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Effects of Thelytokous Worker Reproduction on Kin-Selection and Conflict in the Cape Honeybee, Apis mellifera capensis

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SUMMARY

Apis mellifera capensis workers are able to produce female eggs by the process of thelytoky, whereas the workers of other races of honeybee and most other eusocial Hymenoptera produce males only (arrhenotoky). The maximization of inclusive fitness has been studied in eusocial arrhenotokous species, but not in thelytokous ones. Thelytokous worker offspring are female, consequently the kin-structure of colonies is altered. This difference leads to changes in kin-value asymmetries and kin-selection. Following from these changes many of the predictions regarding conflict in thelytokous species differ quantitatively or even qualitatively from those for arrhenotokous species. In *A. m. capensis* inclusive fitness arguments predict more conflict between workers over reproductive dominance, especially when the colony is queenless. Some of the unique traits of Cape honeybee workers upon queen-loss, for example: (i) extreme aggression amongst workers; (ii) very rapid development of ovaries; and (iii) queen-like pheromones in workers upon queen-loss can be explained as responses to such selection. It is predicted that workers will remove (police) less of their fellow workers' eggs than other races.

1. INTRODUCTION

Hamilton (1964) introduced the concept of inclusive fitness to explain the apparently altruistic behaviour of workers of eusocial species. In essence the concept suggests that related individuals share a number of alleles identical by descent. Hence, by increasing the reproduction of a related individual, a worker indirectly increases the frequency of her own alleles in the next generation. The members of a monogynous eusocial colony (i.e. one queen per colony) are genetically diverse because recombination occurs during the formation of the queen's gametes and because the queen can mate with more than one male leading to different patrilines within the colony. Therefore colony members are related to each other by varied degrees. If all individuals of the colony 'want' to maximize their inclusive fitness by favouring individuals that are more closely related to themselves, some intracolonial conflict can be expected to occur.

Despite the fact that the 'ultimate' outcome of eusociality is seen as the sterility of workers, worker reproduction probably played and still plays an important evolutionary role in the characteristic features of eusocial Hymenopteran colonies (Bourke 1988). Due to the haplodiploid genetic system of the Hymenoptera, workers can produce viable offspring. Unmated workers can lay unfertilized haploid eggs that develop parthenogenetically into males (a process called arrhenotoky; Crozier 1975). Iwasa (1981) showed that production of such males by workers played an important role in the evolution of eusociality. Taylor (1981) argued that worker reproduction of males from queenless colonies causes queen-right (colonies with a queen) colonies to produce more female-biased sex ratios.

The reproductive capabilities of the workers of many species (Bourke 1988; Choe 1988; Davies *et al.* 1994) lead to potential and actual conflicts in eusocial colonies (Ratnieks & Reeve 1992; Heinze *et al.* 1994). The extent of such conflicts between workers and the queen as well as amongst workers themselves depends on how the individuals' inclusive fitness may be affected by these actions. In cases where workers of eusocial Hymenoptera reproduce, they most commonly produce male offspring and conflicts arising from this have been discussed in detail (Trivers & Hare 1976; Starr 1984; Pamilo 1991*a*, *b*; Ratnieks & Reeve 1992).

A few species differ from this general pattern (arrhenotokous reproduction by workers) in that their unmated workers can produce diploid eggs parthenogenetically (a process called thelytoky: Onions 1912; Cagniant 1979; Itow *et al.* 1984; Heinze & Hölldobler 1995; Tsuji & Yamauchi 1995). Being diploid these eggs normally develop into females (Crozier 1975). In *A. m. capensis* the laying workers, more or less 12% of the workers of the colony (Hepburn & Allsopp 1994), produce only female offspring which are reared to workers and a few queens (Hepburn 1994). Unmated queens will also produce females thelytokously, but they produce males as well (Ruttner 1988) and it is not known whether fertilized queens ever produce thelytokously. Although the occurrence of thelytoky is still poorly understood (Bourke 1988; Lenoir *et al.* 1988;

Greeff 1996), it affects the kin-structure of the colony and hence, kin-selection, the most important effect being that worker offspring are females and not males. The effects of thelytokous worker reproduction on kin-selection has, however, not been studied previously.

