

Life History and Population Dynamics of Korean Woodroach (*Cryptocercus kyebangensis*) Populations

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Ecological aspects of *Cryptocercus kyebangensis* life history were investigated via laboratory rearing and field observations. The number of antennal segments and head width were used to classify the first four instars. The results, which combine both the field collection and the laboratory rearing, indicate that eleven instars occur in *C. kyebangensis*. It supports the proposal on the number of instars of Park and Choe (2003c) based on field collections. A total of 388 nymphs from 13 colonies were collected prior to winter to investigate overwintering stages. Of them, 4% (n = 17) were the second instars, 57% (n = 220) were the third instars, and 39% (n = 151) were the fourth instars, respectively. Thus, most of them overwinter in the third or fourth instars. The results indicate that young nymphs of *C. kyebangensis* have to reach at least 3rd or 4th instar to survive low temperature environment of winter. According to seasonal dynamics of populations, *C. kyebangensis* reaches adulthood in the summer of the fourth or fifth year (4-5 yr span) after their birth.

Cockroaches (belonging to the order Blattodea) are among the most ancient winged insects known, the earliest fossils dating back to the Carboniferous (about 400 million years) (McKittrick, 1964). To date, about 4000 species in 460 genera have been described in the world (Roth and Willis, 1960). Cockroaches are ubiquitous in almost all habitat types where insects occur (refer to references in Schal et al., 1984). Our knowledge of the behavioral ecology of cockroaches in forests, grasslands, and deserts has vastly increased over the past decade (Gutrie and Tindall, 1968; Schal et al., 1984; Matsumoto, 1988, 1992; Grandcolas, 1995, 1997; Seelinger and Seelinger, 1983; Nalepa 1984; Park, 2002; Park et al., 2002; Park and Choe, 2003a, b). Studies of tropical habitats where cockroaches are most diverse and abundant indicate a large variety of habitats, including leaf litter, dead leaves trapped above ground, in caves, in hollow trees, rotting logs, pools and streams, in nests of other animals like termites (Grandcolas, 1995, 1997; Roth and Willis, 1960; Seelinger and Seelinger, 1983; refer also to references in Schal et al., 1984).

Wood-feeding cockroaches of the genus *Cryptocercus* are unique among cockroaches because of their unusual life history and wide disjunctive distributions. *Cryptocercus* is the only known oviparous cockroach with well-developed parental care, and it shows nesting behavior (Seelinger and Seelinger, 1983; Nalepa, 1984; Park et

al., 2002). *Cryptocercus* adults live as monogamous pairs with their young and tend to reproduce only a single brood of eggs during their whole life time (Seelinger and Seelinger, 1983; Nalepa, 1984; Park et al., 2002). During early stages, young nymphs have to be provided with some essential nutrients including gut symbionts to digest woody cellulose (Cleveland et al., 1934; Seelinger and Seelinger, 1983; Nalepa, 1984; Park et al., 2002). Adults provide some materials to their young via anal feeding (Cleveland et al., 1934; Seelinger and Seelinger, 1983; Nalepa, 1984; Park et al., 2002). Such advanced social behavior of *Cryptocercus* is not common in other cockroaches and has long been studied in relation to the evolution of social behavior of other cockroaches (Grandcolas, 1997) and the evolution of termite eusociality (Cleveland et al., 1934; Seelinger and Seelinger, 1983; Nalepa, 1984, 1988; Nalepa and Mullins, 1992; Park, 2002).

From the viewpoints of their distribution, *Cryptocercus* are also of special interest. To date, *Cryptocercus* have been found in only some temperate forest mountains of northwestern and eastern North America (Scudder, 1862; Nalepa et al., 1997; Burnside et al., 1999), West China (Bey-Bienko, 1950; Grandcolas, 2000), and Northeast Asia (Bey-Bienko, 1950; Asahina, 1991; Grandcolas et al., 2001). Thus, a prominent feature of its geological distribution is the wide disjunction between the Nearctic and the Palearctic species, between the eastern and northwestern species in North America and between populations in western China and northeastern Asia.

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Recently, the underlying cause and the temporal dynamics of this disjunctive distribution have been the subject of studies on *Cryptocercus* (Nalepa and Bandi, 1999; Grandcolas 1999a, b; Clark et al., 2001; Grandcolas et al., 2001; Park et al., in press).

