Evolution of eusociality in termites

(diploidy/inbreeding/relatedness/supplementary reproductives/sociality)

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ABSTRACT   A model is presented that demonstrates that asymmetries in relatedness such that individuals are more closely related to siblings than to offspring develop in diploid pedigrees under conditions of inbreeding. Given also certain incestuous conditions, the model predicts that eusocial-type helping behavior can be favored by natural selection. Three cases of the model are discussed along with implications for termite eusociality. Several aspects of termite biology, particularly the existence of replacement reproductives, are interpreted as evidence that termite eusociality may have arisen under the special conditions specified in the models.

Eusociality (1) has arisen on 12 separate occasions in the insects: 11 times in the Hymenoptera and once in the protoblattoids ancestral to the Isoptera (1). Hamilton (2, 3) showed that the haplodiploid genetics of the Hymenoptera result in biases in relatedness such that females may increase their inclusive fitness by investing in sisters rather than offspring. His ideas have been tested and expanded to provide an explanation for the evolution of sociality in this group (4, 5).

Because the termites are diploid and because no asymmetries in relatedness exist in the absence of inbreeding, some workers have implied that genetic bases for their eusociality may not exist (6). Cleveland et al. (7) maintain that the termites' intestinal symbiotes are responsible for their evolution. Because these protozoans are lost at each molt and must be replaced by anal feeding, the termite ancestors were forced to aggregate. Taylor (8) argues, from an analogy with ptinellid beetles, that the termites arose under bark. Among these subcortical beetles there exists a reproductive polymorphism in which two types of females are found: one is wingless and remains in galleries under the bark, the other is winged and much more fecund. She suggests that this "reproductive elite" corresponds to what must have been an intermediate condition in the incipient sociality of the prototermites. These explanations are insufficient, however, in that they fail to address the issue: How could selection favor individuals that forego reproduction and invest in relatives?

I will pursue a line of inquiry begun by Hamilton (4) and Flesness (9) and show that in diploid pedigrees inbreeding and incest can lead to substantial biases in relatedness that are favorable to the evolution of eusociality and that termite biology contains the properties suggested by the models as prerequisites for eusocial evolution.

The basic model

Hamilton (2–4) showed that genes for altruistic behavior will spread if

$$C_B b_{BA} > c_A,$$ [1]

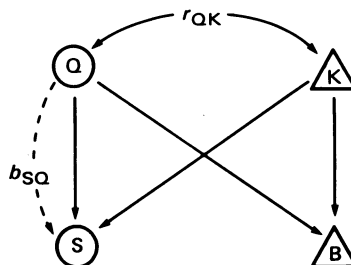in which C_B is the benefit to the recipient, c_A is the cost to the

FIG. 1 The basic model. Individuals K and Q can be considered the king and queen. S and B are sister and brother. Q and K are inbred to the same extent F. r_{QK} indicates the degree to which Q and K are related. b_{SQ} is Hamilton's degree of relatedness of individual Q to S.

altruist, and b_{BA} is a measure of the probability that the altruistic genes in A are also in B. Consequently, b_{BA} is the value that individual A places on a unit of B's fitness·relative to a unit of its own, and is given by the expression

$$b_{BA} = 2f_{AB}/(1 + F_A),$$ [2]

in which f_{AB} is the coefficient of consanguinity between individuals A and B and F_A is the inbreeding coefficient for A. This measure, b_{BA}, is known as A's degree of relatedness to B.

Now, consider the pedigree in Fig. 1. Q and K are diploid and inbred to the same extent F. Q and K may also be related, and this is denoted by the double-headed arrow labeled r_{QK}, Wright's correlation coefficient of relationship (10).

The inbreeding coefficient for an offspring S is given by (11)

$$F_S = (1 + F)r_{QK}/2.$$ [3]

F_B is identical to F_S.

By means of path analysis (12), the coefficients of consanguinity between parents and offspring and between brother and sister can be calculated and the results substituted into Eq. 2 to generate expressions for the degrees of relatedness between siblings and between parents and offspring:

$$b_{BS} = b_{SB} = (1 + F + 2r_{QK})/(2 + r_{QK} + Fr_{QK})$$ [4]

$$b_{SQ} = b_{BK} = (1 + F + r_{QK})/(2 + 2F).$$ [5]

As displayed in Fig. 2, these relations show that as parents become more inbred, their offspring become more closely related to one another while the parents become less closely related to the offspring. This effect can be seen clearly by imagining the situation in which Q and K are completely inbred and yet totally unrelated. In this case, the offspring will be identical and $b_{BS} = 1$. At the same time, each parent is related to the offspring by half that amount ($b_{SQ} = 1/2$).