Here, I develop a model to show how kin-selection operates under thelytokous worker reproduction. I then use the hypothesis developed to interpret the behavioural and biological peculiarities (reviewed in Anderson 1977; Hepburn & Crewe 1991) of the Cape honeybee, *Apis mellifera capensis* (one eusocial Hymenopteran exhibiting thelytoky; Onions 1912; Verma & Ruttner 1983). I will argue that thelytoky exhibited a major selective pressure on *A. m. capensis*. Although I concentrate on *A. m. capensis*, the models developed here can serve as a framework for studies on other species.

2. THE MODEL

Consider two populations comprised of monogynous (one queen per colony) eusocial colonies. The two populations differ in only one respect: workers of the first population produce male offspring arrhenotokously (figure 1*a*), whereas the workers of the other population produce females thelytokously (figure 1*b*). Thelytoky can either involve meiosis, in which case it is called automixis, or no meiosis can occur, in which case we call it apomixis. Because there is no meiosis during apomixis the gametes are already diploid. On the other hand, dipoidy has to be restored after automixis by the fusion of two of the meiotic products i.e. it is almost like self-fertilization. I investigate automixis with central fusion in which the pronucleus and one of the second division products of the first polar nucleus fuse (see Greeff & Villet 1993). Apomixis can be treated as a special case of automixis (see below). Worker reproduction is suppressed when the colony is queen-right. If the generation 1 queen from either population survives till reproduction, she produces males arrhenotokously and females sexually (figure 1). If the generation 1 queen dies and there are no eggs or larvae from which to rear a new queen, workers will start to reproduce. In the arrhenotokous population (figure 1*a*) worker-laid eggs develop into males (drones) that participate in random mating in generation 2. These worker derived males comprise a proportion B of all the males in generation 2. These arrhenotokous colonies will eventually die because the worker force is not replenished. In the thelytokous population (figure 1*b*) worker-laid eggs are reared to workers and queens. A queen derived from a worker-laid egg takes over the colony and mates at random with males from generation 2. Further we will assume that the population is infinitely big. Let n be the number of males a queen is mated to.

The extent to which a worker increases her own inclusive fitness by helping another depends on how many alleles, identical by descent, she shares with the recipient. The relatedness of individual Y to individual X (G_{YX}) can be calculated as:

$$G_{YX} = 2\phi_{YX}/(1+f_X),$$

with ϕ_{YX} equal to the probability that a randomly chosen allele from X and Y will be identical by descent and with $(1+f_X)/2$ equal to the probability that two alleles taken from X are identical by descent (Pamilo & Crozier 1982). This estimate is formally known as the 'pedigree coefficient of relationship' and is analogous to Hamilton's regression coefficient of relatedness (Pamilo & Crozier 1982).

Although both model populations are effectively outbreeding and there is no inbreeding *per se*, automixis leads to inbred queens (Greeff 1993): during automixis with central fusion, crossovers between a locus and the centromere cause half of the zygotes that are formed to have alleles identical by descent at the locus (Greeff & Villet 1993). Hence, if the probability of a crossover between the locus studied and the centromere is S, a proportion $S/2$ of the queens will have alleles identical by descent at that locus. All the offspring of these queens will thus receive an identical allele from their mother and their relatedness to each other will be increased. Let the proportion of colonies that have queens descending from thelytokous eggs be T. Then the proportion of queens inbred for the locus will be equal to $TS/2$. The other variable that affects G is n, the number of males a queen mates with. As n increases, the probability that two workers will have the same father decreases i.e. the probability that they will receive alleles identical by descent from their father decreases. Hence we can calculate relatedness between sisters as follows. In $TS/2$ of all the colonies, sisters will receive identical alleles from their mother. In the remaining colonies, sisters have a probability of 0.5 of receiving an identical allele from their mother. Two sisters' chance of receiving an identical allele from a father is equal to the chance of them having the same father, which is equal to $1/n$. The relatedness can now

