

Appendix from T. Wenseleers and F. L. W. Ratnieks, “Comparative Analysis of Worker Reproduction and Policing in Eusocial Hymenoptera Supports Relatedness Theory” (Am. Nat., vol. 168, no. 6, p. E163)

Table A1

Data on colony kin structure and the occurrence of queen and worker policing and worker-dominance behavior in 48 species of eusocial Hymenoptera

Taxon and species	N_e	r_{w-w}	r_{diff}	Method	Queen policing	Worker policing	Worker-dominance behavior	Aggression or egg eating? (A/E)	References for r_{w-w}
Sweat bees:									
<i>Lasioglossum zephyrum</i>	1	.75 ^a	.125	A	Yes	No	No	A + E	Crozier et al. 1987
Bumblebees:									
<i>Bombus agrorum</i>	1	.75 ^{a,c}	.125		Yes	No ^b	Yes ^b	A	
<i>Bombus ardens</i>	1	.75 ^{a,c}	.125		Yes	?	Yes	A + E	
<i>Bombus bifarius</i>	1	.75 ^a	.125	O	?	?	Yes	A	Hobbs 1967
<i>Bombus ephippiatus</i>	1	.75 ^{a,c}	.125		Yes	?	?	E	
<i>Bombus hypocrita</i>	1	.75 ^{a,c}	.125		Yes	No ^b	Yes ^b	A + E	
<i>Bombus impatiens</i>	1	.67	.085	M	Yes	No	No	E	Cnaani et al. 2002
<i>Bombus lapidarius</i>	1	.75 ^a	.125	M	Yes	No ^b	Yes ^b	A + E	Schmid-Hempel and Schmid-Hempel 2000
<i>Bombus ruderatus</i>	1	.75 ^{a,c}	.125		Yes	?	?	A + E	
<i>Bombus terrestris</i>	1	.75 ^a	.125	M	Yes	No ^b	Yes ^b	A + E	Alaux et al. 2004; Lopez-Vaamonde et al. 2004
Stingless bees:									
<i>Melipona bicolor</i>	1.3	.62 ^d	.085 ^d	M	Yes	No	Yes	E	Peters et al. 1999
<i>Melipona compressipes</i>	1	.75 ^{a,c}	.125		Yes	No	No	E	
<i>Melipona favosa</i>	1	.75 ^{a,c}	.125		?	No	No		
<i>Melipona scutellaris</i>	1	.75 ^a	.125	M	Yes	No	No	E	Tóth et al. 2002b
<i>Melipona subnitida</i>	1	.75 ^a	.125	A	?	No	No		Tóth et al. 2002b
<i>Paratrigona subnuda</i>	1	.75 ^a	.125	M	Yes	No	No	A + E	Tóth et al. 2002a
<i>Scaptotrigona depilis</i>	1	.75 ^{a,c}	.125		Yes	No	No	E	
<i>Scaptotrigona postica</i>	1	.73	.115	M	Yes	No	No	E	Tóth et al. 2002b; Paxton et al. 2003
Honeybees:									
<i>Apis cerana</i>	1	.35	-.075	M	? ^e	Yes ^f	No	E	Palmer and Oldroyd 2000; Oldroyd et al. 2001
<i>Apis florea</i>	1	.29	-.105	M	No	Yes ^f	No	E	Palmer and Oldroyd 2000; Halling et al. 2001
<i>Apis mellifera</i>	1	.29	-.105	M	? ^e	Yes ^f	No	A + E	Estoup et al. 1994; Palmer and Oldroyd 2000

Table A1 (Continued)