Case I: Inbreeding, eusociality, and a problem

To assess the importance of this divergence effect for the evolution of eusociality, consider the pedigree in Fig. 3, in which another generation has been added by allowing S to mate with a male Z. Z is as inbred as S and is as related to S as K was to Q
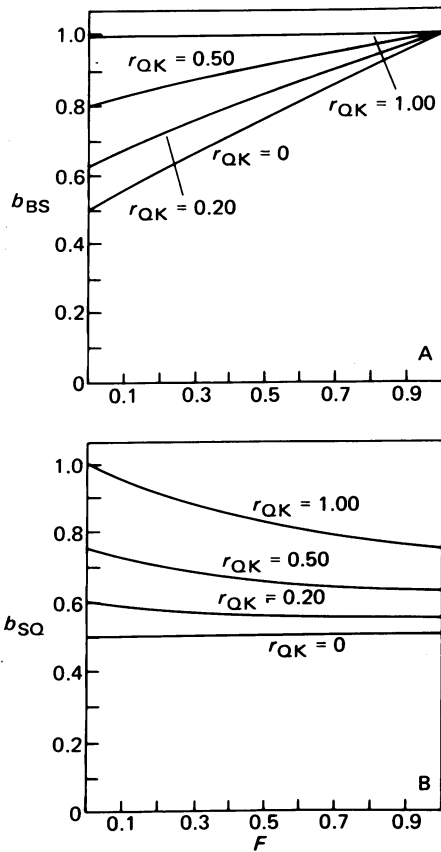
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FIG. 2. Degrees of relatedness in the basic model. F denotes the inbreeding coefficient of the original parents Q and K. (*A*) The value that a sibling places on a unit of its sibling's fitness relative to a unit of its own. (*B*) The value that a parent places on a unit of its offspring's fitness relative to a unit of its own.

so that $F_S = F_Z$ and $r_{QK} = r_{SZ}$. S's degree of relatedness to her offspring O is given by:

$$b_{OS} = \frac{2 + 5r_{QK} + Fr_{QK}}{2(2 + r_{QK} + Fr_{QK})}. \qquad [6]$$

Allow individual S to have the choice of being eusocial and investing in her siblings or mating with Z and investing in her offspring. Assuming that S can raise siblings and offspring with equal facility, the solution to this problem may be found by comparing the value of a sibling with the value of an offspring from S's point of view. This can be done in the form of a ratio of S's relatedness to her siblings and S's relatedness to her offspring:

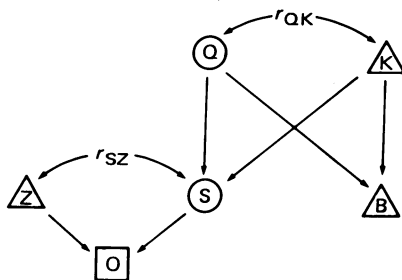$$\frac{b_{BS}}{b_{OS}} = \frac{2(1 + F + 2r_{QK})}{2 + 5r_{QK} + Fr_{QK}}. \qquad [7]$$

FIG. 3. Case I. S has been allowed to mate with an outsider Z. Their offspring is individual O. S and Z are inbred to the same extent and are as related to one another as were Q and K so that $F_S = F_Z$ and $r_{QK} = r_{SZ}$.
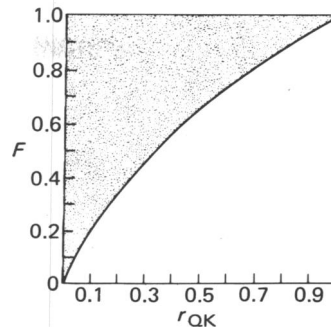

FIG. 4. The values of F and r_{QK} that result in an individual's siblings being more valuable than its offspring. These are therefore the values of F and r_{QK} for which natural selection may favor eusociality.