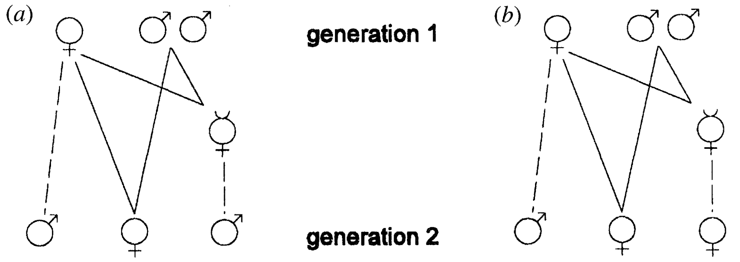

Figure 1. Reproduction in an eusocial species where workers reproduce (*a*) arrhenotokously and (*b*) thelytokously. Note that the workers (☿) themselves falls in between the two generations of 'real' reproductives (♀, ♂). Dashed lines indicate parthenogenetic reproduction.

Table 1. *The relatedness* (G), *reproductive value* (v), *expected mating success* (c) *and kin-value* (K) *of different relatives to workers in a population where workers reproduce thelytokously and in a population where workers reproduce arrhenotokously*

(The abbreviations are defined in the list of abbreviations. These values are the average estimates, for pairs of individuals from the same patriline the term n in G has to be replaced with 1 and for different patrilines $1/2n$ is equal to 0. For apomictic thelytokous populations S is equal to 0.)

	to worker	G	v	c	K
thelytokous population	brother	$(2+ST)/4$	$1/2$	q	$q(2+ST)/8$
	sister	$(2+ST)/8+1/2n$	1	1	$(2+ST)/8+1/2n$
	daughter	1	1	1	1
	niece	$(2+ST)/8+1/2n$	1	1	$(2+ST)/8+1/2n$
arrhenotokous population	brother	$1/2$	$1/(2-B)$	q	$q[2(2-B)]$
	sister	$1/4+1/2n$	1	1	$1/4+1/2n$
	son	1	$1/(2-B)$	q	$q/(2-B)$
	nephew	$1/4+1/2n$	$1/(2-B)$	q	$q(n+2)/[4n(2-B)]$

be written down as $0.5[1 \cdot TS/2+0.5 \cdot (1-TS)/2]+0.5 \cdot 1/n$, which is equal to $(2+ST)/8+1/2n$. Similarly, I calculated G for various relationships (table 1).

These estimates of G are the averages expected in colonies, but if the individuals under consideration are from the same patriline (daughters of the same male), n will be equal to 1 and if they are not, the n term is equal to zero. Similarly, if the colony has a worker-derived queen, T is equal to one, and vice versa.

Haplodiploidy causes females to be twice as valuable as males because females pass on their alleles to sons and daughters whereas males pass their alleles on to daughters only (Hamilton 1972). This ability to pass on alleles to future generations is known as the 'reproductive value' of the sex (Taylor 1988). The reproductive value, v_i, refers to sex i's ability to propagate genes to future generations. In the Hymenoptera the reproductive value of females (v_f) is twice that of males (v_m) (Hamilton 1972; Taylor 1988; Pamilo 1991*a*). When the workers of eusocial species produce males, such as in figure 1*a*, the difference between v_f and v_m is reduced (Pamilo 1991*a*). This reduction is because males can now pass their alleles on to the males of generation 2 via the workers (figure 1*a*). If B is equal to the proportion of males that originate from worker eggs, $v_f : v_m$ is equal to $1 : 1/(2-B)$ (Pamilo 1991*a*). Contrastingly, when workers produce female offspring, such as in figure 1*b*, the reproductive values of males and females are unaffected. Unlike arrhenotoky, thelytoky does not allow males to pass their genes to the males of generation 2 (figure 1).

Another factor which is important in determining how effective a relative will be in propagating one's alleles is the expected mating success of the individual (Hamilton 1972; Ratnieks & Reeve 1992). Let c_i be equal to the ratio of the mating success of a sex i reproductive (queen or male) to that of a queen. By defining it relative to a queen's expected mating success, the resultant kin-values are simplified and c_f is thus per definition equal to 1. c may vary greatly from one species to the next. Assuming that a worker does not have information about the virility of the specific individual and that she will therefore have to respond to the average value of that sex, c is closely related to the sex ratio. Hence if there is for instance, one queen for every four males, c_f will be 1 and $c_m = q = 0.25$, with q equal to the ratio of females to males. Eusocial species that reproduce by colony fission have a high numerical male bias in the sex ratio of the reproductives (Page & Metcalf 1984). In these species c_m will be very small in comparison to c_f. Another factor that needs to be mentioned is the occurrence of polyandry. As a queen mates with n males, the probability that a specific male may mate is qn and not just q. However, any particular male's sperm will only be used for $1/n$ of the fertilizations whereas the queen's gametes will be used for every one, cancelling out the higher probability of mating through sperm competition.

