

<Review>

## Evolution of Social Life in Wood-Eating Cockroaches (*Cryptocercus* spp.) : Effects of the Winter Climate on the Evolution of Subsociality

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**ABSTRACT:** Subsocal behavior of the genus *Cryptocercus* cockroaches has been believed as primitive traits of termite eusociality. Thus, it has been believed that understanding *Cryptocercus* subsociality is a pre-requisite stage to infer evolutionary route of the eusociality in termites. Woodroaches of *Cryptocercus* are also well known because of its peculiar characteristics including adults living monogamously in pairs, semelparous reproduction, xylophagy, obligatory association between adults and their offspring, slow development, and anal trophallaxis by adults. Based on the previously accumulated data, we try to understand two major components of *Cryptocercus* life history, development and reproduction. We hypothesize that harsh winter and length of winter might be one of the main causes driving the appearance of the delayed development and semelparous reproduction in *Cryptocercus* life history.

**Key words:** Climate hypothesis, *Cryptocercus*, Parental care, Subsociality, Wood-eating cockroach

### INTRODUCTION

Subsocial behavior involves parental care behavior that promotes the survival, growth, and development of offspring (Clutton-Brock 1991). In the insects, subsocial behavior has arisen independently in at least 13 different orders (Eickwort 1981, Tallamy and Wood 1986). About 4,000 species in 460 genera of cockroaches (Blattaria) have been described to date (McKittrick 1964). Subsocal behavior comprising a continuum of behavior ranging from a low level of parental care like simple egg caring to an array of complex grooming (Seelinger and Seelinger 1983, Nalepa 1984, Park et al. 2002), feeding (Seelinger and Seelinger 1983, Nalepa 1984, Park et al. 2002, Perry and Nalepa 2003) and protective behavior (Ritter 1964, Roth 1981, Matsumoto 1992, Park and Choe 2003a) has evolved in most cockroaches.

Most studies of subsocial behavior have been focused on cockroaches in the family Blaberidae (Table 1) (Roth 1981, Matsumoto 1988, 1992, Pellens et al. 2002, Maekawa et al. 2005), all of which are xylophagous insects using rotten leaves or woody materials as their food. The subsocial blaberid cockroaches are viviparous or ovoviviparous cockroaches and are distributed in tropical and subtropical forests (Table 1). In contrast with the blaberid cockroaches, the genus *Cryptocercus*, which belongs to the family Polyphagidae, is distributed in temperate forests in areas with harsh winters (Table 1). It is also the only known oviparous cockroach to show advanced

subsocal behavior, including protective behavior and extended parental care (Fig. 1) (Ritter 1964, Seelinger and Seelinger 1983, Nalepa 1984, Park et al. 2002). Because of the close phylogenetic relationship between *Cryptocercus* and termites, *Cryptocercus* subsociality has been described as a primitive form of termite eusociality (Fig. 2). Thus, study of the evolution of *Cryptocercus* subsociality is a prerequisite for understanding the evolutionary of termite eusociality. To date, data on various aspects of *Cryptocercus* life history have been accumulating, resulting in a deeper understanding of the evolution of *Cryptocercus* subsociality. In this paper, we try to infer causes for the evolution of two main components in *Cryptocercus* subsociality, including both abiotic and biotic factors. In particular, we consider two major components of *Cryptocercus* life histories, developmental delay and reproductive mode, in relation to winter climate.

### THE GEOGRAPHIC DISTRIBUTION AND MICROHABITATS OF SUBSOCIAL WOOD-EATING COCKROACHES

Well-developed subsocial behavior has been known in some xylophagous species of cockroaches in the families Blaberidae and Polyphagidae. Most subsocial blaberid cockroaches known to date are distributed in tropical and subtropical forests. *Macropanesthia rhinoceros* are native to Australia and mostly found in tropical parts of Queensland (Matsumoto 1992). *Panesthia australis* is widespread

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Table 1. Brief information of the subsocial wood-eating cockroaches

