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

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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±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±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. Gyebang 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-
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 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. Gyebang, and Mt. Jiri). For the present study, C. kyebangensis was collected from Mt. Gyebang, 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 wintering 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.

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 distributed 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. Gyebang (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.

RESULTS

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).](https://bioone.org/journals/Zoological-Science)
abdomens were flat. When woodroaches of *C. kyebangensis* were exposed out of their gallery, they crawled very slowly or rarely moved. A total of five age stages occurred in *C. kyebangensis* which were collected prior to winter (Fig. 1). They were classified as follows; stage 1: whitish to ivory in color, with a head capsule ≤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 (±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. kyebangensis* 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. kyebangensis* lived in monogamous associations in which parents care for their young. The colony composition of *C. kyebangensis* 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 (±4.89) and that of female nymphs was 9.6 (±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

![Figure 2](https://bioone.org/journals/Zoological-Science/22July2019/figures/135.png) **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.

| Colony composition | Sample size | %
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult pair ( □ or ● )</td>
<td>135</td>
<td>23.24</td>
</tr>
<tr>
<td>Adult □ alone</td>
<td>80</td>
<td>13.77</td>
</tr>
<tr>
<td>Adult ● alone</td>
<td>100</td>
<td>17.21</td>
</tr>
<tr>
<td>Adult pair with nymphs</td>
<td>116</td>
<td>19.97</td>
</tr>
<tr>
<td>Adult □ with nymphs</td>
<td>39</td>
<td>6.71</td>
</tr>
<tr>
<td>Adult ● with nymphs</td>
<td>8</td>
<td>1.38</td>
</tr>
<tr>
<td>Last instar pair ( □ and ● )</td>
<td>20</td>
<td>3.44</td>
</tr>
<tr>
<td>Last instar alone ( □ or ● )</td>
<td>43</td>
<td>7.40</td>
</tr>
<tr>
<td>Group of nymphs</td>
<td>40</td>
<td>6.88</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>581</strong></td>
<td><strong>100</strong></td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Sample size</th>
<th>Mean no. of nymphs</th>
<th>Standard deviation</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Mean brood size</td>
<td>163</td>
<td>21.6</td>
<td>9.4</td>
</tr>
<tr>
<td>B. By age of nymphs</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stage 1</td>
<td>66</td>
<td>26.0*</td>
<td>9.8</td>
</tr>
<tr>
<td>Stage 2</td>
<td>91</td>
<td>19.2†</td>
<td>7.7</td>
</tr>
<tr>
<td>Stage 3</td>
<td>6</td>
<td>9.7‡</td>
<td>5.9</td>
</tr>
<tr>
<td>C. By adult presence</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male and female</td>
<td>116</td>
<td>22.2*</td>
<td>9.6</td>
</tr>
<tr>
<td>Female</td>
<td>39</td>
<td>20.5*</td>
<td>8.8</td>
</tr>
<tr>
<td>Male</td>
<td>8</td>
<td>18.5*</td>
<td>10.1</td>
</tr>
</tbody>
</table>

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 (±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 (±2.3, \( n=10 \)) a day and usually lasted for 43min (±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

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**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 (±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 parents. 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. Gyebang 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. Gyebang, 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 eggar moth Lasiocampa 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).
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.

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