Although studies on *Cryptocercus* have been conducted plentifully because of its life history characteristics, most of the studies are related to sociality, phylogenetics, and biogeography of *Cryptocercus*. The studies were conducted from the viewpoints of the evolution of their sociality including parental care (Cleveland et al., 1934; Seelinger and Seelinger, 1983; Nalepa 1984; Grandcolas, 1997; Park et al., 2002; Park and Choe, 2003a, b), the phylogenetic position of *Cryptocercus* within the Blattaria (Grandcolas, 1994, 1997), and phylogography (Clark, 2001; Grandcolas, 1999a, b; Nalepa et al., 1997; Nalepa and Bandi, 1999; Grandcolas et al., 2001; Park, 2002).

From ecological viewpoints of *Cryptocercus* life history, such as population ecology and life span, however, the information was reported in relatively a small quantity. According to Park et al. (2002), the term of about 4yrs is needed to reach adulthood in the field. Based on head width of field-caught individuals, the categories of 11 instars were also identified (Park and Choe, 2003c). Because size variation in field-collected insects is typically high in later instars of cockroaches, however, further studies are required to determine the number of instars.

The objectives of the current study are to confirm the number of instars via laboratory rearing. The current paper also includes studies on overwintering stages in the field and population ecology of a Korean wood-feeding cockroach, *C. kyebangensis*.

Materials and Methods

Collection

Woodroaches of *C. kyebangensis* were collected from Gyebang-san (Mt.), Gangwon Province, Korea. Collections of *C. kyebangensis* were made periodically from March to November of 1997. Nymphs of the first instar were obtained by incubating oothecae until hatching at $25 \pm 2^\circ\text{C}$ in glass vials furnished with moist woody fragments.

At the collecting sites, all fallen logs and dead standing trees were examined for cockroaches. The undersurface of the fallen logs was examined to determine whether there were the entrances of interconnecting galleries. If cockroaches had been found underneath the log, this was then examined for the entrance holes that corresponded to the position of the collected cockroaches. The galleries were traced from the entrance. The log was then systematically broken up by wood chisel and hammer, beginning from any entrance holes or wounds

on the surface of the log.

Nymphal development

For the investigation of developmental process, individuals were selected from samples preserved in culturing room of laboratory. The study was conducted during the period of April to October in 2000. Each of cockroaches was placed in an observation chamber, a round plastic case. The artificial chambers were transparent and 15cm in diameter and 1.5 cm in depth. Each chamber was provided with rotten wood materials smashed by a mixer. Chambers were kept in D:L=12 h : 12 h at $25 \pm 2^\circ\text{C}$. The debris inside the cages was kept slightly moist by water drops via air holes of cage periodically.

Measurement and morphological investigation

The field-caught *Cryptocercus* were preserved in 70% alcohol. Morphological features were measured using a binocular microscope with a graduated eyepiece (Olympus Model SZ-STU1). The head width and number of antennal segments were measured following Nalepa (1990). To determine the head width, the maximal width of the head, including the eyes, was measured. The number of antennal segments was counted in individuals with at least one antenna undamaged.

For nymphal growth under laboratory environment, each individual was removed from its culturing chamber, measured by upside down position, and moved back in its chamber.

Results and Discussion

Field study on early instars and overwintering stages

Young nymphs of *C. kyebangensis* ($n = 396$), including the first instar obtained by incubating oothecae, were collected and classified into four instar stages based on head width size (Table 1; one-way ANOVA, $p < 0.05$). The number of antennal segments was also discretely grouped into four categories (Table 1). Regression analyses showed that the number of antennal segments and head width were correlated significantly in nymphs of the first four instars ($n = 396$, $y = 19.333x - 0.716$, $r = 0.946$, $P < 0.05$). Damaged antennae, which were characterized by a distinct distal melanization, were found frequently in nymphs of the fourth instar. The present results showed that antennal segmentation, as well as head width, could easily be used for classifying early instars of *C. kyebangensis*.

Park et al. (2002) suggested that young nymphs of *C. kyebangensis* overwinter as the 3rd or 4th instar through field observations. The current study included numerous field surveys to confirm overwintering stages of young nymphs. A total of 388 nymphs from 13 colonies were

collected prior to winter to investigate overwintering stages. Of them, 4% (n = 17) were the second instars, 57% (n = 220) were the third instars, and 39% (n = 151) were the fourth instars, respectively. Thus, most of them overwintered as the third or fourth instars.