Taxon and species	N_e	r_{w-w}	r_{diff}	Method	Queen policing	Worker policing	Worker- dominance behavior	Aggression or egg eating? (A/E)	References for r_{w-w}
<i>Apis mellifera capensis</i> ^g	1	.30 ^a	0 ^g	M	? ^e	Yes ^h	No	E	Moritz et al. 1999
Polistinae wasps:									
<i>Polistes biglumis</i>	1	.75 ^{a,c}	.125		?	No	Yes	E	
<i>Polistes chinensis</i>	1	.75 ^a	.125	M + A	Yes	No	Yes	E	Tsuchida et al. 2003
<i>Polistes dominulus</i>	1.4	.56	.072 ⁱ	M	Yes	No	Yes	E	Queller et al. 2000
Vespinae wasps:									
<i>Dolichovespula arenaria</i>	1	.71 ^a	.104	A	Yes	?	?	A + E	Foster and Ratnieks 2001 ^b ; F. L. W. Ratnieks and J. J. Boomsma, personal communication
<i>Dolichovespula media</i>	1	.71	.105	M	Yes	?	?	E	Foster et al. 2001
<i>Dolichovespula maculata</i>	1	.75 ^a	.125	M	Yes	No	Yes	A + E	Foster et al. 2001
<i>Dolichovespula norwegica</i>	1	.71	.105	M	Yes	No	Yes	A + E	Foster et al. 2001
<i>Dolichovespula saxonica</i>	1	.62	.060	M	Yes	? ^j	?	A + E	Foster and Ratnieks 2000
<i>Dolichovespula sylvestris</i>	1	.68	.090	M	Yes	No	Yes	A + E	Foster et al. 2001
<i>Vespa crabro gribodi</i>	1	.67	.085	M	No	Yes ^f	No	E	Foster et al. 2000
<i>Vespula germanica</i>	1	.46	-.020	M	No	Yes ^f	No	E	Goodisman et al. 2002; T. Wenseleers, R. L. Hammond, K. Vuerinckx, J. Billen, and L. Keller, unpublished data
<i>Vespula rufa</i>	1	.58 ^a	.040	M	Yes	No	Yes	E	Wenseleers et al. 2005 ^a
<i>Vespula vulgaris</i>	1	.51	.005 ^k	M	No	Yes	No	E	Foster and Ratnieks 2001 ^a
Ants:									
<i>Acromyrmex echinator</i>	1	.39	-.055	M	? ^e	Yes ^f	No	E	Bekkevold et al. 1999
<i>Aphaenogaster smythiesi</i>	1	.75 ^a	.125	M	No	Yes ^f	No	A	Iwanishi et al. 2003
<i>Camponotus floridanus</i>	1	.75 ^a	.125	D	? ^e	Yes ^f	No	E	Gadau et al. 1996
<i>Crematogaster smithii</i>	1	.71	.105	M	Yes	No	No	E	Heinze et al. 2000
<i>Diacamma</i> sp. ¹	1	.75 ^a	.125	O	Yes	Yes	Yes	A + E	Kikuta and Tsuji 1999 ^m
<i>Dinoponera quadricaps</i> ^l	1	.75 ^a	.125	O	Yes	No	Yes	A + E	Monnin and Peeters 1997 ^m
<i>Formica fusca</i>	3.3	.31	-.0008 ^k	M	No	Yes	No	E	Helanterä and Sundström 2005
<i>Harpagoxenus sublaevis</i>	1	.75 ^a	.125	A	Yes	No	Yes	A	Bourke et al. 1988 ^b
<i>Leptothorax acervorum</i>	2.1	.52	.083	M	Yes	No	No	E	Chan and Bourke 1994; Hammond et al. 2003
<i>Leptothorax unifasciatus</i>	1	.75 ^a	.125	A + M	No	No	Yes	A	Hammond and Keller 2004

Table A1 (Continued)

Taxon and species	N_e	r_{w-w}	r_{diff}	Method	Queen policing	Worker policing	Worker- dominance behavior	Aggression or egg eating? (A/E)	References for r_{w-w}
<i>Pachycondyla inversa</i>	4.1	.13	-.014 ^a	M	No	Yes	No	E	Kolmer et al. 2002; K. Kellner, A. Trindl, J. Heinze and P. D’Ettorre, personal communication
<i>Platythyrea punctata</i> ^a	1.1	1 ^a	0 ^a	M	Yes	Yes ^f	No	A	Schilder et al. 1999a
<i>Protomognathus americanus</i>	1	.68	.090	M	?	No	Yes	A	Foitzik and Herbers 2001

Note: Queen and worker policing are defined as the killing of worker-laid eggs or aggression toward reproductive workers by the queen or nonreproductive workers. Worker-dominance behavior is defined as worker egg eating or aggression associated with direct reproductive competition among egg-laying workers. Only policing and worker-dominance behavior in queenright colonies are considered. Policing can occur via aggression (A) or egg eating (E) or both (A + E); N_e = effective number of queens; r_{w-w} = worker-worker relatedness; r_{diff} = difference in relatedness between workers’ sons and queen’s sons; Method = method used to estimate relatedness: M (microsatellites), A (allozymes), D (DNA fingerprinting), or O (pedigree relatedness, mating frequency determined through behavioral observation).

