



## **Colony Composition, Social Behavior and Some Ecological Characteristics of the Korean Wood-Feeding Cockroach (*Cryptocercus kyebangensis*)**

Authors: Park, Yung Chul, Grandcolas, Philippe, and Choe, Jae Chun

Source: Zoological Science, 19(10) : 1133-1139

Published By: Zoological Society of Japan

URL: <https://doi.org/10.2108/zsj.19.1133>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# Colony Composition, Social Behavior and Some Ecological Characteristics of the Korean Wood-Feeding Cockroach (*Cryptocercus kyebangensis*)

Yung Chul Park<sup>1\*</sup>, Philippe Grandcolas<sup>2</sup> and Jae Chun Choe<sup>1</sup>

<sup>1</sup>*School of Biological Sciences, Seoul National University, Kwanak-gu Shilim-dong San 56-1, Seoul 151-742, South Korea*

<sup>2</sup>*ESA 8043 CNRS, Laboratoire d'Entomologie, Muséum national d'Histoire naturelle, 45, rue Buffon, 75005 Paris, France*

**ABSTRACT**—Korean populations of the genus *Cryptocercus* occur in forested mountains throughout South Korea. They live in monogamous associations in which parents care for their young in complex woody galleries. Single paired adults (23.2%) and one or both parents with their offspring (28.1%) were found most frequently in the field. Among single-parent families adult females (6.7%) were observed more frequently than adult males (1.4%). In families with single or both parents, the mean brood size was  $21.6 \pm 9.4$ . Oothecae were observed from mid-June to the late July. Oothecae were found in the galleries of only paired adults and never found in families with nymphs. The mean number of eggs per female was  $73.7 \pm 29.8$ . Most of neonates grew to the third or fourth instar prior to the winter. During the winter, *C. kyebangensis* in the field remained almost frozen in their galleries, but ones kept in the laboratory continued to grow during winter. Some characteristics of proctodeal feeding behavior are also described based on laboratory observations. We propose that the cold temperate climate, especially of the winter season, is one of the most important causes for the evolution of unusual life history of *Cryptocercus* including delayed development of nymphs.

**Key words:** *Cryptocercus*, proctodeal feeding, life history, *C. kyebangensis*, prolonged development

## INTRODUCTION

Subsocial behavior, or specialized parent-offspring interactions that terminates before offspring mature, has been well documented in some cockroaches belonging to the genus *Cryptocercus* and to the family Blaberidae (Cleveland *et al.*, 1934; Seelinger and Seelinger, 1983; Nalepa, 1984; O'Neill *et al.*, 1987; Matsumoto, 1988, 1992; Park and Choe, 2002a). The woodroaches of the genus *Cryptocercus* occur in temperate regions and live as families in complex galleries in rotten logs in temperate forests (Cleveland *et al.*, 1934; Seelinger and Seelinger, 1983; Nalepa, 1984; Park, 2002; Park and Choe, 2002a, b, c). Especially the xylophagy shown by *Cryptocercus* is not common in cockroaches and has been considered as a trait associated to delayed nymphal development and the evolution of parental care in *Cryptocercus* (Nalepa, 1984, 1988; reviewed by Nalepa, 1994).

There are currently nine *Cryptocercus* species recognized in the world. Five of them occur in the Nearctic region (Cleveland *et al.*, 1934; Bey-Bienko, 1950; Nalepa *et al.*, 1997; Burnside *et al.*, 1999). The other species occur in the Palearctic region. Some Asian populations including *C. primarius* were found in Sichuan Province and Yunnan Province, West China (Bey-Bienko, 1950; Grandcolas, 2000; Nalepa *et al.*, 2001b). The other *Cryptocercus* populations known as *C. relictus* were found in Northeast Asia (Bey-Bienko, 1950; Asahina, 1991). Recently Grandcolas *et al.* (2001) described another Asian species, *C. kyebangensis* from Mt. Gyeong in the northeastern region of South Korea.

Although woodroaches of *Cryptocercus* occur widely in forests of Asia, most studies on *Cryptocercus* social behavior have focused until now on North American species, especially *C. punctulatus* (Cleveland *et al.*, 1934; Ritter, 1964; Seelinger and Seelinger, 1983; Nalepa, 1984, 1988, 1990). From the viewpoint of *Cryptocercus* social evolution, little is known from Asian populations of the genus. We conducted an extensive survey of *Cryptocercus* in South Korea since 1997. In the present study, we describe some ecolog-

\* Corresponding author: Tel: +82-2-880-8157;  
FAX: +82-2-882-7195.  
E-mail: parkyungchul@hotmail.com

ical characteristics including habitat conditions of the Korean *Cryptocercus*. We also report on colony composition, characteristics of life history and social behavior of Korean woodroach, *C. kyebangensis*, recently described by Grandcolas *et al.* (2001). The objective of the present study is to provide information on social life of East Asian *Cryptocercus* via Korean *Cryptocercus*.