These three values: relatedness, reproductive value and expected mating success can be multiplied to give an estimate of how valuable a relative will be in propagating one's own alleles (Ratnieks & Reeve 1992). This product is called the kin-value (K; Ratnieks & Reeve 1992) of the relative. The kin-value of individual Y to individual X can be calculated as

$$K_{YX} = G_{YX} \cdot v_i \cdot c_i, \tag{2}$$

3. RESULTS

Here I discuss the kin-values in table 1 and how they are affected by the variables. One very important thing to keep in mind is that the kin-values are really ratios, because both v and c are arbitrarily defined. For example, it seems as if the kin-value of a daughter is unaffected by all the variables because it is equal to 1. However, we could have defined c_m as 1 and c_f as $1/q$ and similarly $v_f = 2$ and $v_m = 1$, which will alter all the kin-values. The kin-values are thus the *ratios* of the inclusive fitness returns a worker can expect from different classes of relatives.

All kin-values of male relatives to workers are affected by q: if the sex ratio is male biased such as in many species, q can lead to a dramatic devaluation of a male relative's (brother, son or nephew) kin-value in comparison to a female's and vice versa (see *A. m. capensis* below). The effect of ST and B on kin-values are similar in the two populations, that of B being larger. Increases in ST increase the kin-values of brothers, sisters and nieces to the workers by increasing G between these relatives (table 1). Whereas increases in B increase the kin-value of brothers, sons and nephews to workers by increasing the value of males. Queen-loss leads to worker reproduction and should thus correlate with B and T. However, the same proportion of queen-loss in ecologically similar thelytokous and arrhenotokous populations will not necessarily cause B to be equal to T. The effect of n is similar in both populations and increases in n leads to a decrease in the kin-value of sisters, nieces and nephews by decreasing G.

4. KIN-SELECTION IN THELYTOKOUS POPULATIONS

In this section I will make predictions based on table 1. Most of this discussion will apply to all thelytokous species. However, in a few specified cases the predictions will apply to *A. m. capensis* only. In order to apply the model to *A. m. capensis* I obtained estimates for the variables from data.

Lobo & Kerr (1993) estimated that honey bee queens mate with an average of 16.1 males. Honey bees reproduce by colony fission and European honeybees produce an average of ±20000 drones (Page & Metcalf 1984) and 0.96 swarms per year (Seeley 1978). As each swarm has one queen the operational sex ratio is very male-biased and consequently males have a very low probability of mating compared to queens. c_m is thus very small: in the order of 5×10^{-5}. African races generally produce more swarms and c_m will thus be more for these races. However, the conclusions of this work will not be altered, unless c_m is more than one.

The specific type of thelytokous parthenogenesis observed in *A. m. capensis* workers is known as automixis. It is characterized by a normal meiosis followed by diploidization through fusion of two of the meiotic products (Verma & Ruttner 1983; Hepburn & Crewe 1991). Cytological work (Verma & Ruttner 1983), breeding experiments (Tucker 1958) and heritability estimates (Greeff & Villet 1993) suggest that crossovers and recombination occur during thelytoky in *A. m. capensis*. However, Moritz & Haberl (1994) using multilocus DNA fingerprinting, did not find evidence of any recombination. In calculating kin-values I assume that recombination occurs. Should further empirical tests show that there is no recombination, S (the probability of a crossover between the locus studied and the centromere), only needs to be set equal to zero i.e. no crossovers. Similarly, species reproducing apomictically (non-meiotic thelytoky) can be accommodated by setting S equal to zero. The kin-values for apomictic species can also be calculated (table 1) and these are actually very similar to that of automictic species (assuming T is not very large). If S is zero for a species, only sections 4*a*(ii) Sex allocation; and 4*c* Intragenomic conflict, will become redundant, all the other predictions will hold fast. Regardless of the amount of recombination, it is important to note that parthenogenetically produced individuals, whether male or female, receive all their DNA from their mothers. Moritz (1986) argued that 0.3 might be a liberal estimate of the probability of queen-loss, but variation in T and B will not affect the predictions of this discussion qualitatively.