When this ratio is greater than 1, S is more closely related to her siblings than to her offspring and may thus be selected to remain with her parents and invest in siblings. The values of F and r_{QK} for which this is true satisfy the relation

$$F > r_{QK}/(2 - r_{QK}) \qquad [8]$$

and are shaded in Fig. 4. These are the values of F and r_{QK} for which eusocial tendencies may be selected. Note that for low values of r_{QK}, even very low degrees of parental inbreeding will result in siblings being more valuable than offspring.

It is the extent to which the parents are inbred that determines the relative values of siblings and offspring. As the parents become more related, however, the effect of devaluing ego's offspring becomes smaller for any given degree of parental inbreeding. However, unless the parents are related, the offspring will themselves not be inbred, and in the following generation S's or B's offspring will be related equally to both their siblings and offspring. Thus the selection pressure to remain and raise siblings disappears in a single generation if the parents are unrelated. Cases II and III show that when an incestuous breeding system is imposed, these biases in relatedness are maintained.

Case II: Brother-sister incest

Consider the pedigree in Fig. 5, in which a generation of brother-sister incest has been added by allowing S to mate with B to produce offspring S′ and B′. What is S″'s solution to the problem of whether to invest in her siblings or her offspring by Z? (Again, Z is as inbred as S′ and as related to S′ as K was to Q so that $F_Z = F_{S'}$ and $r_{QK} = r_{S'Z}$.) The relative value of siblings and offspring to S′ is given by the ratio of S″'s relatedness to her siblings and S″'s relatedness to her offspring:

$$\frac{b_{BS'}}{b_{OS'}} = \frac{2(3 + F + 3r_{QK} + Fr_{QK})}{5 + F + 10r_{QK}}. \qquad [9]$$

When this ratio is greater than 1, S′ is more closely related to her siblings than to her offspring, and selection will favor S″'s
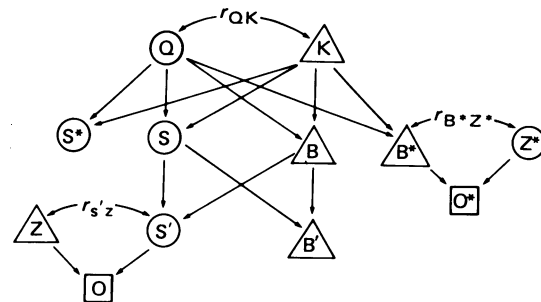

FIG. 5. Case II. Individuals S, B, S*, and B* are all siblings. S and B have mated to produce individuals S′ and B′. Z* is an outsider who is as inbred as individual B*. O* is the offspring of B* and Z*. Z is another outsider who is as inbred as individual S′. Again, $r_{QK} = r_{B*Z*} = r_{S'Z}$.
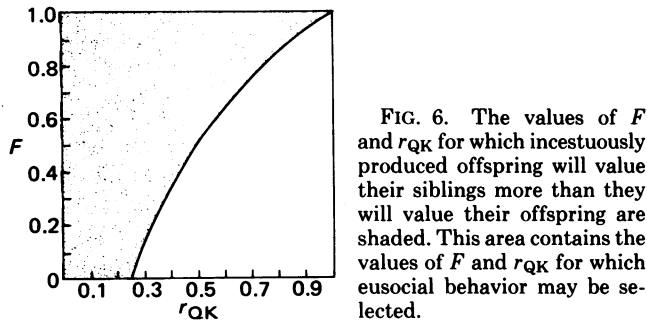
FIG. 6. The values of F and r_{QK} for which incestuously produced offspring will value their siblings more than they will value their offspring are shaded. This area contains the values of F and r_{QK} for which eusocial behavior may be selected.

FIG. 8. The ratio of the relatedness of incestuously produced siblings to one another ($b_{sib,sib}$) and the relatedness of these siblings to their own outbred offspring ($b_{sib,offspring}$). Here, any value greater than 1 will indicate favorable selection for eusocial behavior. —, $F = 0$; – – –, $F = 0.5$; - - -, $F = 1.0$.

altruistic tendencies toward her siblings more so than toward her offspring. The values of F and r_{QK} for which this will be true are shaded in Fig. 6. This shows that the conditions for the evolution of eusociality are less severe for these incestuously produced individuals than for siblings in case I.

Similarly, by comparing the relatedness of S's sibling to its own "outbred" offspring with its relatedness to S's incestuously produced offspring, it can be shown that the values of F and r_{QK} for which these siblings will be selected to invest in their siblings' offspring are the same that will favor siblings investing in siblings in case I (see Fig. 4). However, because any individual is more closely related to its own incestuously produced offspring than to offspring of siblings, each sibling in the F_1 generation would prefer that it be the one involved in the incestuous production of offspring. Consequently, one may expect conflict among these siblings concerning just who it is that becomes reproductive.