## MATERIALS AND METHODS

### Collection

We conducted an extensive survey of *Cryptocercus* in Korea, during the periods of 1997–2001. Korean populations of the genus *Cryptocercus* occurred in most of the forested regions from the North (Mt. Seorak) to the South (Mt. Jiri) of South Korea. Korean *Cryptocercus* were found in mountainous regions including both small fragments with vegetation in poor state of preservation (Mt. Cheongok, Mt. Yumyeong, and Mt. Songni) and large and quite undisturbed reserves (Mt. Seorak, Mt. Gyeong, and Mt. Jiri). For the present study, *C. kyebangensis* was collected from Mt. Gyeong, Gangwon Province, in 1997–2001. For laboratory observations, *Cryptocercus* was also collected from Mt. Yongmun, Gyeonggi Province, in mid-September 2000. All the connecting chambers in a gallery system were opened with a hammer and wood chisel. All woodroaches which were found in the connecting chambers were considered to be a family unit. Age stages were assigned to the field-caught woodroaches of *C. kyebangensis*, based on head width and body color (slightly modified from Nalepa, 1984).

### Effects of winter on nymphal growth

The overwintering age stages of *C. kyebangensis* were investigated using colonies collected prior to the winter of 1997. To investigate the effects of winter climate on the development of young nymphs, five families of young nymphs were collected in November, 1998. Head width and body weight were measured within two days since the collection, and then each family was placed into a plastic box (25×17×13 cm) which had minute air holes on the floor and sides, and was filled with pieces of rotten wood. Three families were returned to their collection sites and the others were kept in laboratory conditions (25±2°C) during the winter season. All boxes were examined in March of the following year. Habitat conditions of *C. kyebangensis* were investigated during 22–25 February, 1999.

### Social behavior

Two families which included young nymphs were used for behavioral observations. Each family was introduced into an observation chamber, a round plastic case. The artificial chambers were 15 cm in diameter and 1.5 cm deep and transparent. Each chamber was provided with rotten wood materials smashed by a mixer. Chambers were kept in D:L=12h:12h at 25±2°C. The woodroaches were allowed to accustom themselves to the plastic chambers for one week before observation.

## RESULTS

### Habitat

Korean *Cryptocercus* occurred in mountains ranging from 720 m (Mt. Juwang) to 1915 m (Mt. Jiri) in elevation. Most of them were observed on the ridge or near the top of the mountains. The mountains in which Korean *Cryptocercus* were found harbor deciduous forests with patchily dis-

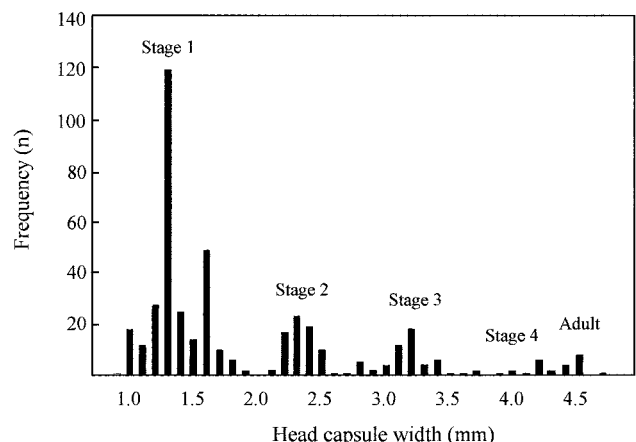
tributed coniferous trees. *Cryptocercus kyebangensis* used for the present study were collected from nearby cultivated land (around 800 m in elevation) and valleys to the top of Mt. Gyeong (1577 m). *Cryptocercus kyebangensis* occurred in the galleries of rotting tree trunks. The size of these trunks ranged from 5 cm to about 120 cm in diameter, but individuals of *C. kyebangensis* were found most often in dead trunks of 36.5 cm (±16; *n*=31) in mean diameter. The gallery structure comprised irregular chambers and tunnels. Generally the chambers were about 0.8 cm (±0.3, *n*=20) in depth and less than 7 cm (±0.2, *n*=15) in diameter, and connected with tunnels. Paired adults without nymphs usually inhabited in relatively simple galleries, whereas families with nymphs constructed fairly complicated galleries, including small galleries (<about 1 cm in diameter) probably built by nymphs. The galleries were often located right beneath the hard bark of rotting logs.