Field studies on *C. punctulatus*, a North American species, have been conducted (Nalepa, 1984, 1990). Young nymphs of *C. kyebangensis* had somewhat larger head width than that of *C. punctulatus* reported by Nalepa (1990), but the number of antennal segments appeared to be similar between the two species. According to Nalepa (1990), young nymphs of *C. punctulatus* reach the 3rd or 4th instar before the first winter after their hatch. Overwintering stages of *C. kyebangensis* also appeared to be similar to those of *C. punctulatus* reported by Nalepa (1990).

The environment in which an insect develops has a profound effect on its growth and behavior (Woodhead and Paulson, 1983; Schal et al., 1984; Park et al., 2002). Unlike tropical cockroaches, *Cryptocercus* live only in temperate forests and experience distinct, periodic climate changes. The winter in temperate regions may seriously affect the life history of *Cryptocercus*. Physiological observations suggest that *Cryptocercus* has adapted to cope with low temperature of the winter. In *C. punctulatus*, critical thermal temperatures were 40.3°C and -7.8°C for maxima and minima, respectively, and these are not similar to those of related taxa (Appel and Sponsler, 1989). According to Hamilton et al. (1985), winter-acclimated *C. punctulatus* are able to withstand ice crystal formation within their bodies. Ribitol, a sugar alcohol, accumulates in their hemolymph during winter (Hamilton et al., 1985).

Cryptocercus kyebangensis remain frozen in their natural habitat during the winter season, spanning from November to March (Park et al., 2002). Thus, temperature, which falls significantly during winter, will affect seriously the survivorship of *Cryptocercus*. The results may indicate that *C. kyebangensis* has to regulate their life cycle to cope with the extreme environment of the winter. That is, young nymphs of *C. kyebangensis* have to reach at least 3rd or 4th instar for the regulation of physiological mechanisms needed for freeze-tolerance.

Development of laboratory-reared older nymphs

Recently, Park and Choe (2003c) categorized older nymphs as well as the young. Based on head widths of field-caught individuals, Park and Choe (2003c) suggested 11 instars of *C. kyebangensis*. Their finding that instar classes of early nymphs were distinguished obviously by head width corresponds well to the present results (Table 1). According to the peaks in the graph (Park and Choe, 2003c; Fig. 1), however, the determination of instars are not always obvious in older nymphs, especially in individuals with head width between about 2.5 mm and

Table 1. Head capsule width and the number of antennal segments in the first four instars of *C. kyebangensis*

Instar	n	Head capsule widths (mm)		No. of antennal segments	
		Mean ± SD	Range	Mean ± SD	Range
1st	57	0.88 ± 0.05	0.75 - 0.95	15.00 ± 0.00	15 - 15
2nd	94	1.13 ± 0.06	1.00 - 1.23	21.28 ± 0.56	20 - 23
3rd	186	1.38 ± 0.07	1.20 - 1.50	26.16 ± 0.80	25 - 29
4th	59	1.66 ± 0.06	1.53 - 1.78	31.41 ± 1.16	30 - 34

Each instar did differ significantly in means of head capsule width and the number of antennal segments (one way ANOVA; df=3, 392 F=1924, p<0.05 and F=5434, p<0.05, respectively).

3.5 mm. To clear up some of the ambiguous instar categories in older nymphs, the changes in head width were investigated by rearing nymphs in the laboratory. A total of 93 individuals used for the experiment were grouped into 6 categories (Table 2). Head width of each individual was checked periodically once every month from May to September. Most individuals of Category I and II molted twice during the experiment. The first molt was observed in June and the second molts occurred sporadically from July to September (Table 2). Individuals belonging to Category III-V, however, molted only once during the experiment. Molts were observed frequently in June and July for the individuals of Category III and IV, and in May for those in Category VI. Individuals of Category I had head width of 1.97 ± 0.06 mm) and it corresponds to that (1.92 ± 0.06 mm) of the fifth instar previously reported by Park and Choe (2003c; Table 1).