Family or subfamily	Species	Presence of adults <sup>2</sup>	Gut protozoa	Development	Reproductive mode	Association with adults	Micro-habitat <sup>3</sup>	Climate	Reference
Cryptocercidae/ Polyphagidae <sup>1</sup>	<i>Cryptocercus</i> sp.	Both/ rarely F	Present	4.5~7 yrs	Semelparity	Whole development	DL	Harsh winter temperate	Nalepa et al. 1997 Park and Choe 2003 Park et al. 2004
Blaberidae: Panesthiinae	<i>Panesthia</i> <i>australis</i>	F/ rarely both	Absent	Un- known	Ite- rarity	About half of whole development	DL	Mild winter temperate	Matsumoto 1988
Blaberidae: Panesthiinae	<i>Panesthia</i> <i>cribrata</i>	One M/ several Fs	Absent	4~7 yrs	Ite- rarity	About half of whole development	DL	Mild winter temperate	O'Neil et al. 1987 Rugg and Rose 1990
Blaberidae : Zetoborinae	<i>Parasphaeria</i> <i>boleiriana</i>	M or F	Present	At least 1 yr	Ite- rarity	Within one month (about the first two instars)	DL	Tropical	Pellens et al. 2002
Blaberidae: Panesthiinae	<i>Salganea</i> sp.	Both	Absent	Un- known	Ite- rarity	Whole development	DL	Tropical	Maekawa et al. 2005
Blaberidae : Geoscapheinae	<i>Macropanesthia</i> <i>rhinoceros</i>	F/ rarely both	Un- known	About 2.5 yrs	Ite- rarity	Disperse at the 6th instar(total 9 instars)	UG	Tropical	Matsumoto 1992

<sup>1</sup> The phylogenetic placement of the genus *Cryptocercus* is still on discussion, *Cryptocercidae* or *Polyphagidae*.

<sup>2</sup> M and F mean male and female adults, respectively.

<sup>3</sup> DL and UG indicate dead log and underground.



Fig. 1. The monogamous reproductive system of *Cryptocercus* cockroaches. Pairs consisting of a single male and a single female live with their young.

in most eucalyptus forests of the eastern Australia (Matsumoto 1988). *Salganea matsumotoi* is distributed in Southeast Asia, especially Myanmar (Maekawa et al. 2005) and *Parasphaeria boleiriana* in South America (Pellens et al. 2003). With the exception of *Macropanesthia rhinoceros*, which lives in tunnels and galleries

under ground, all of the subsocial blaberids live in complex galleries of humid rotten logs and feed on woody materials. Since they obtain their woody foods by chewing on the humid wall of the galleries, the galleries become complex and expand as time goes on.

In contrast with the subsocial blaberids, the genus *Cryptocercus* is only subsocial cockroach distributed in temperate forests. Distributions of *Cryptocercus* cockroaches are limited to some high mountainous forests in Northeast Asia (South Korea, Manchuria, and eastern Russia), West China and North America (Cleveland et al. 1934, Bei-Bienko 1950, Nalepa 1984, Nalepa et al. 1997, Burnside et al. 1999, Grandcolas et al. 2001, Park et al. 2004). Wood-eating cockroaches of the genus *Cryptocercus* also live in complex woody galleries and feed on woody materials like xylophagous blaberid cockroaches.

#### PREVIOUS HYPOTHESES FOR THE EVOLUTION OF *CRYPTOCERCUS* SUBSOCIALITY

Peculiar characteristics of *Cryptocercus* life history include adults living monogamously in pairs, semelparous reproduction occurring only once in a lifetime, xylophagy, or using woody materials as food, long-lasting association between adults and their offspring, slow