### Reproduction

Oothecae were found at various dates ranging from mid-June to late July. Oothecae were only found in the galleries of paired adults and never found in families with nymphs (*n*=46 families). Oothecae were embedded in the grooves of rotting logs with the finely-chewed woody material and packed to about two thirds of their height, with the keel upside. The mean number of oothecae per female was 2.5 (±0.9; range, 1–5; *n*=15), the mean number of eggs per ootheca was 29.1 (±3.9; range, 18–36; *n*=38), and the mean number of eggs per female was calculated to 73.7 (±29.8; range, 25–133; *n*=15). The oothecae kept in the laboratory hatched between mid-July to late July of 1997 and 1998, respectively. The proportion of neonates hatched per ootheca was 79.1% (±14.6; *n*=15).

### Effect of winter on nymphal growth

During the winter months, the trunks were laid under the snow cover (mean deep 43±13 cm, *n*=7). Members of the families were found deeper in the galleries and their



**Fig. 1.** Frequency distribution of head capsule widths of the field-caught *Cryptocercus kyebangensis* (*n*=466).

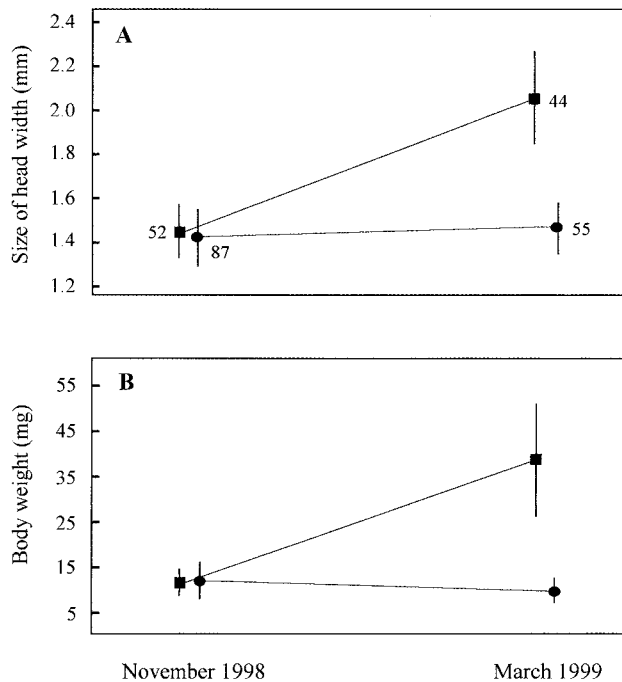
abdomens were flat. When woodroaches of *C. kye bangensis* were exposed out of their gallery, they crawled very slowly or rarely moved. A total of five age stages occurred in *C. kye bangensis* which were collected prior to winter (Fig. 1). They were classified as follows; *stage 1*: whitish to ivory in color, with a head capsule  $\leq 1.8$  mm, *stage 2*: ivory to gold, between 1.8 and 2.7 mm, *stage 3*: gold to reddish-brown, between 2.7 and 3.5 mm, and *stage 4*: darker reddish-brown, between 3.5 and 4.2 mm. Adults were nearly black, approximately 25 mm in length with a mean head capsule width of 4.45 mm ( $\pm 0.16$ ,  $n=30$ ). Although age stages were not always clearly defined, especially in the older nymphs, female adults had lateral emarginations in the

caudal margin of the 7th sternum. Thus, they could be distinguished easily from nymphs of the last instar.

In young nymphs of *C. kye bangensis* kept in the field, the size of head width did not change during the winter months. Rather, a decrease in body weight occurred (Fig. 2A, B). Nymphs kept in the laboratory condition, however, continued to grow throughout the season (Fig. 2A, B). Nymphal molts were often observed in ones kept in the laboratory in winter.

### Colony composition

Families of *C. kye bangensis* lived in monogamous associations in which parents care for their young. The colony composition of *C. kye bangensis* which were collected in the field was summarized in Table 1. In colonies where adults were present ( $n=21$ ), the mean number of male nymphs was 9.1 ( $\pm 4.89$ ) and that of female nymphs was 9.6 ( $\pm 4.96$ ). Brood sex ratio was not significantly biased (Chi-Square test;  $\chi^2=0.027$ ,  $P>0.05$ ). Paired adults without offspring (23.2%) and one or both parents with their offspring (28.1%) were found most frequently in the field. In the case of families with single parents, the presence of female adults within families (6.7%) was noted more frequently than that



**Fig. 2.** Size of head width (A) and body weight (B) of offspring kept in the laboratory condition and in the field during the winter (□ and ● indicate laboratory conditions and natural conditions, respectively). Numbers within boxes indicate the number of individuals.