The overall data for the laboratory-reared individuals (Table 2) are summarized by mean head width of individuals in each category (Fig. 1). The first Group (a) within Category I corresponds to the fifth instar (refer to Park and Choe, 2003c). Thus, the Group (b) and (c) in the category, derived from continuous molts of the Group (a), will be assigned to the 6th and 7th instar, respectively. Since head width did not differ among the Groups (b)s and (c)s in Category I-III [Mann-Whitney U test for Group (b)s, P>0.05; Kruskal-Wallis test for Group (c)s, P>0.05]. The Group (b) and (c)s within Category II-III could also be assigned to the 6th and 7th instar, respectively. Instar categories can be assigned in the same way to each group in Category III-VI.

Although complete molting series of the 5th instar to adulthood were not monitored, the number of molts was confirmed by checking the degree of overlap between the mean head widths of groups in the six categories (Fig. 1). The results indicate that the 5th instar developed to adult after 5 molts, and it supports the suggestion of Park and Choe (2003c; Table 1) based on head width of field-caught individuals.

According to Nalepa et al. (1997), *C. punctulatus*, an American *Cryptocercus*, requires 4 or 5 yr to reach adulthood and *C. clevelandi*, another American species,

Table 2. Changes of head capsule width of *Cryptocercus kyebangensis* reared in laboratory environment

Ca ¹ .	In ²	Sex	Change of head capsule width (mm)							Ca	In	Sex	Change of head capsule width (mm)						
			Apr.	May	Jun.	Jul.	Aug.	Sep.	Apr.				May	Jun.	Jul.	Aug.	Sep.		
I	1	m	1.87	2.19		2.46					48	f	2.80		3.23				
	2	m	1.93		2.17						49	f	2.80		3.27				
	3	f	1.93		2.19				2.43		50	f	2.83				3.20		D ³
	4	f	1.93		2.15						51	m	2.87			3.20			
	5	m	1.99		2.28				2.67		52	m	2.89				3.20		
	6	f	2.01		2.32			2.72			53	m	2.90		3.20				
	7	f	2.03		2.34				2.73		54	f	2.90		3.22				
	8	m	2.03		2.34			2.69			55	m	2.93				3.2		
											56	f	2.93				3.40		
	9	m	2.17		2.46	2.83					57	f	2.95				3.40		
	10	f	2.18		2.53			2.90		IV	58	f	2.97			3.40		D	
	11	f	2.18		2.46	2.97					59	f	2.97		3.45				
	12	f	2.18		2.53			2.90			60	f	2.97		3.45				
	13	f	2.20		2.50						61	f	2.98			3.33			
	14	f	2.20	2.57							62	m	3.00		3.36				
	15	f	2.20		2.48	2.87					63	f	3.00				3.35		
	16	f	2.20		2.50	2.90					64	m	3.00		3.33				
	17	f	2.21			2.56					65	m	3.00			3.40			
	18	m	2.22		2.50			2.83			66	f	3.03		3.28				
	19	m	2.23		2.57			2.95			67	m	3.05		3.44				
20	f	2.23	2.54			D													
21	f	2.23		2.54						68	m	3.32		3.77					
22	f	2.23		2.53						69	m	3.32		3.75					
23	m	2.23		2.57			2.90			70	m	3.35	3.81						
24	f	2.24		2.50			2.83			71	f	3.40		3.76					
25	m	2.25		2.57				2.80		72	f	3.48		3.95					
26	m	2.25		2.57				2.83		73	f	3.48		3.95					
27	f	2.25			2.53					74	f	3.56		3.95					
28	f	2.25		2.57						75	f	3.56		3.90					
29	m	2.25			2.49				V	76	m	3.60		4.07					
30	f	2.25		2.52			2.87			77	m	3.60		3.91					
31	f	2.25	2.57		2.86					78	m	3.60		4.00				D	
32	f	2.25		2.57			2.93			79	m	3.60		4.07					
33	f	2.25		2.53	2.90					80	f	3.63		4.10					
34	m	2.25		2.56			2.80			81	f	3.64				4.15			
35	m	2.25		2.57						82	f	3.64				4.05			
36	m	2.27						2.60		83	m	3.65	4.15						
37	m	2.27			2.49					84	f	3.65	4.03						
38	f	2.28		2.52				2.90											
39	f	2.28		2.57			2.87			85	m	3.80	4.30						
40	f	2.30		2.63				2.87		86	f	3.90	"4,45"						
41	f	2.30		2.63			2.90			87	m	4.00	4.38						
42	f	2.32			2.63			2.83		88	m	4.10	4.58						
									VI	89	m	4.05	4.55						
	43	m	2.50		2.85					90	f	4.05	4.55						
	44	m	2.57			2.89				91	m	4.10	4.48						
III	45	m	2.60		2.93					92	m	4.10	4.50						
	46	m	2.63		3.00					93	f	4.05	4.55						
	47	f	2.65		3.00		3.50												