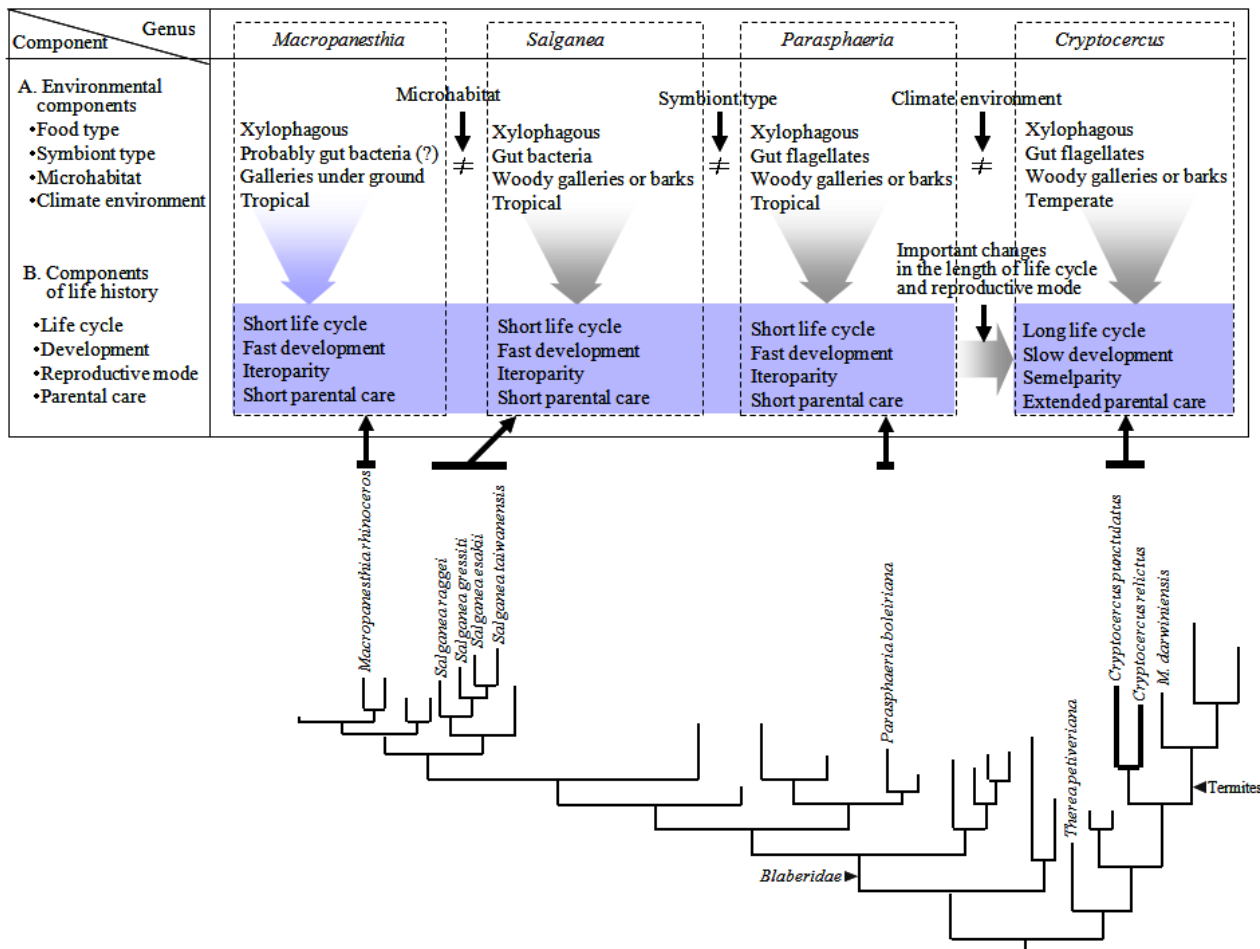


Fig. 2. Evolution of cockroach life histories with environmental change and phylogenetic relationships. The phylogenetic tree was cited from Pellens et al. (2007).

development, and anal trophallaxis by adults (Seelinger and Seelinger 1983, Nalepa 1984, Park et al. 2002). Two ultimate questions must be addressed to understand the evolution of *Cryptocercus* subsociality. First, why has the obligatory association between adults and offspring evolved in the genus? Second, what are the primary factors driving the evolution of extended parental behavior, or advanced subsociality?

Most studies to date of *Cryptocercus* life histories have only focused on the role of proctodeal trophallaxis in explaining the evolution of *Cryptocercus* social system (Cleveland et al. 1934, Seelinger and Seelinger 1983, Nalepa, 1984, 1990, 1994). Two hypotheses have been proposed to explain the link between the proctodeal feeding and the evolution of *Cryptocercus* subsociality.

Cleveland et al. (1934) hypothesized that the obligatory transfer of symbiotic gut protozoa resulted in subsociality in *Cryptocercus* (the symbiotic gut protozoa-transfer hypothesis). *Cryptocercus* are xylophagous insects, and gut protozoa are required to digest woody

materials. Neonates of *Cryptocercus* are clearly dependent on the symbiotic gut protozoa provided by their parents because they hatch devoid of gut fauna (Cleveland et al. 1934, Seelinger and Seelinger 1983). Thus, *Cryptocercus* adults provide these protozoa via proctodeal feeding (anal feeding) of their young, which is terminated prior to the nymphal stage at about the fourth instar (Nalepa 1990, Park et al. 2002). It has been suggested that this proctodeal feeding behavior led up to the obligatory social association between adults and offspring (Cleveland et al. 1934, Nalepa 1990).

Another hypothesis for the link between proctodeal feeding and the evolution of *Cryptocercus* sociality involves the nutritional ecology of *Cryptocercus* (Nalepa 1988, 1994). According to Nalepa and Bell (1997), proctodeal feeding has to be understood in the context of an unfavorable nutrition-ecological environment. Woody diets are low in nitrogen compounds, which may cause the delayed nymphal development in *Cryptocercus*; about 5 years are required for nymphs to reach adulthood. Thus, Nalepa (1988, 1994) proposed

that the nutritional environment of *Cryptocercus* may have resulted in the evolution of parental care (the nutrient-transfer hypothesis), and that the primary role of the anal material is to provide essential nutrients required in the early stages as well as to transfer symbiotic gut protozoa.