**Table 1.** Colony composition of the field-caught *C. kye bangensis* in South Korea

Colony composition	Sample size	%
Adult pair ( or )	135	23.24
Adult alone	80	13.77
Adult alone	100	17.21
Adult pair with nymphs	116	19.97
Adult with nymphs	39	6.71
Adult with nymphs	8	1.38
Last instar pair ( and )	20	3.44
Last instar alone ( or )	43	7.40
Group of nymphs	40	6.88
Total	581	100

**Table 2.** Brood size of *C. kye bangensis* families in South Korea

	Sample size	Mean no. of nymphs	Standard deviation	Range
A. Mean brood size	163	21.6	9.4	4–48
B. By age of nymphs				
Stage 1	66	26.0 <sup>+</sup>	9.8	7–48
Stage 2	91	19.2 <sup>†</sup>	7.7	7–40
Stage 3	6	9.7 <sup>‡</sup>	5.9	4–20
C. By adult presence				
Male and female	116	22.2 <sup>*</sup>	9.6	7–48
Female	39	20.5 <sup>*</sup>	8.8	4–39
Male	8	18.5 <sup>*</sup>	10.1	4–35

Different symbols in each group indicate differences in mean.



of males (1.4%).

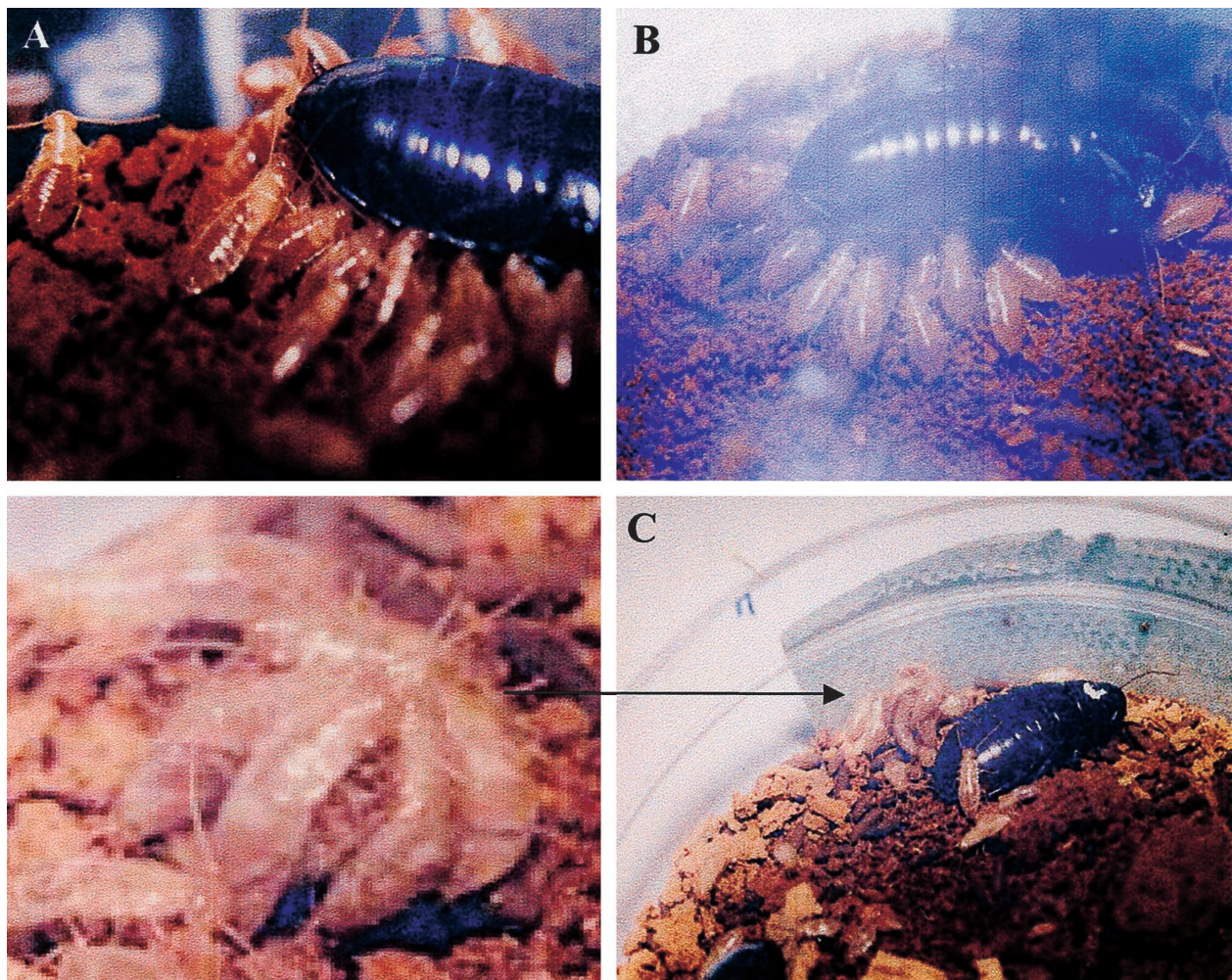
In families with single or both parents, the mean brood size was 21.6 ( $\pm 9.4$ ;  $n=163$  families) (Table 2A). Mean brood size varied significantly depending on age stages (Table 2B). Families with nymphs of *stage 2* had significantly smaller broods than those with nymphs of *stage 1* (Mann-Whitney *U*-test;  $U=1763.5$ ,  $P<0.0001$ ). The brood size was also significantly different between families with nymphs of *stage 2* and *stage 3* (Mann-Whitney *U*-test;  $U=76.5$ ,  $P<0.05$ ). The brood size of families with both adults was not significantly different from that of families with single adults (Kruskal-Wallis test;  $\chi^2=1.51$ ,  $df=2$ ,  $P>0.05$ ) (Table 2C).