In this incestuous situation, is the inbreeding produced effect of devaluing offspring maintained or is it lost as it was in case I? To answer this question, the ratio of the relatedness between siblings and the relatedness between siblings and their outbred offspring has been calculated for successive generations (see Fig. 7 for the mating/pedigree scheme). Fig. 8, in which this ratio is plotted, demonstrates that the effect remains through at least five generations.

The surprising result from this multigenerational view is that this ratio approaches an asymptote that is independent of pa-
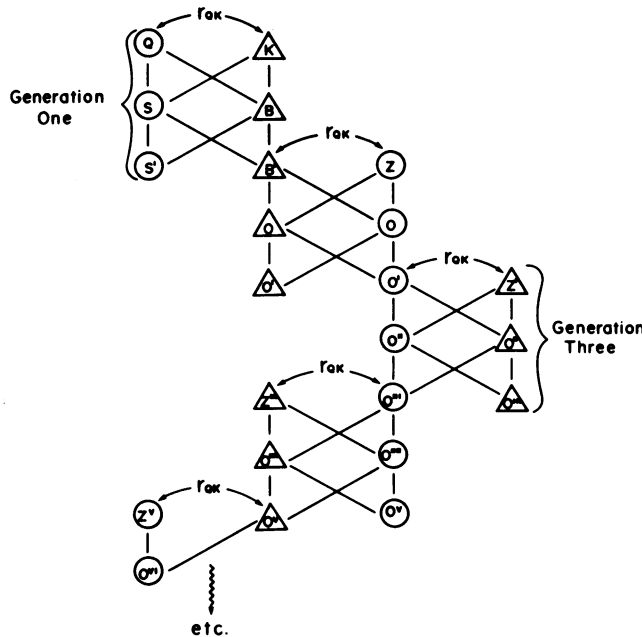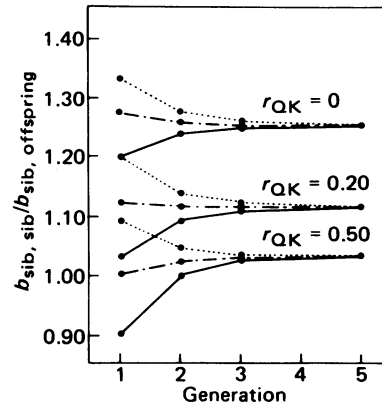
rental inbreeding and is entirely determined by r_{QK}. The more related the original parents are, the smaller the eventual difference between the value of a sibling and the value of an offspring.

Case III: Parent-offspring incest

In this case, intergenerational incest will be briefly examined. As the pedigree in Fig. 9 shows, only one of the original reproductives, Q or K, is being replaced by an offspring. Attention focuses on the ratio of individual S''s relatedness to her siblings and her relatedness to offspring:

$$\frac{b_{B'S'}}{b_{OS'}} = \frac{12 + 6F + 11r_{QK} + 3Fr_{QK}}{2(5 + F + 10r_{QK})}. \quad [10]$$

The values of F and r_{QK} for which this ratio is greater than 1 are shaded in Fig. 10. Contrasted with the brother-sister incest case, in this situation the effect of devaluing offspring is less sensitive to changes in either F or r_{QK}.

As in the last case, under conditions of inbreeding, the "nonreproductive" siblings' interests are better served by investing in the incestuously produced offspring rather than in their own "outbred" offspring. Also true is that among these siblings each would prefer that it be the one involved in the incest.

The course of the worth of ego's sibling as compared to an offspring through the generations, each generation composed of a unit like that depicted in Fig. 9, is plotted in Fig. 11. The ratio again approaches an asymptote that depends only on the value of r_{QK}. Note that the asymptotes lie at values greater than those for the case of brother-sister incest. This confirms the

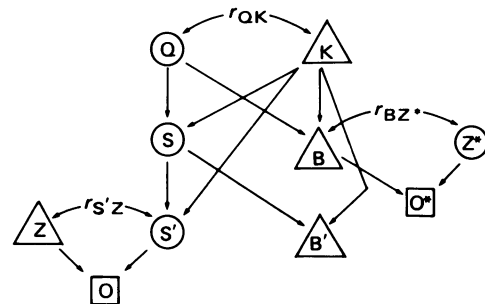

FIG. 7. Several generations of case II-type incest.