The proctodeal materials appear to contain both essential nutritious material and the gut protozoa required in the early stages of nymphal development (Nalepa 1990). It is apparent that parental care in the form of parental care is essential in the early stages of nymphal development (Cleveland et al. 1934, Nalepa 1994), resulting in the evolution of subsociality. However, this is not sufficient to explain the extended relationship between adults and their young. Young nymphs develop a full complement of gut symbiotic protozoa at an early stage of development, i.e., prior to the third or fourth instar, within about three or four months of hatching (Nalepa 1990). In addition, proctodeal feedings by adults are mainly observed at the early nymphal stages. Thus, according to the two hypotheses based on proctodeal feeding behavior, the obligatory social association between adults and offspring should be restricted to the early stages. However, adults and their offspring live together beyond the critical early stages (3th or 4th instar stages) (Park and Choe 2003b). Thus, further factors have to be considered to explain the evolution of the extended parental care.

#### CLIMATE AND THE EVOLUTION OF SUBSOCIALITY IN THE GENUS *CRYPTOCERCUS*

##### Evolution of Long Life Cycles

Climate has been almost completely overlooked in studies of the evolution of *Cryptocercus* life histories (but see Grandcolas 1995, Park et al. 2002), although *Cryptocercus* live in areas with pronounced seasonality. Weather and climate are commonly accepted by entomologists as dominant influences on the behavior, abundance, and distribution of insects (Andrewartha and Brich 1954). The importance of temperature in the growth, seasonal development, and ecological adaptations of insects has long been recognized (Tauber et al. 1986, Danks 1992, Anderson and Brower 1996). The rate of development and survival of insects can be constrained by the length of the winter as well as low temperatures in the winter (Danks 1992). Thus, the climate in winter may affect the evolution of many aspects of life histories, including the length of the life cycle, patterns of parental care, and the reproductive mode (e.g., semelparity vs. iteroparity). In the temperate forests where *Cryptocercus* is distributed, one of the most apparent climatic features is the cold winter. Like other perennial insects which occur in temperate regions, the *Cryptocercus* life cycle includes physiological mechanisms and behavioral responses that permit survival in cold

winters (Hamilton et al. 1985, Appel and Sponsler 1989, Park et al. 2002). Thus, the evolution of extended parental care and semelparous reproductive mode of *Cryptocercus* may be responses to climate.

The climate in the Korean forests is harsh during the long winter (about four and half months) (refer to Fig. 4 in Park et al. 2002), which lasts from November to March of every year, and snowcover persists almost to the end of March in Korea. *Cryptocercus* nymphs remain frozen in their natural habitat during the winter months, while under the laboratory condition they can still feed and grow (Park et al. 2002). The nymphal groups in the lab molted at least one or twice more than the control groups in their natural habitat during the winter after they hatched.

In Northeast Asia, *Cryptocercus* species are distributed throughout Manchuria, Siberia (Ussuri of Russia), and Korea (Bei-Bienko 1950, Park et al. 2004). *Cryptocercus* live in similar microhabitats in these locations, but there is some variation in temperature and the length of cold periods (Park et al. 2004). Since the former two regions are located in higher latitudes than South Korea, *Cryptocercus* there might have had to adapt to colder climates than Korean *Cryptocercus*.

Manchurian and South Korean *Cryptocercus* live in environments that differ by about 7°C in annual mean temperature (Table 2). Korean *Cryptocercus* starts moving slowly at a minimum temperature of 3~4°C and eat at higher temperatures (Park et al. 2002). This might indicate that overwintering Korean *Cryptocercus* restart their growth every spring and develop for a periods of about 8 months from mid-March to mid-November of every year, i.e. in the months when the average temperature is at least 0°C. If Manchurian *Cryptocercus* have similar physiology to that of Korean *Cryptocercus*, and respond similarly to temperature variation, their growth should occur for a period of about 6 months from mid-April to mid-October of every year (Table 2).