According to nymphal stages, parental presence in families was investigated. In 68 families with young nymphs (*Stage 1*), 66 families had one or both of parents and 70.6% of them had both parents. In 20 families with old nymphs (*Stage 3*), adults were present in only 6 families.

### Social behavior

Nymphs of *C. kyebangensis* collected for laboratory

observations belonged to the first stage. They showed a series of typical proctodeal feeding behavior. Nymphs often fed on woody materials around the mouth of feeding adults. Nymphs also spent their time for group feeding, and grooming various body parts of one or both adults, especially around anus, spiracles, neck membrane, and coxal segments. Nymphs sometimes showed great interest in one of the adults, more often the female. Most nymphs began following around the adult and assembled around the abdominal tip or under the abdomen of the adult (Fig. 3A). Most nymphs (about 20 individuals) attended in sitting side by side in semicircular pattern with their heads directed toward the adult abdomen with antennae vibrating actively (Fig. 3B). This type of behavior occurred 6.5 times ( $\pm 2.3$ ,  $n=10$ ) a day and usually lasted for 43min ( $\pm 14$ ;  $n=18$ ) at once. Among the anal feeding patterns observed ( $n=35$ ), 64% were terminated at the semicircular feeding stage. The termination of the feeding session occurred by the adult walking off from nymphs. In the rest, however, some peculiar behavioral patterns were observed following the semicircular stage. Nymphs stopped feeding in semicircular fashion in



**Fig. 3.** Behavioral patterns of nymphs during proctodeal feeding. Nymphs which assembled around under abdomen of one of their parents, with antennae vibrated actively (A). Semicircular position (B). Clumping behavior (C).

35 min ( $\pm 16$ ,  $n=23$ ) and clumped around themselves at the anal tip of the adult with their heads facing the inside of the clump (Fig. 3C). Most nymphs joined to form the clump. The adult turned around to face the nymphs shortly after they formed the clump-and then walked away from it. A few nymphs failed to join in clumping continued to follow the adult.

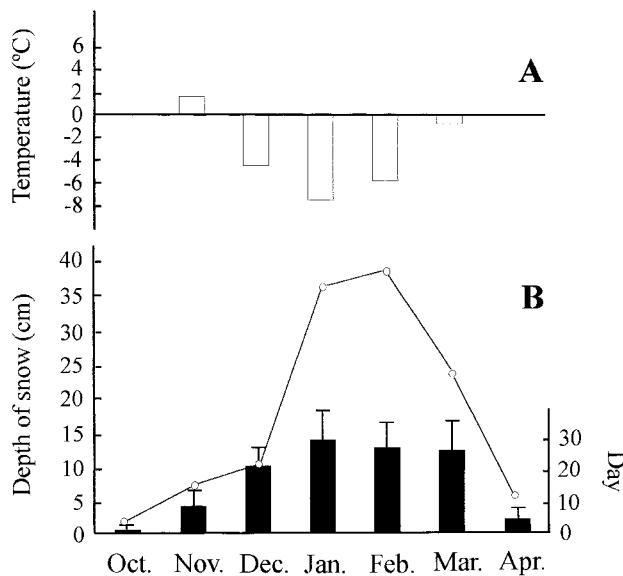
## DISCUSSION

Asian *Cryptocercus* have been found primarily at high elevations, over 1000–4,270 m until now (Bey-Bienko, 1950; Asahina, 1991; Grandcolas, 2000; Nalepa *et al.*, 2001b). Korean *Cryptocercus* were distributed at much lower elevations than those known to date in Asia. These differences in the distribution of *Cryptocercus* populations with respect to elevation could be interpreted in terms not only of historical paleogeographical constraints (Grandcolas, 1999; Nalepa and Bandi, 1999) but also of the present regional climate and latitude, northern populations being present at lower altitudes.