The nature of the following predictions depends heavily on whether the colony is queen-right or queenless. The following discussion is divided accordingly. The kin-values for the thelytokous population will contain a capital T in their subscript to differentiate them from those of the arrhenotokous population, which will be denoted by a capital A.

(*a*) *Queen-right colonies*

(i) *Worker-worker conflict*

Worker reproduction

Pamilo (1991*b*) showed that the evolution of worker reproduction depends on its cost to the colony's total reproductive output and on the level of polyandry of the species. If the queen mates with two or more males, worker reproduction will evolve only if it increases the total reproductive success of the colony. The more polyandrous the species, the greater this increase must be. If the queen mates with fewer than two males, worker reproduction can evolve even if it incurs a cost on the colony's total reproduction, but there is a limit to the magnitude of the cost, which is inversely related to the number of mates the queen has (Pamilo 1991*b*). We can adjust Pamilo's (1991*b*) eq (2) to allow for the differences in the genetic system as follows: if a colony in which workers produce a proportion ψ of the colony's queens has a total success of $U\psi$, the non-laying worker's inclusive fitness is equal to

$$W = U\psi\{[(1-\psi)G_{\mathrm{siw}}+\psi G_{\mathrm{niw}}]v\mathrm{f}+G_{\mathrm{bw}}v_{\mathrm{m}}\}, \tag{3}$$

As $G_{\mathrm{siw}} = G_{\mathrm{niw}}$, it follows from eq (3) that the workers' inclusive fitness is unaffected by the size of ψ and only depends on $U\psi$, the colony's total success. Hence, if worker reproduction increases total colony success, it will be selected for and if it decreases colony success likewise it will be selected against. Unlike arrhenotokous worker reproduction the degree of polyandry of queens plays no role in selection for this trait. Worker reproduction will thus evolve more easily in polyandrous thelytokous species than in polyandrous arrhenotokous species.

An *A. m. capensis* worker's own offspring have more kin-value to her than that of her mother's offspring (compare K_{dwT} to K_{siwT} and K_{sowA} to K_{bwA}). This difference is far greater for *A. m. capensis* than for arrhenotokous races of honeybee, because q reduces the kin-values of males dramatically. Some workers may be expected to cheat and produce eggs, but with a far greater incidence in *A. m. capensis* than in other races. However, thelytokous workers will only increase their inclusive fitness if these eggs are reared as queens; there is no male worker-caste and all males are thus reared to reproductives. There will be much higher conflict between thelytokous workers about the identity of worker eggs that are reared as reproductives than in arrhenotokous races, because the difference between the kin-values of an automictic worker's daughter and her niece is far greater than that between an arrhenotokous worker's son and her nephew ($K_{\mathrm{dwT}} - K_{\mathrm{niwT}} \gg K_{\mathrm{sowA}} - K_{\mathrm{newA}}$).

Policing

Ratnieks (1988) looked at the evolution of policing behaviour (when workers eat their sisters' eggs) in arrhenotokous species and found that it will evolve when the queen is mated to more than two males. This is because they are more closely related to their brothers than to their nephews ($G_{\mathrm{bw}} > G_{\mathrm{new}}$, when $n > 2$). In thelytokous species, workers' sisters and nieces are related to them by the same magnitude regardless of the degree of polyandry and should thus not prefer the one above the other. Hence, the intensity of policing will depend on a play off between the cost of policing and the cost of worker reproduction to overall colony reproduction. We would thus expect that *A. m. capensis* workers would either not police at all or will do so less frequently than other races.