¹Category, ²Individual number, ³Death

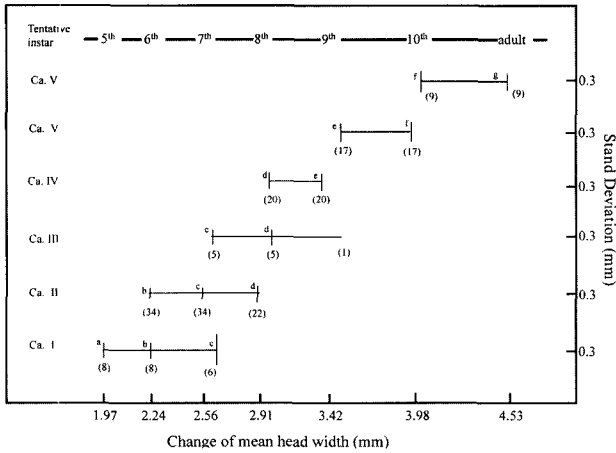


Fig. 1. The change of mean head widths of the laboratory-reared individuals described in Table 2. The letters in each category indicate the names of groups in the category. Groups with same letters did not differ significantly in head width [Mann-Whitney *U* test for Group (b)s, (e)s, and (f)s, $P > 0.05$; Kruskal-Wallis test for Group (c)s and (d)s, $P > 0.05$]. Ca. indicates the abbreviation of category. The numbers in parentheses indicate the number of individuals.

requires 5-7 yr. It is known that a larger body size is associated with longer postembryonic development in several cockroach species. Greater adult weight was, for example, due to longer duration of larval development (Landowski, 1938; Wharton et al. 1967; Woodhead and Paulson, 1983; refer to the discussion in Park and Choe, 2003c). Head widths of *C. kyebangensis* adults were similar in size to those reported for *C. punctulatus* (Seelinger and Seelinger 1983; Nalepa 1984; Nalepa et al., 1997), but smaller than that described for *C. clevelandi* (Nalepa et al., 1997). Since *C. kyebangensis* has a smaller head width size than *C. clevelandi*, the former may have a shorter developmental period than the latter (Nalepa et al., 1997). In addition to similar habitat requirements, the similar head width between *C. kyebangensis* and *C. punctulatus* suggests that the developmental span of *C. kyebangensis* may be similar to that (4-5 yr) of *C. punctulatus* (Nalepa et al., 1997).

Population dynamics of C. kyebangensis

The frequency distribution of head widths of field-caught individuals is presented in Fig. 2 and instars were determined following the criteria of Park and Choe (2003c). The 1st instar was only collected during June-July (Fig. 2B). The 2nd instar was frequently observed from the collections of June-July and September-October (Fig. 2B, C). The 3rd or 4th instar was frequently collected during March-April (Fig. 2A) and September-October (Fig. 2C). Thus, young nymphs of *C. kyebangensis* reach the 3rd or 4th instar until September-October after hatch in June. Since they stop growing while overwintering, they still remain in the 3rd or 4th instar in the next year.