In Korean *Cryptocercus*, reproduction occurs between the middle and the end of June (Park et al. 2002). In Korea, the average temperature in June is 21.5°C (Table 2). June in Korea is similar to July in Manchuria in average temperature (22.5°C) as well as high and low temperatures (27.8°C and 17.2°C, respectively) (Table 2). If other environmental factors such as photoperiod and humidity do not have an additional influence, then reproduction of Manchurian *Cryptocercus* is predicted to occur between the middle and the end of July. Thus, Manchurian *Cryptocercus* neonates would grow for 3~3.5 months to the middle or end of October after their hatch in July, whereas Korean *Cryptocercus* neonates would have about 5 months to grow after hatching. Since this only includes the difference of 1~2 months in the first year of their life cycle, a much greater difference may accumulate over their whole life cycle. Therefore, the length of cold temperature in winter may significantly

Table 2. Comparison of monthly average temperatures between Manchuria and South Korea

Location	Temp (°C)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Mean
Manchuria <sup>1</sup>	High	-11.1	-6.7	2.2	13.3	21.1	25.0	27.8	26.7	21.1	12.8	1.1	-8.3	10.4
	Low	-23.9	-20.6	-10.6	-0.6	6.7	12.8	17.2	16.1	8.3	-0.5	-10.6	-20.0	-2.1
	Mean	-17.5	-13.7	-4.2	6.4	13.9	18.9	22.5	21.4	14.7	6.2	-4.8	-14.2	4.2
South Korea <sup>2</sup>	High	1.6	4.7	11.2	19.1	24.0	27.8	29.7	30.1	25.8	19.9	11.3	4.2	17.5
	Low	-11.6	-8.9	-3.0	2.9	8.9	15.2	19.9	19.8	13.6	5.4	-1.7	-8.2	4.4
	Mean	-5.0	-2.1	4.1	11.0	16.5	21.5	24.8	25.0	19.7	12.7	4.8	-2.0	11.0

<sup>1</sup> Monthly average temperature of Mudangiang city near the collection sites for the period from 1951 to 1988 (these average temperatures were calculated based on raw data from the website: <http://www.fwcc.org/climate.htm>).

<sup>2</sup> Monthly average temperature of Hongcheong city near the collection sites for the period from 1971 to 2000 (these average temperatures were calculated based on raw data from the website of Korean Metrological Administration: [http://www.kma.go.kr/kor/weather/climate/climate\\_06\\_02.jsp](http://www.kma.go.kr/kor/weather/climate/climate_06_02.jsp)).

affect the time required to reach adulthood, i.e., their life span may depend on the length of developmental stasis during the winter, *ceteris paribus*.

We collected specimens in the field in South Korea and Manchuria during similar time periods (early to mid October and mid to late October in 1998, respectively), and found differences in the developmental stages of *Cryptocercus* nymphs between the two regions (Fig. 3). In the Korean *Cryptocercus* (*C. kyebangensis*), most nymphs belonged to the 3th (28.0%) and 4th (60.1%) instars, whereas most Manchurian nymphs (*C. parvus*) were in the 2nd (21.6%) and 3rd (64.0%) instars. Since winter starts in late October or early November in Manchuria (Table 2), the Manchurian nymphs overwinter at a younger stage than South Korean nymphs (Fig. 3). In contrast with Korean *Cryptocercus*, Manchurian *Cryptocercus* collected in late October moved slowly and had a flattened abdomen, indicating that the contents of their gut had been emptied to avoid gut freezing injury. This indicates that Manchurian *Cryptocercus* start overwintering at least one month earlier than South Korean *Cryptocercus*. Nymphal development will also be delayed by the earlier and longer winter (Table 2), resulting in the longer life cycles. Thanks to the shorter Korean winter (Table 2), Korean *Cryptocercus* nymphs may spend more time feeding and growing than those in Manchuria.

If *Cryptocercus* life spans depend on the length of developmental stasis during winter, the length of winter may significantly affect the time required to reach adulthood. Since *Cryptocercus* nymphs spend about four months per year overwintering, it suggests that they may be able to reach adulthood within 3~3.5 years, if there were no winters, instead of 5~7 years, (Seelinger and Seelinger 1983, Nalepa 1984, Park and Choe 2003).

#### Evolution of Extended Parental Care

To date, the evolution of extended parental care in *Cryptocercus*

has been explained based on the need for proctodeal trophallaxis for transferring symbiotic protozoa (Cleveland et al. 1934) or essential nutrients (Nalepa 1988, Nalepa 1994), resulting in the evolution of an obligatory association between adults and their young. Since the anal feeding behavior is terminated within a few months after neonates hatch, however, further explanations for the evolution of the long-lasting association between adults and their offspring are needed.

An environmental prime mover that creates conditions favorable to extended parental care in *Cryptocercus* might be the stressful winter environment. Cold temperatures, in particular, may promote extended parental care as well as the long life cycle resulting from delayed nymphal development. The harsh winter conditions that nymphs face may be mitigated by extended parental care, as *Cryptocercus* adults block some tunnels with chewed woody debris when temperatures are cold, and lead up their young to deeper areas in their woody galleries (Park et al. 2002).