The present results showed that the life history of *C. kyebangensis* is similar to that of North American *C. punctulatus*. *Cryptocercus kyebangensis* was also monogamous and lived in families. Oothecae of *C. kyebangensis* were observed in galleries of only paired adults without their young and never occurred in galleries of families with nymphs. It suggests that *C. kyebangensis* females have only a single reproduction in her lifetime as do females of *C. punctulatus* (Seelinger and Seelinger, 1983; Nalepa, 1984). Gallery structures were more complex in families with older nymphs. Tunneling by older nymphs with stronger mandibles appeared to lead to a rapid expansion of the gallery system. Rapid tunneling by older nymphs could be important to *Cryptocercus* dispersal. The proctodeal feeding behavior displayed in *C. kyebangensis* is also similar to that of *C. punctulatus* (Seelinger and Seelinger, 1983; Nalepa, 1984). However, a new pattern of feeding behavior, the clumped feeding behavior, was observed in *C. kyebangensis* during proctodeal feeding. Until now, it was unknown in the well-studied North American species, *C. punctulatus*. Since neonates of *Cryptocercus*, xylophagous cockroaches, hatch without gut fauna needed to digest woody diets (Cleveland *et al.*, 1934; Nalepa, 1990; Park, unpublished data), they have to obtain gut fauna via proctodeal trophallaxis provided by their adults (Cleveland *et al.*, 1934; Seelinger and Seelinger, 1983; Nalepa, 1984). According to Nalepa (1984, 1988, 1994) and Nalepa and Bell (1997), *Cryptocercus* nymphs need essential nutrients required for early development as well as gut fauna via proctodeal trophallaxis from their adults (refer to Park and Choe, 2002a). In addition, flagellates provided by adults may be digested in gut system and assimilated as food for their young (reviewed by Nalepa *et al.*, 2001a). Park and Choe (2002a) recently reported that *Cryptocercus* growth was more facilitated in young nymphs with parents than those without par-

ents. Although droplets of gut content were not directly observed, the clumping behavior suggests that gut fluids are transferred by excreting droplets and they play a role in transfer of essential nutrients as well as gut fauna from parents to their young.

Woodroaches of *C. kyebangensis* stopped growing in winter, generally from the end of November. At this moment, five age stages were present in the colonies of *C. kyebangensis*. Stage 1 nymphs hatched in the previous summer of the collection (refer to Park and Choe, 2002a), Stage 2 nymphs were probably born in the second summer prior to the collection, and those in stage 3 and 4 were probably about in the third and fourth year after their birth, respectively (also see Nalepa, 1984). Thus, *C. kyebangensis* appeared to reach adulthood in the summer of the fifth year (approximately 4-year long) after their birth. In North American species, the time required to reach adulthood was 4–5 years in *C. punctulatus* and 5–7 years in *C. clevelandi* (Nalepa *et al.*, 1997). In *Cryptocercus* spp., the delayed nymphal development has often been explained from the viewpoint of wood diet poor especially in nitrogen (Nalepa, 1984, 1988, 1994; Nalepa and Bell, 1997). According to this viewpoint, diets low in nutrients are a prime cause of delayed nymphal growth and the evolution of subsociality in *Cryptocercus*. This delayed growth has been also subsequently hypothesized to have allowed the successful invasion of seasonal temperate regions, making *Cryptocercus* perennial and relatively independent of seasonality changes (Grandcolas, 1995). However, little was known about the life history of *Cryptocercus* in relation to their environment. Our results suggest that climatic environment as well as low quality nutrients of woody diet may be an important cause in the evolution of *Cryptocercus* life history. The winter climate can affect the evolution of their life history by delaying nymphal growth. The mean temperature of the Daegwallyeong region, to which Mt. Gyeongju is adjacent, falls significantly during winter, i.e., November to March of every year (Fig. 4A). Snowcover exists nearly to the end of March (Fig. 4B). In Mt. Gyeongju, the winter season also begins from mid-November and ends in mid-March, lasting nearly four months of the year. The field and laboratory observations showed that *C. kyebangensis* remain frozen in their natural habitat during the winter months, but under the laboratory condition they can still feed and grow. According to Danks (1992), developmental rate can be constrained by low temperature as well as poor food quality and large body size. Species with the longest life cycles tend to be found in cool climates or microhabitats of temperate regions. Boreal and arctic insect species tend to have longer life cycles than their temperate relatives (Danks, 1992). When a species also spans a range of temperature, the life cycle can vary in response. For example, the mayfly *Habrophlebia vibrans* (Lauzon and Harper, 1986) and the oak egg moth *Lasio-campa quercus* (Bulmer, 1977) have 2-year periodical life cycles in colder areas, but 1-year non-periodical life cycles in warmer areas (also reviewed by Heliövaara *et al.*, 1994).



**Fig. 4.** Mean temperature (A), and mean depth of snowcover (—) and the number of days ( ) which snowcover was observed in each month (B) during autumn and winter 1991 to 2001 at Daegwallyeong region adjacent to Mt. Gyebang. \*Raw data were provided from the Daegwallyeong Weather Station.