Notes with evidence used to infer presence or absence of policing. **Sweat bees: *L. zephyrum*.** Queens aggress workers with active ovaries and eat worker-laid eggs (Michener and Brothers 1974; see also Batra 1968; Buckle 1982). Workers do not usually kill eggs, so there is no evidence for worker policing or worker-dominance behavior. **Bumblebees: *B. agrorum*.** A single reproductive worker was observed to be repeatedly attacked by the queen (Brian 1951). The reproductive worker eventually succeeded in laying a few eggs. Reproductive workers also show dominance behavior to each other (Free 1955; see also Brian 1952). Egg eating by the queen or workers was not observed (Brian 1951). ***B. ardens*.** The queen aggressed workers that attempted to kill her eggs and also aggressed egg-laying workers and ate worker-laid eggs (Katayama 1997). Workers were also observed eating worker-laid eggs. This was probably linked to direct competition over egg laying since three out of 13 workers who were seen to eat eggs later laid eggs themselves (Katayama 1997). The data are insufficient to determine whether worker policing by nonreproductive workers occurs or whether all egg eating is by egg-laying workers. The data show clearly that some egg eating was by egg-laying workers. ***B. bifarius*.** Workers with active ovaries show mutual aggression (Foster et al. 2004). No data on worker egg laying or the fate of worker-laid eggs were presented. ***B. ephippiatus*.** The queen has been observed to eat worker-laid eggs (J. I. Cuadriello-Aguilar, personal communication). ***B. hypocrita*.** Laying workers kill the queen’s eggs and other workers’ eggs and replace them with their own (Katayama 1974). Egg laying workers are also aggressive toward one another. The queen was mildly aggressive toward egg-laying workers and sometimes pushed them off their cell to prevent them from laying eggs. However, she was not observed to eat any worker-laid eggs and in a few cases just added her own eggs to the workers’ batch of eggs (Katayama 1974). Hence, this species has worker-dominance behavior and a mild form of queen policing. ***B. impatiens*.** One worker was seen to lay a batch of eggs, but the eggs were all eaten by the queen (Cnaani et al. 2002). The reproductive worker was also aggressive toward the queen (Cnaani et al. 2002). No worker-worker aggression occurred in queenright colonies, and worker oophagy was not reported. ***B. lapidarius*.** Hoffer (1882–1883), Lindhard (1912) and Plath (1923) showed that the queen aggresses egg-laying workers and eats worker-laid eggs. Free et al. (1969) also reported that the queen attacks workers who have active ovaries and workers who attempt to build their own egg cups, and that she frequently kills worker-laid eggs. In addition, workers sometimes attempted to open existing egg cups and steal eggs from them, although the queen defended her eggs vigorously to prevent them from being eaten (Free et al. 1969). Workers with active ovaries also aggressed other workers to maintain their dominance position; workers with active ovaries, however, were not aggressed by other workers. ***B. ruderatus*.** Queens have been observed to eat worker-laid eggs (Pomeroy 1979). However, no details on worker oophagy or aggression were given, so we consider it uncertain whether worker policing or worker-dominance behavior might also occur. ***B. terrestris*.** Worker egg laying is common near the end of season (Sladen 1912; Cumber 1949; Free and Butler 1959; Röseler and Honk 1990; Bloch and Hefetz 1999). However, the queen aggresses egg-laying workers (Röseler and van Honk 1990), and the majority of the worker-laid eggs are eaten by the queen and by other egg-laying workers (Duchateau 1989, 1996; Velthuis et al. 2002). Workers often destroy queen-laid eggs and then replace them by their own (van Honk and Hogeweg 1981; van Honk et al. 1981; Duchateau and Velthuis 1988; Bloch and Hefetz 1999). Aggression among egg-laying workers is also common (Van Doorn 1987; Duchateau 1989). **Stingless bees: *M. bicolor*.** Workers lay reproductive eggs, but competing reproductive workers frequently eat and replace these by their own eggs (Velthuis et al. 2002; Koedam et al. 2007). The queen also eats worker-laid eggs. Although these eggs were initially thought to have a purely trophic function, they are in fact viable (Koedam et al. 2001). Hence, both worker-dominance behavior and queen policing occur. ***M. compressipes*.** Workers lay eggs of similar form to queen-laid eggs, presumably indicating that they are reproductive and viable (Sakagami and Oniki 1963). All 18 eggs laid by workers, however, were observed to be eaten by the queen. In any one cell, up to six workers successively oviposited, but after each worker oviposition, the queen ate the worker-laid egg. Eventually, all cells contained queen-laid eggs. ***M. favesa*.** Worker production of males is widespread, with 94.5% of all adult males being workers’ sons (Sommeijer et al. 1999; Chinh et al. 2003). Eggs laid by workers are never eaten by other workers, implying that worker policing is absent (Chinh et al. 2003). The eating of worker-laid eggs by the queen is also common, but most of these eggs are thought to be trophic and nonviable. ***M. scutellaris*.** Sommeijer et al. (1984) observed that a worker who had just laid a reproductive egg and was in the process of sealing the cell was pushed aside by the queen. The queen then reopened the cell, ate the worker-laid egg and mounted the cell for egg laying. In that particular instance, however, the queen’s oviposition attempt failed as she was pushed aside by another reproductive worker before she could lay her egg. ***M. subnitida*.** Worker production of males is widespread, with ~36% of the adult males being workers’ sons (Koedam et al. 1999, 2005; table A2). Eggs laid by workers are never eaten by other workers, implying that worker policing is absent (Koedam et al. 1999, 2005). The eating of worker-laid eggs by the queen is also common, but most of these eggs are thought to be trophic and nonviable. ***P. subnuda*.** Worker production of males is widespread in this species, with 64% of the males being workers’ sons (Tóth et al. 2002a). Worker reproduction proceeds in an unusual way. Workers reopen sealed cells and drop in reproductive eggs through a small hole in the cell (Tóth et al. 2002a). The queen also sometimes aggresses workers while they are doing this. This implies the presence of a form of queen policing. Nevertheless, the strategy of reopening cells evidently makes it much harder for the queen to effectively police the workers. Workers never interfere with other egg-laying workers. Workers also lay eggs in approximately one in four cells before cells are sealed, and these eggs are always eaten by the queen. It is unknown, however, whether these eggs are viable. ***S. depilis*.** da Silva et al. (2001) showed that workers lay both trophic and reproductive eggs. The trophic eggs could be distinguished by their more flaccid and rounder appearance. The queen, however, always ate both types of eggs, before laying her own egg. ***S. postica*.** As in *S. depilis*, workers in this species were found to lay both trophic and reproductive eggs (Bego 1990). Workers were observed to lay 118 trophic and 73 reproductive eggs. Out of the 73 reproductive eggs, however, 69 were eaten by the queen (Bego 1990). This implies that the queen policed worker reproduction through the eating of the workers’ eggs. Competition among egg-laying workers sometimes resulted in up to five eggs being laid in a single cell. Workers were also found to lay more eggs when the colony was in a male producing period, that is, when the queen was laying haploid eggs. This would reduce the cost of worker reproduction as workers’ sons would be traded off against queen’s sons and not against new workers, who are part of colony female reproduction via swarm production. **Honeybees: *A. cerana*.** Worker-laid eggs from queenless nests are preferentially removed compared with queen-laid eggs when introduced into queenright discriminator colonies (Oldroyd et al. 2001). In the experiments performed, queens had access to the eggs