FIG. 9. Case III. Individual K has mated with his daughter to produce individuals S' and B'. Z* and B are equally inbred. In this case, B is known as the "nonreproductive" individual.

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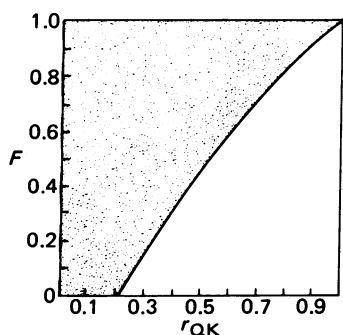*Proc. Natl. Acad. Sci. USA 76 (1979)*   5767

FIG. 10. The values of F and r_{QK} for which the right-hand side of Eq. **10** is greater than 1 are shaded. This area represents values of F and r_{QK} for which eusocial-type helping behavior may be favored among the intergenerational incestuously produced offspring.

indication that in this intergenerational incest situation a greater degree of relatedness between the original parents can be tolerated.

Discussion

It has been shown that, in diploid pedigrees, conditions of inbreeding and incest lead to asymmetries in relatedness that may promote the evolution of eusociality. Several properties of the biology of the termites suggest that eusociality in this group may indeed have arisen under the special conditions specified in the models.

Supplementary Reproductives. In at least 28 genera, in all of the families of the Isoptera, there exist supplementary reproductives (13–19). These individuals are offspring of the colony-founding pair, and in the lower termites they assume the reproductive role upon the death of one (or both) of the founders. In the Termitidae, very often many supplementary reproductives coexist with the founders. According to the theory presented here, these supplementary reproductives are essential to the maintenance of termite social organization and should be expected in every colony.

The theory not only predicts that supplementary reproductives should occur, but in fact it also predicts that alates should be the offspring of supplementaries. This prediction follows
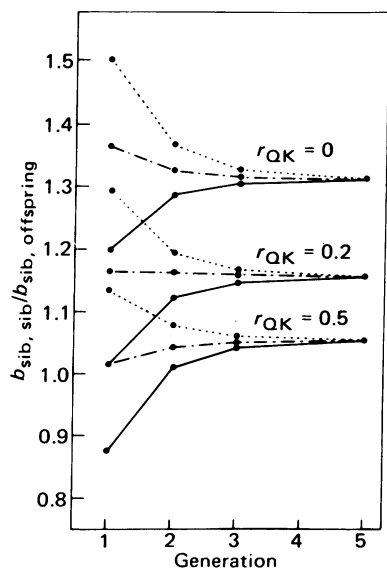

FIG. 11. The ratio of the relatedness of incestuously produced offspring to one another ($b_{sib,sib}$) and the relatedness of one of these offspring to its own outbred offspring ($b_{sib,offspring}$). The ratio is plotted against generation number, each generation composed of a unit like that depicted in the pedigree in Fig. 9. ——, $F = 0$; – – –, $F = 0.5$; - - -, $F = 1.0$.

from the problem raised in case I, where it was shown that unless the founders are related, their offsprings' offspring will not be more closely related to their siblings than to their offspring, and the selection favoring eusociality will then be nonexistent.

Data from 30 nests of desert termite species studied by Nutting (20) for which he was able to find both male and female reproductives is presented in Table 1. If all of the species are included in the test, the association between the occurrence of alates and the existence of supplementary reproductives is significant ($\chi^2 = 7.46$; $P < 0.01$). If only nests of single species are examined, the association is still significant: for $M.\ hubbardi$ $\chi^2 = 6.00$ ($P < 0.025$) and for $N.\ larseni$ $\chi^2 = 5.96$ ($P < 0.05$). Thus it seems that one of the requirements for maintaining degrees of relatedness congenial to eusociality, that alates be produced by supplementaries, is met among these termites.

Unfortunately no comparative data exist for *Zootermopsis* and *Incisitermes*, the colonies showing production of alates in the absence of supplementaries. However, Heath (21) has reported that in species of *Termopsis* (very closely related to *Zootermopsis*) there exist male and female soldiers that are reproductively competent. If these individuals were mating with the primary reproductives, or among themselves, then alates could be incestuously produced in the absence of supplementaries. It would be interesting to know whether these fertile soldiers also occur in *Zootermopsis* and *Incisitermes*.