(ii) *Queen-worker conflict*

Identity of new queens

When workers produce a proportion of the colony's males, the queen compromises her inclusive fitness because she is more related to her own sons ($Gv = 1/2$) than to her grandsons ($Gv = 1/4$) (Ratnieks & Reeve 1992). When workers produce a portion of the colony's queens the present queen does not incur any cost due to differences in relatedness, because she is equally related to her daughters and granddaughters. We would thus not expect queens to resist thelytokous worker reproduction as long as it does not reduce the colony's total success. In fact a queen who allows workers to replace her eggs with theirs will not suffer a reduction in inclusive fitness, unless the colony's total fitness is reduced. In contrast, the egg-laying worker will increase her reproductive success substantially (K_{dwT} versus K_{siwT}). This result is contrary to the normal scenario in eusocial Hymenoptera.

Sex allocation

Trivers & Hare (1976) argued that the workers and queens of arrhenotokous species are in conflict about the magnitude of the sex ratio. Pamilo (1991*a*) showed that when the reproductive success of offspring is a linear function of the investment in them then the equilibrium investment in males, r, is given by

$$r = G_{\mathrm{m}}v_{\mathrm{m}}/(G_{\mathrm{f}}v_{\mathrm{f}} + G_{\mathrm{m}}v_{\mathrm{m}}), \qquad (4)$$

where G_i is the relatedness of the controlling individual to the sex i offspring. By substituting the appropriate values into eq (4) we find that the equilibrium investment ratio, when determined by the queen is

$$r = 0.5, \qquad (5)$$

whereas that determined by workers is

$$r = (2 + ST)/[2(2 + ST + 2/n)]. \qquad (6)$$

The optimal sex ratio from the workers' point of view is 0.25 when ST is equal to 0 and n equal to 1. As n and/or ST increase the optimal sex ratio for workers nears that of the queen. Hence, like polyandry (Trivers & Hare 1976), thelytoky reduces the conflict between the queen and workers about the sex ratio.

(*b*) *Queenless colonies*

(i) *Worker–worker conflict*

In arrhenotokous species a worker will increase her inclusive fitness most by rearing her own sons, followed by rearing nephews of the same patriline and then by rearing nephews from a different patriline (table 1). In thelytokous species the order of preference is similar: daughters, then nieces from the same and then from a different patriline (table 1). However, the difference in inclusive fitness gains is more than c_{m} times greater in *A. m. capensis* than in other races of honeybee and we can thus expect much more serious conflicts than in arrhenotokous races.

(*c*) *Intragenomic conflicts*

This conflict occurs when queens are reared from an automictic worker-laid egg and is thus unique to automictic species. S may vary from one locus to the next i.e. for loci close to the centromere there may never be crossovers between the locus and the centromere, $S = 0$, and for loci close to the telomere, there may always be a crossover, $S = 1$. Any other second crossovers will not affect the model (assuming that they occur independently from the first; see Suzuki *et al.* 1981). Hence, the kin-value of a relative is larger for loci closer to the telomere than to those closer to the centromere. The opposite is true for automixis with terminal fusion. Resolution of this conflict is only possible if crossovers in all arms are localized to either the centromere or the telomere. Selection will maximize the inclusive fitness of the locus affecting the behaviour under selection. For traits that are polygenic an average situation will evolve.

5. *APIS MELLIFERA CAPENSIS* REINTERPRETED

In this section I will contrast data from previous work on *A. m. capensis* to that on other races. The differences in their behaviour is consistent with the differences in kin-value asymmetries between the races. It has been argued that there is reproductive conflict between subfamilies and individuals of honeybee colonies that may select for traits which enhance a subfamily's or individual's ability to skew reproduction in their favour (Starr 1984; Page & Erickson 1988; Ratnieks 1993; Page & Robinson 1994). When we compare the potential conflict between workers that may arise due to kin-value asymmetries it is clear that if ecological factors are similar, thelytokous species will be far more prone to conflict than arrhenotokous species. Therefore, we can expect thelytokous species to show more traits that result from this potential conflict. Here we will concentrate on conflict that arise after queen-loss. Each worker will gain most if her daughter is reared as the new queen. Or if the worker is incapable of laying eggs, she will increase her inclusive fitness most by favouring full sibs rather that half sibs. I can identify three main responses to such selection in *A. m. capensis*.