that were tested for survival. Hence, although most of the eggs are probably killed by the workers, it cannot presently be excluded that the queen also polices some of the worker-laid eggs. *A. florea*. Worker-laid eggs from queenless nests are preferentially removed when introduced into queenright colonies (Halling et al. 2001). In the experiments performed, queens had access to the eggs that were tested for survival. Nevertheless, queen policing was inferred to be absent, since during the experiments, the queen was not observed on the introduced drone comb. By contrast, workers were observed inserting their heads into cells, removing eggs, and eating them on several occasions. *A. mellifera*. In three races of *Apis mellifera*, *A. mellifera mellifera*, *A. mellifera ligustica*, and *A. mellifera scutellata*, it has been shown that worker-laid eggs from queenless nests are preferentially removed when introduced into queenright colonies (*A. m. ligustica* or hybrid: Ratnieks and Visscher 1989; Ratnieks 1995; Visscher 1996; Katzav-Gozansky et al. 2001; Miller and Ratnieks 2001; Martin et al. 2002b, 2005; Halling and Oldroyd 2003; Beekman et al. 2004; Beekman and Oldroyd 2005; *A. m. scutellata*: Beekman et al. 2002; Martin et al. 2002a; Neumann et al. 2003; Pirk et al. 2003). In all these experiments, the queen was denied access to the eggs under test by using a queen excluder. Hence, all the observed policing was carried out by workers. At present, it is unknown whether queens ever police worker-laid eggs. Velthuis et al. (2002) and Pirk et al. (2004) suggested that worker-laid eggs have lower viability than queen-laid ones, and that workers merely police dead eggs. This idea, however, has since been disproven (Beekman and Oldroyd 2005). Ratnieks (1993) showed that eggs that are naturally laid by workers in queenright colonies are also quickly removed. Finally, it has been shown that reproductive workers from queenless colonies are aggressed by other workers when introduced into queenright colonies (Visscher and Dukas 1995; Dampney et al. 2002). *A. mellifera capensis*. In the Cape honeybee, workers can produce diploid female offspring through thelytokous parthenogenesis (Anderson 1963). Since the relatedness to sister workers' daughters is the same as to the mother's daughters (sisters), $r_{\text{diff}} = 0$, and worker policing should not be selected for on relatedness grounds (Greiff 1996). Genetic analysis has shown that unpoliced worker-laid brood indeed is common in this species (Moritz et al. 1999). Beekman et al. (2002) also showed that out of three colonies of mixed *A. mellifera scutellata* and *A. mellifera capensis* race, introduced worker-laid eggs were not differentially policed in the colony where workers were most *capensis*-like but were in the two others, where workers were more *scutellata*-like. Pirk et al. (2003), by contrast, concluded that introduced worker-laid eggs were differentially policed in *A. m. capensis*. Nevertheless, the policing was much less effective than in *A. mellifera mellifera* (ca. 50% effective in *A. m. capensis* vs. 98% effective in *A. m. mellifera*). On relatedness grounds, a low level of worker policing may also remain to be selected for if workers not only produce female but also male eggs. Genetic analysis has shown that this can be the case (Moritz et al. 1999), particularly in colonies of mixed *A. mellifera capensis* and *A. m. scutellata* race. In our analysis, however, we assumed that workers only produce female offspring and hence that $r_{\text{diff}} = 0$. Microsatellite analysis of one *capensis* colony showed that the effective queen mating frequency was 10.1, giving $r_{\text{w-w}} = 0.30$ (Moritz et al. 1999). **Polistinae wasps: *P. biglumis***. Yamane (personal communication), cited in Miyano (1983), mentions that egg-laying workers in this species compete for reproduction by eating each other's eggs. ***P. chinensis***. Both the queen and the workers remove worker-laid eggs (Saigo and Tsuchida 2004). However, when workers eat each others' eggs, they always immediately replace the killed egg by one of their own. The percentage of eggs that are worker laid can be very high, sometimes approaching 100% (Miyano 1983; Tsuchida et al. 2003; Saigo and Tsuchida 2004). ***P. dominulus***. In this species, the queen polices worker-laid eggs, and workers also replace other workers' eggs with their own eggs (Liebig et al. 2005). **Vespinine wasps: *D. arenaria***. The queen commonly eats worker-laid eggs (Greene et al. 1976; Greene 1979). It has also been observed that ovipositing workers may be chased over the comb by the queen and that they may be vigorously mauled by her if caught (Greene 1979). ***D. media***. Foster et al. (2001) mention that the queen may police worker-laid eggs. ***D. maculata***. The queen commonly eats worker-laid eggs and may aggress egg-laying workers (Greene 1979). ***D. norwegica***. Worker-laid eggs are removed both by the queen and by other competing egg-laying workers (T. Wenseleers, A. Tofilski, F. S. Nascimento, K. Vuerinckx, and F. L. W. Ratnieks, unpublished data). The queen may also aggress workers with active ovaries. In addition, aggression among egg-laying workers is common. ***D. saxonica***. Foster et al. (2001) mention that the queen may police worker-laid eggs. Genetic analysis also suggests that worker policing is facultatively expressed in multiple paternity colonies (Foster and Ratnieks 2000). However, this remains to be confirmed by direct behavioral observation. ***D. sylvestris***. An initial study showed that worker-laid eggs were removed both by the queen and by other workers (Wenseleers et al. 2005b). However, a later analysis showed that 95% of the eggs eaten by workers were removed by workers who themselves laid eggs (T. Wenseleers, A. Tofilski, F. S. Nascimento, and F. L. W. Ratnieks, unpublished manuscript). Hence, the worker egg eating