence, new adults have likely not yet changed color. New adults that started mature feeding after escaping the pupal chamber become colored after 1–26 days (mean 4.8 days, n = 35). After escaping the pupal chamber, the adult body does not become colored (i.e., does not solidify) unless it enters water. The longer it takes from emergence to escape from the pupal chamber (the periods from transition to land to emergence were nearly the same), the longer it takes for the body to color. From these observations, we concluded that if the habitat is flooded within a certain period after emergence and mature feeding has not started, there is increased risk of death by predators or starvation.

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要　　約

渡部晃平・林　成多・加藤雅也：コセスジゲンゴロウ *Copelatus parallelus* ZIMMERMANN, 1920（鞘翅目ゲンゴロウ科）の卵・幼虫・蛹および繁殖生態の記載．———— コセスジゲンゴロウ *Copelatus parallelus* ZIMMERMANN, 1920 は，環境省版レッドデータブックにおいて絶滅危惧IA類に選定されている希少種である．しかし，本種の生態的な知見はほぼ皆無であり，卵，幼虫および蛹の形態は明らかにされていない．本研究では，飼育により得られた卵，幼虫（1齢，2齢，3齢），蛹の形態および繁殖生態について記載するとともに，本種の飼育方法を示した．

飼育下において，京都府で採集した1雌から108日間で少なくとも115個の産卵が確認された．各成育段階における成育期間は卵（7日以内），1齢幼虫（2–43日），2齢幼虫（3–23日），3齢幼虫（5–56日），上陸から蛹化（3–8日），蛹（4–6日）であった．卵と幼虫期は水中で過ごし，上陸後には土中で蛹室を作って蛹化した．3齢幼虫は乾燥に対する耐性が確認され，46日間陸上で過ごし，周囲の土が乾燥していても死ぬことはなかった．蛹の表面には毛が生えており，水に浮くのを確認した．羽化した新成虫は基本的に自力では蛹室から脱出せず蛹室内に留まるが（最長68日まで確認），容器に水を入れることで降雨や増水と同様の状況を再現すると蛹室から脱出した．以上の観察結果から，野外においても不安定な水域での発育や生息によく特化した生態を持った種であることが推察される．

羽化後の新成虫は水に入って数日が経過するまで体が色づくことはなかった．体が色づくまでの期間は羽

化から脱出までに時間がかかる程長くなることから，羽化後のある一定期間内に生息地が湛水されなければ，新成虫が捕食者に食べられたり，餓死したりすることなどにより死滅するリスクが高まると考えられる．

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