Winter climate can affect both nymphal development and parental care. If *Cryptocercus* nymphs were capable of growing normally even in winter, as they do under laboratory conditions (Park et al. 2002), then they could reach earlier adulthood and *Cryptocercus* adults could be relieved of their caring duty earlier. In addition, since overwinter caring for overwinter would not be necessary in the absence of low winter temperatures, the association between adults and their young might be restricted only to the earlier stages when the proctodeal trophallaxis occurs.

#### Evolution of Semelparous Reproductive Mode

Semelparous reproduction and extended parental care are the main components of *Cryptocercus* subsociality. Semelparity is defined as reproducing only once in a lifetime (in contrast to iteroparity, which involves reproduction more than once in a lifetime) (Fritz et al. 1982). In *Cryptocercus*, which inhabits only temperate

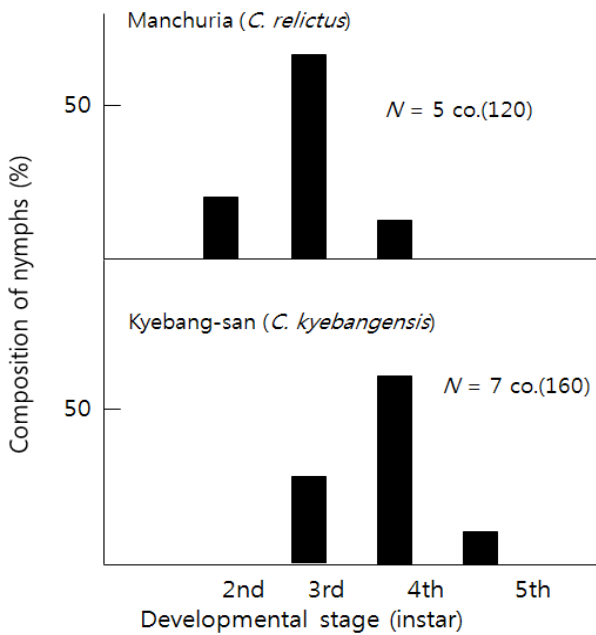


Fig. 3. Comparison of nymphal development in South Korean and Manchurian cockroaches. Seven colonies of *Cryptocercus kyebangensis* were collected in South Korea and 5 colonies of *Cryptocercus parvus* were collected in Manchuria. The Manchurian *Cryptocercus* has been known as *C. relictus* to date (Bey-Bienko 1950, Park et al. 2004). However, this species was recently renamed as *C. parvus* (Grandcolas et al. 2005). Field collections were conducted 10~15 October 1998 in South Korea and 22~25 October 1998 in Manchuria. The Manchurian samples were collected from Laotudingzi (> 1000 m) near the Shuang feng tree farm, 100 km W-SW of Hailin city (43° 3' ~44° 3' N and 128° 5' ~129° 0' E). The Korean samples were collected from Gyebang-san (1,577 m; 37° 43' N and 128° 28' E), Gangwon Province. The collection localities were described by Grandcolas et al. (2001), Park et al. (2004), and Grandcolas et al. (2005). Monthly average temperatures in Manchuria and South Korea are shown in Table 2. Head capsule widths of nymphs were measured to determine age stages and stages of nymphal development were defined according to Park and Choe (2003c).

forests, semelparous reproduction might be caused by the delayed nymphal development resulting from developmental stasis during winter, leading to extended costs of parental care. Nalepa (1988) reports that when young nymphs of *C. punctulatus* are removed, adults tend to reproduce again. This suggests that shortening the length of nymphal development might allow *Cryptocercus* adults to reproduce repeatedly during their lifetime, transitioning from being semelparous to being iteroparous.

Comparable life histories have been reported in other cockroach

species (Table 1). *Panesthia australis* is a wood-eating cockroach distributed throughout the tropical forests of Australia. *Panesthia australis* adults provide relatively short and casual parental care (Matsumoto 1988), different from the extended parental care shown in *Cryptocercus*. *P. cribrata*, which lives in regions with mild winters, has a long life span like *Cryptocercus*, but extended parental care and monogamy did not evolve in this species. These cockroaches are found in aggregations, most commonly containing a number of adult females, a single male, and nymphs of various sizes (O'Neill et al. 1987). The giant cockroaches, *Macropanesthia rhinoceros* (Blaberidae), live in complex galleries beneath the Australian desert. Their nymphs live independently within a relatively short period after their birth (Matsumoto 1992). The wood-eating cockroach *Salganea matsumotoi* is distributed throughout the tropical forests of Myanmar. They are thought to finish nymphal development within two years, display a short relationship between parents and offspring, and have more than one reproductive episode (Mae-kawa et al. 2005). These wood-eating cockroaches live in similar forest habitats to *Cryptocercus* (Pellens et al. 2002). The most important factor distinguishing the life histories of *Cryptocercus* species and the tropical species appears to be temperature, i.e., *Cryptocercus* experiences cold winters whereas the tropical species do not.