Conflict. As indicated earlier, the theory suggests that there may be conflict among individuals concerning who replaces

Table 1. Data from 30 nests of desert termites*

Termite species	No. of alates	Total colony size
With replacement reproductives		
Neotermes larseni	385	1052
Pterotermes occidentis	0	221
	0	1111
	1688	5828
Marginitermes hubbardi	110	312
	75	450
	1477	3119
Without replacement reproductives		
N. larseni	0	10
	0	12
	0	16
	0	33
	16	167
	0	210
	0	566
	0	614
	0	760
	0	813
	0	1828
	0	2911
Incisitermes marginipennis	503	1871
I. minor	0	9200
I. platycephalus	0	15
M. hubbardi	0	122
	0	2045
	0	2267
Cryptotermes fatulus	0	366
Zootermopsis laticeps	0	137
	370	585
	0	1086
	298	2367

* Data from Nutting (19). See the text for discussion.

the primary reproductives because each individual prefers to assume this role. In the normal course of replacement in *Kalotermes*, a number of individuals will develop reproductive potential simultaneously. These individuals then fight until only a single pair of reproductives remains (22–24). The fighting itself is seldom mortal, but once wounded, a reproductive is attacked by workers and soldiers and killed. It is not always the case that the replacements are eliminated until only a pair remains. In many species there are frequently several replacements or supplementaries coexisting peacefully in the same colony (13, 25).

Outbreeding. Because of the effects that increasing relatedness between the founding pair of reproductives has on the relative value of siblings and offspring, the theory predicts that selection favoring outbreeding should occur at the level of the colony because in colonies founded by related individuals the asymmetries congenial to eusociality will not exist among offspring (see Figs. 8 and 11).

Observers do not agree on the incidence of outbreeding. Grasse and Noirot (22), studying *Bellicositermes* species, suggested that colonies are most often founded by brother-sister pairs. Harris and Sands (25), Weesner (26), and Herfs (27), however, argue that termites are not such poor fliers as they are supposed and, in addition, the great masses of termites that swarm simultaneously from many different colonies provide excellent arenas for outbreeding. Also on this point, Grassi and Sandias (28, 29) report for *Kalotermes flavocollis* in Sicily, that during a swarm, the males invariably leave the nest 2–3 hr after the females. It is difficult to understand this phenomenon as anything but a device to promote outbreeding.

Unfortunately, data concerning colony foundation are scant. It is clear, however, that in every case colonies are founded by a single male and a single female. This situation of obligate monogamy implies that there can be no "limiting sex" in the sense of Hamilton (30), and means that the skews in the sex ratio of alates [predominantly in the direction of an overabundance of females (5, 31, 32)] cannot possibly be due to local mate competition as Alexander and Sherman (33) suggested. Just why these skews in the sex ratio exist remains a mystery and certainly warrants further study.

Origin of the Termites. The models presented here shed new light on the circumstances that might have prevailed in the evolution of eusociality in the termites. In particular, inbreeding assumes a crucial role by establishing the appropriate biases in relatedness. Consequently the suggestion of Taylor (8) and of Hamilton (34), that termites arose in an underbark or rotting wood habitat, now appears eminently reasonable because it is in this type of habitat, where movement is restricted, that much inbreeding occurs (34). I suggest that this peculiar type of habitat, by enforcing inbreeding, is one of the prime movers of termite eusociality.

Termite evolution might, therefore, have proceeded roughly along the following line: Omnivorous cockroaches, living in detritus, were forced by the pressures of predation and the elements into the underbark or rotting wood habitat. Once there, these roaches acquired symbiotic protozoa that digest cellulose, allowing them to remain under the bark and exploit the energetic wealth of their wooden refuge. However, by doing this, they became confined under the bark and much inbreeding ensued. This inbreeding then generated biases in relatedness that allowed the evolution of eusocial-type helping behavior.

The underbark or rotting wood habitat is also one that would facilitate the maintenance of these biases in relatedness. Once the local wood has been consumed, these prototermites would have had to move to another food source, facilitating outbreeding. This "bonanza" (1) pattern of resource exploitation might have resulted in a life cycle with alternating periods of inbreeding and outbreeding like that depicted in Fig. 7.

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