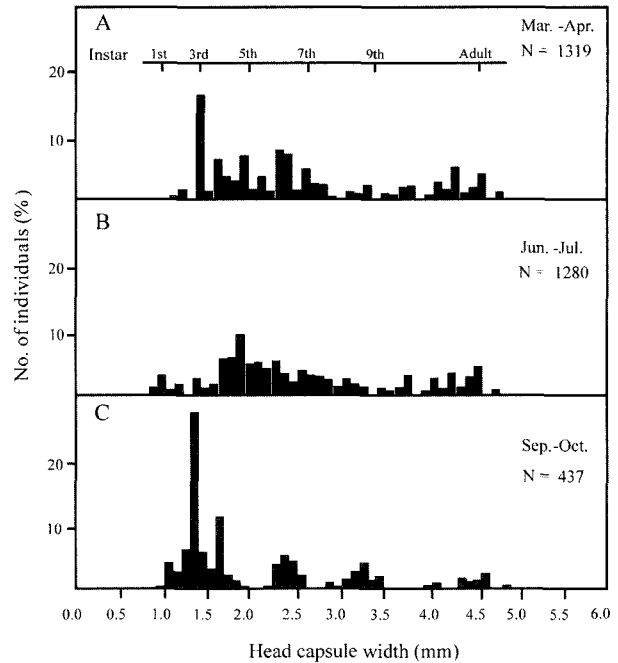


Fig. 2. Frequency distribution of head widths of the field-caught individuals during March and April (A), June and July (B), and September and October (C).

In addition to the 1st instar, the 5th or 6th instar was frequently observed in the collections of June-July (Fig. 2B). It indicates that the 3rd or 4th instar of March-April (Fig. 2A) developed to the 5th or 6th instar in June-July (Fig. 2B) and most of them overwinter as the 6th or 7th instar (Fig. 2C). Thus, the 6th or 7th instar was frequently observed in the collections of March-April (Fig. 2A). The 6th or 7th instar of March-April (Fig. 2A) grows to the 8th or 9th instar by the end of the year (Fig. 2C) and they will develop to the 9th or 10th instar by the summer of the following year (Fig. 2B). Since they overwinter without further molts, the 9th or 10th instar observed frequently in the collections of March-April (Fig. 2A). The 9th or 10th instar will develop to the 10th instar or adults in June-July. The life history of *C. kyebangensis* was investigated via the changes of head width of individuals

	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.
Hatch year				Reproduction and hatch				3rd or 4th instar	
1st year				5th, 6th, 7th instar				6th or 7th instar	
2nd year				8th or 9th instar				8th or 9th instar	
3rd year				9th or 10th instar				9th or 10th instar	
4th year				10th instar or adult				10th instar or adult	
5th year				Adult					
				Molting stages				Overwintering stages	

Fig. 3. Life history of *Cryptocercus kyebangensis*.

during laboratory rearing (Table 2) and the frequency distribution of head widths of populations according to seasons in the field (Fig. 2). *Cryptocercus kyebangensis* reaches adulthood in the summer of the 4th or 5th year (4-5 yr span) after their birth (Fig. 3).

According to Park et al. (2002), adults of *C. kyebangensis* tend to die in the 3rd year after their offspring hatch. In both species of American *Cryptocercus*, adult males and females pair up as soon as they mature, but do not reproduce until the following summer (Nalepa et al., 1997). Thus, the time needed for reproduction after adults pair will be one year. If *C. kyebangensis* appear to have a similar reproduction pattern to that of American species, total life span seems to correspond at least 8-9 yr including developmental time and adults life length. In *Cryptocercus*, such long lifespan would be related to woody diet and their habitat condition. From the viewpoint of nutrient environment (Nalepa, 1988; Nalepa and Jones, 1991), the woody diet on which *Cryptocercus* feed is extremely poor in terms of quality nutrients such as nitrogen. Thus, diet condition has been considered as a prime cause of long lifespan including delayed nymphal development. Climate condition may also be an important cause for the evolution of long life history in *Cryptocercus*. According to Park et al. (2002), *C. kyebangensis* overwinter frozen in their natural habitat, whereas *Cryptocercus* under the laboratory condition grow continuously. It suggests that the delayed nymphal development may be related to the length of winter. Thus, the evolution of long lifespan in *Cryptocercus* spp., including *C. kyebangensis*, has to be understood in terms of the effect of the poor nutritional condition and climate environment.

Conclusions

The results confirm instar categories of *C. kyebangensis* via field and laboratory study. A total of 11 stages, including adulthood, occur in *C. kyebangensis*. The results also indicate that young nymphs of *C. kyebangensis* overwinter as the 3rd or 4th instar, and it suggest that neonates have to reach at least the 3rd or 4th instar to survive during overwintering. The results also suggest that *C. kyebangensis* reaches adulthood in the summer of the 4th or 5th year (4-5 yr span) after their birth.

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