#### CLIMATE HYPOTHESIS FOR THE EVOLUTION OF CRYPTOERCUS SUBSOCIETY

We propose that the environmental prime mover that creates conditions favorable to extended parental care in *Cryptocercus* is the stressful winter environment. The effects of the harsh winters that nymphs endure may be mitigated by extensive parental care, resulting in a lasting association between adults and their young (Fig. 4). The association between adults and offspring should vary depending on the length of winter and temperature regime of winter. We propose that adaptation to the low temperatures experienced during winter might be one of the main causes of the delayed nymphal development (Fig. 4) and the evolution of the semelparous reproductive mode (Fig. 5), though we do not exclude the possibility that the low quality of woody diets may also promote delayed nymphal development (Nalepa 1994). The extraordinary delay in nymphal development may result in a prolongation of costly parental care, resulting in the evolution of semelparous reproduction (Fig. 5). In addition to studies of Manchurian *Cryptocercus* living in habitats with longer winters, further studies on wood-eating cockroaches living in habitats with less extreme winters will provide valuable information about the evolution of life cycles in *Cryptocercus*.

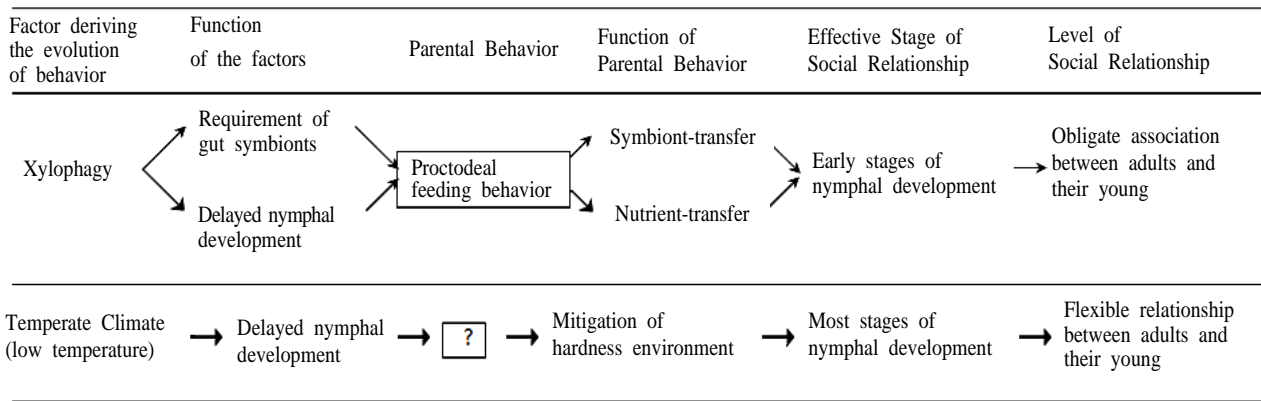


Fig. 4. The xylophagous diet of *Cryptocercus* leads to the requirement for symbiotic gut protozoa (the gut protozoa-transfer hypothesis; Cleveland et al. 1934) and essential nutrients (the nutrient-transfer hypothesis; Nalepa 1988, 1994). *Cryptocercus* adults transfer gut protozoa and nutrients via proctodeal feeding behavior. Parental care is most important in the early stages of nymphal development, and the social relationship between adults and their young is obligatory at that time. However, the extended association beyond the early stages (the 3th or 4th instar) cannot be explained by proctodeal feeding behavior because this behavior only occurs in the three or four months after hatching. The duration of the cold period (winter) may be one of the factors leading to delayed growth in *Cryptocercus* nymphs. By extending parental care, *Cryptocercus* adults may help their young endure the cold temperatures of winter. Thus, parental care may be important in all stages of nymphal development. The social relationship between *Cryptocercus* adults and their nymphs may be flexible, depending on the duration of the cold period, i.e., if *Cryptocercus* live in environments with short or no winters, the social association between adults and their young might be terminated at the early stages, probably within two or three months after hatching, when their young complete the establishment of gut protozoa.