Like perennial insects which occur in temperate regions (Tauber *et al.*, 1986; Leather *et al.*, 1993), *Cryptocercus* also have to regulate their life cycle to cope with unfavorable environment in winter (Hamilton *et al.*, 1985; Appel and Sponsler, 1989). If *Cryptocercus* nymphs can grow normally even in winter as ones kept under the laboratory condition, they would reach the adulthood earlier. Thus, the adults could be relieved earlier from the duty of caring their offspring. According to Nalepa (1988), when young nymphs of *C. punctulatus* were removed, the adults tended to reproduce again. Shortened nymphal development could allow *Cryptocercus* adults to reproduce more than once during their lifetime, which means the transition of semelparity to iteroparity. *Cryptocercus* in China live in colder regions than Korean *Cryptocercus* because their habitats are located in mountains at higher elevations and latitudes (Bey-Bienko, 1950; Grandcolas, 2000; Nalepa *et al.*, 2001b). If the life cycle of *Cryptocercus* can vary along the range of temperature, *Cryptocercus* in China should have longer life cycles than Korean *Cryptocercus*. In addition to studies on *Cryptocercus* in China, further studies of cockroaches belonging to Blaberidae or Polyphagidae, which live in habitats with shorter or no winter (as those in Southeast Asia) will provide valuable information on the evolution of life cycles in *Cryptocercus* (e.g., Matsumoto, 1988, 1992; Pellens *et al.*, 2002).

We believe that the present study adds interesting comparative results to the literature of *Cryptocercus* studies. First, it confirms that the main subsocial and developmental characteristics observed in *C. punctulatus* and *C. clevelandi* can be safely generalized for the genus. Second, it shows that elevational distributions of *Cryptocercus* have considerable variations along their latitudinal positions. Finally, the

present study shows that climate may have played an important role in the evolution in *Cryptocercus* long life span and semelparity.

## ACKNOWLEDGEMENTS

We are grateful to the exchange program KOSEF/CNRS for grants to Jae C. Choe (KOSEF No. 985-0500-007-2) and P. Grandcolas (CNRS No. 5389/7066, 1998/1999). This study was also supported by grants from the BK21 Research Fellowship from the Korean Ministry of Education and Human Resources Development.

## REFERENCES

- Appel AG, Sponsler RC (1989) Water and temperature relations of the primitive xylophagous cockroach *Cryptocercus punctulatus* scudder (Dictyoptera: Cryptocercidae). *Proc Entomol Soc Wash* 91: 153–157
- Asahina S (1991) Notes on two small collections of the Blattaria from China and Korea. *Akitu* 121: 1–5
- Bey-Bienko GY (1950) Fauna of the USSR. Insects. Blattodea. Inst Zool Acad Sc URSS, Moscow (in Russian).
- Bulmer MG (1977) Periodical insects. *Am Nat* 111: 1099–1117
- Burnside CA, Smith PT, Kambhampati S (1999) Three new species of the woodroach, *Cryptocercus* (Blattodea: Cryptocercidae), from the eastern United States. *J Kans Entomol Soc* 72: 361–378
- Cleveland LR, Hall SR, Sanders EP, Collier J (1934) The wood-feeding roach *Cryptocercus*, its protozoa, and the symbiosis between protozoa and roach. *Mem Am Acad Arts Sci* 17: 85–342
- Danks HV (1992) Long life cycle in insects. *Can Entomol* 124: 167–187
- Grandcolas P (1995) The appearance of xylophagy in cockroaches: two case studies with reference to phylogeny. *J Orth Res* 4: 177–184
- Grandcolas P (1999) Systematics, endosymbiosis, and biogeography of *Cryptocercus clevelandi* and *C. punctulatus* (Blattaria: Polyphagidae) from North America: a phylogenetic perspective. *Ann Entomol Soc Am* 92: 285–291
- Grandcolas P (2000) *Cryptocercus matilei* n.sp., du Sichuan de Chine (Dictyoptera, Blattaria, Polyphaginae). *Rev Fr Entomol* 22: 223–226
- Grandcolas P, Park YC, Choe JC, Piulachs MD, Bellés X, D'Haese C, Farine JP, Brossut R (2001) What does reveal *Cryptocercus kyebangensis*, n. sp. from South Korea about *Cryptocercus* evolution? A study in morphology, molecular phylogeny and chemistry of tergal glands (Dictyoptera, Blattaria, Polyphagidae). *Proc Acad Nat Sci Phila* 151: 61–79
- Hamilton RL, Mullins DE, Orcutt DM (1985) Freezing tolerance in the woodroach *Cryptocercus punctulatus* (Scudder). *Experientia* 41: 1535–1536
- Heliövaara K, Väisänen R, Simon C (1994) Evolutionary ecology of periodical insects. *Trends Ecol Evol* 9: 475–480
- Lauzon M, Harper PP (1986) Life history and production of the stream-dwelling mayfly *Habrophlebia vibrans* Needham (Ephemeroptera: Leptophlebiidae). *Can J Zool* 64: 2038–2045
- Leather SR, Walters KFA, Bale JS (1993) The ecology of insect overwintering. Cambridge University press, Cambridge
- Matsumoto T (1988) Colony composition of the subsocial wood-feeding cockroaches *Panesthia australis* Brunner (Blattaria, Blaberidae, Panesthinae) in Australia. *Zool Sci* 5: 1145–1148
- Matsumoto T (1992) Familial association, nymphal development and population density in the Australian giant burrowing cockroach, *Macropanesthia rhinoceros* (Blattaria: Blaberidae). *Zool*