is caused by direct reproductive competition and is not genuine worker policing. The queen may also aggress egg-laying workers, and reproductive workers frequently fight each other. ***V. crabro gribodi***. Worker-laid eggs from queenless nests are differentially removed when introduced into queenright colonies (Foster et al. 2002). Since the queen did not visit the comb with introduced eggs during the larger part of the trials, queen policing was probably absent. Since only ~2% of the workers had active ovaries in queenright colonies (Foster et al. 2000), most policing was probably carried out by nonreproductive workers. ***V. germanica***. Worker-laid eggs from queenless nests are differentially removed when introduced into queenright colonies (T. Wenseleers, R. L. Hammond, K. Vuerinckx, J. Billen and L. Keller, unpublished data). Since the queen did not visit the comb with introduced eggs during the larger part of the trials, queen policing was probably absent. Since only ~1.5% of the workers had active ovaries in queenright colonies, most policing was probably carried out by nonreproductive workers. ***V. rufa***. In queenright colonies, 12% (28/232) of the eggs were laid by workers (Wenseleers et al. 2005a). Out of the 28 eggs laid by workers, 11 were eaten by the queen and eight were eaten by workers. The remaining nine eggs were not eaten (Wenseleers et al. 2005a). In two out of the eight cases where a worker removed a worker-laid egg, the policing worker laid an egg soon after (table S1 in Ratnieks et al. 2006). For the remaining six cases it was not known whether the policing workers had active ovaries or not. Overall, these results show that most of the policing was by the queen and that egg eating by workers probably reflected direct reproductive competition rather than true worker policing. ***V. vulgaris***. Worker-laid eggs from queenless nests are differentially removed when introduced into queenright colonies (Foster and Ratnieks 2001a). Experiments have shown that the workers who police do not have active ovaries (T. Wenseleers and A. Tofilski, unpublished data). Since the queen did not visit the comb with introduced eggs during the larger part of the trials, queen policing was probably absent (Foster and Ratnieks 2001a). It has also been shown that worker-laid eggs have a similar viability as queen-laid ones (Helanterä et al. 2006), thereby eliminating the possibility that workers might police for hygienic reasons (Pirk et al. 2004). **Ants: *A. echinator***. Worker-laid eggs collected from queenless colonies were differentially removed by workers when introduced into queenright nests (Dijkstra and Boomsma 2004). Worker-laid eggs were removed by nonreproductive workers, since all workers in queenright nests are effectively sterile (Dijkstra et al. 2005). The presence or absence of queen policing could not be studied. ***A. smythiesi***. Reproductive workers from queenless colonies were preferentially aggressed when introduced into queenright nests (Iwanishi et al. 2003). The attacking workers were nonreproductive, since workers in queenright nests never have fully developed ovaries (Iwanishi and Ohkawara 2005) and are thought to lay only unviable, trophic eggs (Iwanishi et al. 2003). The eggs laid by workers from queenless colony fragments were seen to be eaten by other workers and by the queen. It is unknown, however, whether this egg eating was differential and whether it represented genuine queen or worker policing. ***C. floridanus***. Worker-laid eggs collected from queenless colonies were differentially removed by workers when introduced into nests from which the queen was temporarily removed (Endler et al. 2004). Worker-laid eggs were almost certainly removed by nonreproductive workers, since workers in queenright nests do not lay eggs (Endler et al. 2004). The occurrence of queen policing could not be studied due to the experimental design that was used, whereby the queen was temporarily removed. ***C. smithii***. This species has a subcaste of large workers morphologically specialized to lay unfertilized eggs (Heinze et al. 1999). Because many of these worker-laid eggs were eaten by the queen, these eggs were initially thought to have a purely trophic function (Heinze et al. 1999). However, a later genetic study (Heinze et al. 2000) showed that a significant percentage of the adult males (11%; table A2) were workers' sons, implying that many of the eggs were in fact viable. Hence, egg eating by the queen is probably best interpreted as queen policing. Workers were not seen to consume eggs laid by other workers. ***Diacamma* sp.** In this species, colonies are headed by a single queen (who is actually a mated worker or “gamergate”; Nakata and Tsuji 1996; Kikuta and Tsuji 1999). Studies on the occurrence of queen and worker policing are slightly conflicting. On the one hand, Nakata and Tsuji (1996) reported that in natural queenright colonies there is only queen policing and some worker-dominance behavior but no genuine worker policing. The fate of nine eggs laid by workers could be followed, and eight of these were eaten by the gamergate; the remaining egg was added to the egg pile. Workers in natural queenright colonies were never observed to consume any eggs (Nakata 1995). Aggressive interactions were common but mostly restricted to dominant, egg-laying workers. Using an alternative approach, whereby reproductive workers from orphaned nests were introduced into queenright colonies, Kikuta and Tsuji (1999) confirmed that the majority (89%) of the worker-laid eggs are eaten and that most of the egg policing was by the gamergate (60/89 = 67% of the eggs killed). However, the remainder of the eggs were eaten by workers. Kikuta and Tsuji (1999) show that although some of the policing workers likely had active ovaries (especially when the policing was by workers from the orphaned colony fragment), 32% of the worker policing