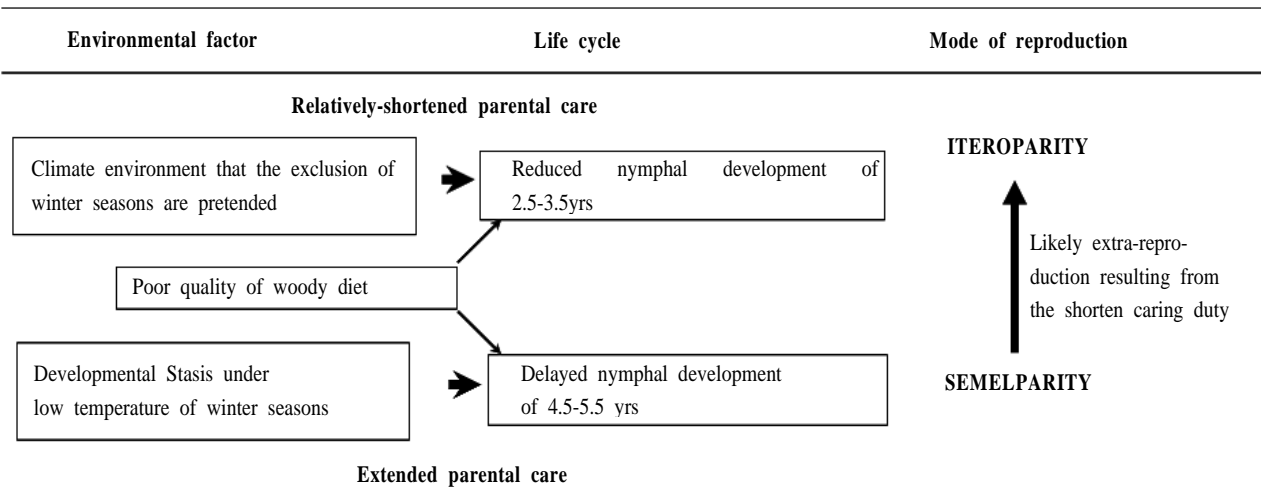


Fig. 5. The relationship between the length of winter and the mode of *Cryptocercus* reproduction. Our hypothesis suggests that the duration of the cold season may significantly affect the time required to reach adulthood. Under artificial conditions that did not include seasonal variation, *Cryptocercus* nymphs appear to mature faster (in 2.5 to 3.5 years) than the 4.5~5.5 years to maturation observed in natural environments. Adults in an artificial environment might therefore be free from the need for parental care earlier, potentially resulting in a shift from a semelparous reproductive strategy to iteroparous breeding.

This study suggests that wood-eating cockroaches are a useful model organism for testing the semelparity hypothesis (Tallamy and Brown 1999) and the origins of extended parental care. Semelparity

and the evolution of parental care in insects is a classic topic in evolutionary studies (Wilson 1975, Tallamy and Brown 1999). According to the semelparity hypothesis (Tallamy and Brown 1999),

the presence or absence of maternal care is better explained by the opportunities for iteroparous reproduction. The duration of care may vary with increasing opportunities for repeated reproduction as predicted (Tallamy and Brown 1999). Wood-eating cockroaches reproduce at different rates in taxa with extensive geographical ranges. We predict that taxa restricted to highly seasonal habitats (in the northern latitudes) should show higher rates of maternal care (and semelparity) than taxa occupying less seasonal environments (which should be iteroparous). We suggest that future studies should examine whether cockroaches of the genus *Cryptocercus* are iteroparous when climatic circumstances permit.

## CONCLUSIONS

The gut protozoa-transfer and nutrient-transfer hypotheses about the origins of parental care in *Cryptocercus* are based on the observation of proctodeal trophallaxis in the genus. Since the proctodeal behavior by adults is terminated at the early stages of nymphal development, however, it cannot explain the lengthy relationship between adults and their young beyond the critical early period. Our hypothesis can explain the evolution of extended parental care beyond the critical developmental stages as well as the semelparous reproductive mode.

The climate in winter may affect the evolution of the *Cryptocercus* life span, for example by delaying nymphal growth. Our hypothesis suggests that developmental stasis during the winter may explain the slow nymphal growth. Extraordinary delays in nymphal development may result in extended parental care, resulting in the evolution of semelparous reproduction. If the length of nymphal development is shortened, it could allow *Cryptocercus* adults to reproduce repeatedly during their lifetime; i.e., to change their reproductive mode from semelparous to iteroparous (Fig. 5). For our hypothesis to be tested, comparative studies including wood-eating cockroaches that live in environments with milder winters, or with no seasonal change in temperature regimes, will be required. In addition, future studies should be conducted to determine whether cockroaches of the genus *Cryptocercus* are opportunistically iteroparous in non-seasonal environments.

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