(*a*) *Pheromonal exploitation*

Honeybee queens secrete pheromones that suppress reproduction in workers. Due to the presence of this communication system, there is already a fine-tuned mechanism by which a single individual can monopolize reproduction. Hence, the occurrence of trace amounts of 9-ODA (a queen-pheromone which suppress ovary development in other individuals, Hepburn *et al.* 1991) in workers of orphaned colonies of arrhenotokous races (Crewe 1988; Plettner *et al.* 1993) has been interpreted as a result of selection for dominance (Page & Robinson 1994). In *A. m. capensis* the selection coefficient for such domination is much higher ($K_{\mathrm{dwT}} - K_{\mathrm{niwT}} \gg K_{\mathrm{sowA}} - K_{\mathrm{newA}}$). In line with this expectation, orphaned *A. m. capensis* workers produce a pheromonal bouquet that is very similar to that of the queen and produce it in much larger amounts than other races (Crewe & Velthuis 1980; Crewe 1988; Velthuis *et al.* 1990; Plettner *et al.* 1993). Like queens, workers with queen-like pheromones can suppress queen-cell construction and even cause queen-cell destruction (Hepburn *et al.* 1988), can lead to the abortion of queen rearing (Hepburn 1994), can inhibit the development of other workers' ovaries (Hepburn *et al.* 1991) and can dominate other workers (Hillesheim *et al.* 1989). Keller & Nonacs (1993) argued that a colony member cannot stably deceit other colony members to act altruistically against their own interest with the use of pheromones. However, the case of *A. m. capensis* might be an exception with certain workers selfishly using the pheromones to deceive their fellow colony members into rearing their young. This coercive use of the pheromone is probably stable because it reflects an honest signal more often than not. The fact that hybrid *A. m. capensis* × *A. m. carnica* workers produce intermediate amounts of pheromone (Velthuis & van der Kerk 1988) suggests that it is under genetic control and hence may have been selected for. Crewe (1988) stated that 'Whether this conjunction (between thelytoky and pheromonal secretions) is fortuitous or adaptive has yet to be determined'. My theoretical considerations indeed suggest that this association is adaptive.

(*b*) *Overt aggression*

Upon queen-loss, arrhenotokous colonies experience an increase in aggressive interactions between workers (Velthuis 1976). This aggression is orientated towards half sisters rather than to full sisters (Getz & Smith 1983; Evers & Seeley 1986). Presumably the aggression may increase full sisters' probability of becoming laying workers over half sisters, although this could not be demonstrated (Van der Blom & Verkade 1991). In some *A. m. capensis* colonies extreme fighting occurs upon queen-loss (Anderson 1968; Hepburn & Crewe 1991). In the 12 days following queen-loss the amount of dead bees removed daily from the colony increases ninefold. This increase is due to attacks by workers on nest mates. It is thus possible that the bigger asymmetry in the kin-values of nieces of the same and different patrilines compared to nephews of the same and different patrilines (table 1) leads to selection for more effective elimination of laying workers of other patrilines, hence the massacre. These killings do not occur in all colonies and the variation may be due to variation in kin-value asymmetries. Increased relatedness within a colony means that the elimination of laying workers from other patrilines will increase an individual's inclusive fitness less. In fact, the reduction in the worker force due to fighting may outweigh advantages gained by fighting. Because the advantages gained by fighting are less when individuals are more closely related, an increase in relatedness may lead to a decrease in the amount of fighting. Such an increase in the relatedness of a colony can result from queens that originated from automictic eggs, or if queens mate with related drones, or to fewer drones. Because eusocial insects seem to be able to perceive the genetic variation within their colony (Sundström 1994) this explanation may be tenable.

(*c*) *Ovary function*

Workers show two egg laying adaptations. First, they have twice as many ovarioles as the workers of their closest relatives, *A. m. scutellata* (Allsopp 1988) and more than all other races (Ruttner & Hesse 1979). Second, worker ovaries are very well developed in queen-right colonies, causing the onset of egg laying by workers within 4 days of queen-loss (Anderson 1963; Hepburn *et al.* 1988) which is more rapid than in other races (Ruttner & Hesse 1979). Given that a quicker onset of oviposition and more ovarioles lead to a higher reproductive output, this difference is also consistent with expectations from kin-value asymmetries.