was by workers from the gamergate-right colony fragment, none of whom had active ovaries. Hence, the Kikuta and Tsuji (1999) study shows that there was a mixture of queen policing, worker-dominance behavior, and genuine worker policing. Finally, a third study by Kawabata and Tsuji (2005) showed that reproductive workers from orphaned nests are also attacked by nonreproductive workers when introduced into gamergate-right colonies. This implies that worker policing also occurs through aggression. In our analysis, we therefore scored worker policing as being present, although the above discussion shows that in natural colonies, this behavior may actually be rare. *D. quadricaps*. In this species, colonies are also headed by a mated worker or gamergate (Monnin and Peeters 1997). Twelve out of 18 worker-laid eggs were policed by the queen (Monnin and Peeters 1997). One gamergate-laid and one worker-laid egg were also eaten by a subordinate worker, but since this type of egg cannibalism was very rare and nondifferential, it does not represent genuine worker policing. The top-ranking unmated egg layers also show aggressive interactions toward workers of lower rank (Monnin and Ratnieks 2001). Hence, there is also worker-dominance behavior. *F. fusca*. Egg introduction experiments showed that worker-laid eggs were policed by workers but not by queens (Helanterä and Sundström 2005). *H. sublaevis*. Workers in queenright colonies lay eggs, and reproductive workers engage in dominance interactions (Bourke 1988a). The queen also aggresses reproductive workers (Bourke 1988a). Egg cannibalism by nonreproductive workers is thought to be absent. An allozyme study was unable to demonstrate any adult worker-produced males (Bourke et al. 1988). Nevertheless, this may be due to a lack of power (number of assignable males = 29; table A2). *L. acervorum*. Bourke (1991) reported that four out of 16 reproductive worker-laid eggs were eaten by queens. In addition, the queens consumed two nonviable, trophic eggs laid by workers. It was further shown that the eating of intact eggs was unique to queens and that workers never ate undamaged eggs. Although these observations of egg eating were from polygynous nests, in which the queens also consumed eggs laid by other queens (Bourke 1991), it seems that the egg eating was discriminatory and hence represents genuine queen policing. Evidence for differential eating of worker-laid eggs comes from a comparison of the percentage of male eggs and adults that are workers' sons. Based on the data in Bourke (1991) and assuming the queen-laid male and female eggs in an equal ratio, 12.4% of the male eggs can be inferred to be worker-laid. By contrast, a microsatellite study showed that only 2.8% of the adult males are workers' sons (Hammond et al. 2003). This suggests that some of the worker-laid eggs are differentially removed. On the other hand, in a genetic study, Hammond et al. (2003) found no difference between the proportion of male eggs and adults that were workers' sons. Nevertheless, as acknowledged in that study, this may have been because the eggs that were genotyped likely contained a bias of older eggs, so that the actual percentage of newly laid male eggs that were workers' sons would have been underestimated. Worker-worker aggression has also been noted in this species, although it could not be clearly connected to conflict over egg laying (Bourke 1991). *L. unifasciatus*. Queen and worker policing was absent, since worker-laid eggs from orphaned nests were not differentially removed by either the queen or the workers when introduced into queenright colonies (N. Stroeymeyt, E. Brunner, and J. Heinze, personal communication). Egg-laying workers, however, received targeted aggression from other workers who later become dominant and started laying eggs. Hence, worker-dominance behavior does occur. *P. inversa*. Worker-laid eggs collected from orphaned nests were differentially removed when introduced into queenright colonies (D'Ettore et al. 2004). *P. punctata*. In this species, workers produce diploid females from unfertilized eggs by thelytokous parthenogenesis, which results in a clonal colony structure (Heinze and Hölldobler 1995; Schilder et al. 1999a, 1999b). All individuals are morphologically identical and equally capable of laying eggs, but each colony nevertheless contains only one, or rarely two, egg layers (Schilder et al. 1999b). When additional reproductive workers from orphaned nests are added to colonies, they are attacked by other workers (Hartmann et al. 2003), and when the introduced reproductive workers are older than 2 months, they are also attacked by the resident reproductive (Hartmann et al. 2005). *P. americanus*. Workers in queenright colonies lay eggs and reproductive workers engage in dominance interactions (Heinze 1996). A microsatellite analysis showed that a large percentage, 41%, of the adult males are workers' sons (Foitzik and Herbers 2001; table A2), indicating that worker-laid eggs are not policed.