Sci 9: 835–842

- Nalepa CA (1984) Colony composition, protozoan transfer and some life history characteristics of the woodroach *Cryptocercus punctulatus* Scudder (Dictyoptera: Cryptocercidae). *Behav Ecol Sociobiol* 14: 273–279
- Nalepa CA (1988) Cost of parental care in *Cryptocercus punctulatus* Scudder (Dictyoptera: Cryptocercidae). *Behav Ecol Sociobiol* 23: 135–140
- Nalepa CA (1990) Early development of nymphs and establishment of hindgut symbiosis in *Cryptocercus punctulatus* (Dictyoptera: Cryptocercidae). *Ann Entomol Soc Am* 83: 786–789
- Nalepa CA (1994) Nourishment and the origin of termite eusociality. In “Nourishment and evolution in insect societies” Ed by JH Hunt, CA Nalepa, Westview Press, Boulder, pp 57–104
- Nalepa CA, Bandi C (1999) Phylogenetic Status, Distribution, and Biogeography of *Cryptocercus* (Dictyoptera: Cryptocercidae). *Ann Entomol Soc Am* 92: 292–302
- Nalepa CA, Bell WJ (1997) Postovulation parental investment and parental care in cockroaches. In “The Evolution of Social Behavior in Insects and Arachnids” Ed by JC Choe, BJ Crespi, Cambridge University Press, Cambridge, pp 26–51
- Nalepa CA, Bignell DE, Bandi C (2001a) Detritivory, coprophagy, and the evolution of digestive mutualisms in Dictyoptera. *Insect Soc* 48: 194–201
- Nalepa CA, Byers CW, Bandi C, Sironi M (1997) Description of *Cryptocercus clevelandi* (Dictyoptera: Cryptocercidae) from the Northwestern United States, molecular analysis of bacterial symbionts in its fat body, and notes on biology, distribution, and biogeography. *Ann Entomol Soc Am* 90: 416–424
- Nalepa CA, Li LI, Wen-Hua Lu, Lazell J (2001b) Rediscovery of the wood-eating cockroach *Cryptocercus primarius* (Dictyoptera: Cryptocercidae) in China, with notes on ecology and distribution. *Acta Zootaxonom Sin* 26: 184–190
- O'Neill SL, Rose HA, Rugg D (1987) Social behavior and its relationship to field distribution in *Panesthia cribrata* Saussure (Blattodea: Blaberidae). *J Aust Entomol Soc* 26: 313–321
- Park YC (2002) Behavioral ecology, molecular phylogeny and biogeography of the Korean wood-feeding cockroaches (Blattaria: *Cryptocercus*). Ph. D. thesis, Seoul National University, Seoul
- Park YC, Choe JC (2002a) Effects of parental care on offspring growth in the Korean wood-feeding cockroaches, *Cryptocercus kyebangensis*. *J Ethol* DOI 10.1007/s10164-002-0080-9 [published online]
- Park YC, Choe JC (2002b) Territorial behavior of Korean wood-feeding cockroaches (*Cryptocercus kyebangensis*). *J Ethol* DOI 10.1007/s10164-002-0081-8 [published online]
- Park YC, Choe JC (2002c) Structure of female genitalia in the Korean wood-feeding cockroach (*Cryptocercus kyebangensis*). *Korean J Biol Sci* 6: 65–68
- Pellens R, Grandcolas P, Domingos da Silva-Neto I (2002) A new and independently evolved case of xylophagy and the presence of intestinal flagellates in cockroaches: *Parasphaeria boleiriana* (Dictyoptera, Blaberidae, Zetoborinae) from the remnants of the Brazilian Atlantic forest. *Can J Zool* 80: 350–359
- Ritter HJr (1964) Defense of a mate and the mating chamber of a wood-eating cockroach. *Science* 143: 1459–1460
- Seelinger G, Seelinger U (1983) On the social organization, alarm and fighting in the primitive cockroach *Cryptocercus punctulatus* Scudder. *Z Tierpsychol* 61: 315–333
- Tauber MJ, Tauber CA, Masaki S (1986) Seasonal adaptations of insects. Oxford University Press, New York

(Received April 30, 2002 / Accepted July 1, 2002)