There are no data to test a number of the predictions of the previous section, but because such experiments will be valuable I will briefly discuss them. In arrhenotokous races worker reproduction is very low (Visscher 1989; Robinson *et al.* 1990; Ratnieks 1993) and most eggs are policed (Ratnieks & Visscher 1989; Ratnieks 1993). However, some colonies show dramatic retaliation by workers (Oldroyd *et al.* 1994). In the colony studied by Oldroyd *et al.* (1994) one subfamily produced eggs that were not policed by workers. In *A. m. capensis* we expect far more such retaliations and queens should not resist these as much as in arrhenotokous races. As several researchers (Page & Erickson 1984; Noonan 1986; Visscher 1986; Page *et al.* 1989) have argued that arrhenotokous workers preferably rear full sisters to queens, an investigation of nepotism in queenless *A. m. capensis* colonies may shed further light on the controversy of kin-recognition (Hogendoorn & Velthuis 1988; Carlin & Frumhoff 1990; Oldroyd & Rinderer 1990; Page & Robinson 1990; Page *et al.* 1990).

The high degree of actual conflict observed in *A. m. capensis*, predicted by the greater kin-value asymmetry, suggests that thelytoky played an important role in the evolution of the behaviour of *A. m. capensis*. Further comparative work on this race will thus be of importance. Moritz (1989) discussed an important point that has been neglected in this treatment of the problem. He argued that although an increase in competitive ability between workers will lead to a higher personal fitness in the short run, it may in fact reduce the colony's fitness to such an extend that overall, the individual is less fit. The playoff between these two selective hirarchies is an important factor confining the extend of individual selection.

(*d*) *Thelytoky in eusocial Hymenoptera*

There are four ant species that have been unambiguously shown to have thelytokous worker reproduction, *Pristomyrmex pungens* (Itow *et al.* 1984), *Cataglyphis cursor* (Cagniant 1979), *Platythyrea punctata* (Heinze & Hölldobler 1995) and *Cerapachys biroi* (Tsuji & Yamauchi 1995). The thelytokous workers of *P. punctata* interacted aggressively, but their behaviour closely resembled that of other ponerines (Heinze & Hölldobler 1995). To evaluate this species more information about its mating behaviour will be necessary. Like *A. m. capensis*, *C. cursor* colonies reproduce by budding, implicating a male-biased sex ratio, and their queens appear to be polyandrous (Lenoir *et al.* 1988). In agreement with the theory presented here, *C. cursor* workers bite each other on queen-loss (Retana & Cerdá 1991). Heinze (1993) also interpreted this aggression as evidence for competition between reproductive workers. Aggression between workers in *P. pungens* has also not been recorded, but the present lack of conflict in *P. pungens* is probably due to the importance of inter-demic selection (Tsuji 1994, 1995). This species lacks queens altogether and this model does not really apply to them. However, if we consider its evolution from a species with queens, eq (3) is probably of some importance. Equation (3) shows that worker reproduction may evolve as long as it does not reduce the colony's total reproduction. A major cause of such a reduction will be conflict between workers to reproduce. If the ancestral species was monandrous this source of conflict will be considerably reduced. Another important factor is that the queen, being equally related to her granddaughters and daughters, will not resist worker reproduction.

By viewing eusocial thelytokous species from a kin-value perspective we not only gain greater understanding of their functioning, but new areas of research are also suggested. Because many of these kin-based predictions for thelytokous species differ qualitatively from arrhenotokous species, they are good alternatives for comparative tests.

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APPENDIX

List of variables

B	the proportion of males from worker descent
c_i	the expected reproductive success of sex i
G_{YX}	the pedigree coefficient of relationship of individual Y to individual X
K_{YX}	the kin-value of individual Y to individual X
$_{\mathrm{b}}$	brother
$_{\mathrm{d}}$	daughter
$_{\mathrm{ne}}$	nephew (sister's son)
$_{\mathrm{ni}}$	niece (sister's daughter)
$_{\mathrm{si}}$	sister
$_{\mathrm{so}}$	son
$_{\mathrm{w}}$	worker
q	the ratio of queens to males
S	the probability of a crossover between the locus and the centromere
T	the proportions of colonies with queens from worker descent
n	the number of males a queen mates to