^a Pedigree relatedness estimate.

^b Worker egg eating does occur but is not differential and is usually carried out by egg-laying workers (see notes).

^c Formal relatedness estimate not available, but single mating is the rule in bumblebees, stingless bees, and polistine wasps (Peters et al. 1999; Schmid-Hempel and Schmid-Hempel 2000; Strassmann 2001). In bumblebees, a male mating plug also prevents queens in some species from mating multiply (Baer et al. 2001). In addition, putative evidence for multiple mating in a few species of stingless bees has been overturned and has since been shown to be due to the accidental inclusion of drifted workers (Paxton et al. 2001a; Palmer et al. 2002).

^d Effective number of queens and r_{diff} were calculated from the worker-worker relatedness, assuming that queens are related by 0.5.

^e Presence of queen policing unknown since the queen did not have access to the eggs that were tested for survival.

^f Reproductive workers very rare in queenright colonies; worker-laid eggs most likely eaten by nonreproductive workers.

^g Workers produce diploid female offspring through thelytokous parthenogenesis (Anderson 1963; Heinze and Hölldobler 1995; Schilder et al. 1999a, 1999b). Since the relatedness to the worker's daughters is the same as to the mother's daughters (sisters), $r_{\text{diff}} = 0$.

^h In some colonies of *A. mellifera capensis*, worker policing has been shown to be absent (Beekman et al. 2002) and policing is generally less effective than in *A. mellifera mellifera/ligustica* (Pirk et al. 2003).

ⁱ The relatedness among gynes in the fall is $r = 0.56$ (Queller et al. 2000) and the average relatedness among foundresses is $G = 0.44$ (Queller et al. 2000). From the formula $r = [3 + G \times (N_e - 1)]/4N_e$, the mean effective number of queens can be estimated at $N_e = 1.4$. The difference in relatedness between workers' sons and queen's sons $r_{\text{diff}} = r_{w-wm} - r_{w-qm} = r_{w-w}/2 - [1 + G(N_e - 1)]/4N_e = 0.072$ (Pamilo 1991).

^j Genetic analysis suggests that worker policing is present in multiple paternity colonies, but this remains to be demonstrated by direct behavioral observation (Foster and Ratnieks 2000).

^k r_{diff} is not significantly different from 0.

^l Colonies are headed by a single mated worker or “gamergate” (Monnin and Ratnieks 2001).

^m Gamergates are single mated, since after mating, the genitals of the male and part of its abdomen remain attached to the female. This acts as a mating plug and prevents further matings.

ⁿ Nests are usually polygynous, and microsatellite analysis has shown that relatedness among queens $G = 0.097$ (Kolmer et al. 2002) and that queens are multiple mated (harmonic mean paternity $k = 2.4$, K. Kellner, A. Trindl, J. Heinze, and P. D'Ettore, personal communication). In the most recent and extensive study, worker-worker relatedness has been measured at $r_{w-w} = 0.13$ (K. Kellner, A. Trindl, J. Heinze, and P. D'Ettore, personal communication). From the formula $r_{w-w} = (2 + k)/(4kN_e)$, the mean effective number of queens can be estimated at 4.1. Using these parameters, $r_{\text{diff}} = r_{w-wm} - r_{w-qm} = r_{w-w}/2 - [1 + G(N_e - 1)]/4N_e = -0.014$ (Pamilo 1991).

Table A2

Data on colony kin structure and male parentage in 90 species of eusocial Hymenoptera

Taxon and species	Colony class or study	N_e	r_{w-w}	r_{diff}	WPM	n_c	n_m	n_a	Met	SIV	References
Sweat bees:											
<i>Augochlorella striata</i> (*)	Eusocial cols.	1	.75 ^a	.125	0	12	49	28.4	D	NS	Mueller et al. 1994
<i>Lasioglossum laevissimum</i> (*)		1	.75 ^a	.125	52.0	83	108	54	A		Packer and Owen 1994
<i>Lasioglossum malachurum</i> (*)		1.1	.74	.120	4.7	7	80	63.8	M		Richards et al. 2005
<i>Lasioglossum zephyrum</i> (*)		1	.75 ^a	.125	15.0	14	176	88	A		Crozier et al. 1987; Kukuk and May 1991
Bumblebees:											
<i>Bombus hypnorum</i>	LP, study 1	1	.65	.075	0	7	162	81	M		Paxton et al. 2001b; R. J. Paxton, personal communication
<i>B. hypnorum</i>	LP, study 2	1	.75 ^a	.125	18.5	10	1,193	595.5	M		Brown et al. 2003; M. Brown, personal communication
<i>B. hypnorum</i>	LP, comb. est.	1	.71	.105	16.4	17	1,355	676.5	M	NS ^b	
<i>B. hypnorum</i>	HP	1	.48	-.010	0	1	71	35.5	M		Paxton et al. 2001b; R. J. Paxton, personal communication
<i>B. hypnorum</i>	All	1	.69	.095	15.4	28	1,426	712	M		
<i>Bombus melanopygus</i> (*)		1	.75	.125	19.1	15	1,125	562.5 ^c	P		Owen and Plowright 1980, 1982
<i>Bombus terrestris</i> (*)	Study 1	1	.75 ^a	.125	3.8 ^d	32	1,501	1,357.4	M		Lopez-Vaamonde et al. 2004
<i>B. terrestris</i> (*)	Study 2	1	.75 ^a	.125	4.8	10	395	395	M		Alaux et al. 2004
<i>B. terrestris</i> (*)	Study 3	1	.75 ^a	.125	2.3	5	1,853	926.5 ^c	P		Velthuis et al. 2002; M. J. Duchateau, personal communication
<i>B. terrestris</i> (*)	Comb. est.	1	.75 ^a	.125	3.4	47	3,749	2,678.9	M + P		
Stingless bees:											
<i>Austroplebeia australis</i>		1	.75 ^a	.125	7.0	1	94	70.5	M		Drumond et al. 2000
<i>Austroplebeia symei</i>		1	.75 ^a	.125	5.0	4	130	65	M		Palmer et al. 2002
<i>Melipona beecheii</i> (*)		1	.75 ^a	.125	0	13	108	54 ^c	M		Paxton et al. 2001a
<i>Melipona favosa</i> (*)		1	.75 ^a	.125	94.5	4	604	604	B		Sommeijer et al. 1999; Chinh et al. 2003
<i>Melipona marginata</i>		1	.75 ^a	.125	37.1	3	41	20.5 ^c	M		Tóth et al. 2002b
<i>Melipona quadrifasciata</i>		1	.75 ^a	.125	64.2	2	47	23.5 ^c	M		Tóth et al. 2002b
<i>Melipona scutellaris</i>		1	.75 ^a	.125	28.3	5	46	23 ^c	M		Tóth et al. 2002b
<i>Melipona subnitida</i> (*)	Study 1	1	.75 ^a	.125	39.3	17	300	150 ^c	A		Contel and Kerr 1976
<i>M. subnitida</i> (*)	Study 2	1	.75 ^a	.125	33.6	3	292	292	B		Koedam et al. 1999, 2005
<i>M. subnitida</i> (*)	Comb. est.	1	.75 ^a	.125	36.3	20	592	442	A + B		Tóth et al. 2002a
<i>Paratrigona subnuda</i>		1	.75 ^a	.125	64.0	6	418	209 ^c	M		Tóth et al. 2002a
<i>Plebeia droryana</i>	Study 1	1	.75 ^a	.125	0	1	19	9.5 ^c	M		Tóth et al. 2002b
<i>P. droryana</i> (**)	Study 2	1	.75 ^a	.125	16.2	14	281	140.5 ^c	A		Machado et al. 1984
<i>P. droryana</i> (**)	Comb. est.	1	.75 ^a	.125	15.2	15	300	150	M + A		
<i>Plebeia remota</i>		1	.75 ^a	.125	2.4	5	83	41.5 ^c	M		Tóth et al. 2002b
<i>Plebeia saiqui</i>		1	.75 ^a	.125	0	3	66	33 ^c	M		Tóth et al. 2002b
<i>Scaptotrigona postica</i>	Study 1	1	.72	.109	13.1	8	160	144.6	M		Paxton et al. 2003
<i>S. postica</i>	Study 2	1	.75 ^a	.125	18.5	3	62	31 ^c	M		Tóth et al. 2002b
<i>S. postica</i>	Comb. est.	1	.73	.115	14.7		222	111 ^c	M		
<i>Schwarziana quadripunctata</i>		1	.75 ^a	.125	0	16	314	157 ^c	M		Tóth et al. 2003
<i>Tetragona clavipes</i>		1	.75 ^a	.125	65.0	5	47	23.5 ^c	M		Tóth et al. 2002b
<i>Trigona carbonaria</i>		1	.75 ^a	.125	0	1	20	10	M		Green and Oldroyd 2002
<i>Trigona clypearis</i>		1	.75 ^a	.125	0	4	46	42	M		Palmer et al. 2002
<i>Trigona hockingsi</i>		1	.75 ^a	.125	0	4	79	33	M		Palmer et al. 2002
<i>Trigona mellipes</i>		1	.75 ^a	.125	0	4	42	23	M		Palmer et al. 2002
Honeybees:											
<i>Apis cerana</i>		1	.35	-.075	0	5	652	365	M		Palmer and Oldroyd 2000; Oldroyd et al. 2001

Table A2 (Continued)

Taxon and species	Colony class or study	N_e	r_{w-w}	r_{diff}	WPM	n_c	n_m	n_a	Met	SIV	References
<i>Apis dorsata</i>		1	.29	-.105	0	4	660	521	M		Palmer and Oldroyd 2000; Wattanachaiyingcharoen et al. 2002
<i>Apis florea</i>		1	.29	-.105	0	4	564	269	M		Palmer and Oldroyd 2000; Halling et al. 2001
<i>Apis mellifera</i> (*)		1	.29	-.105	.1	11	57,960	28,980	P		Visscher 1989; Estoup et al. 1994; Palmer and Oldroyd 2000
Sphecidae wasps:											
<i>Microstigmus comes</i> (*)		1	.67	.085	0	21	63	31.5	A		Ross and Matthews 1989
Polistinae wasps:											
<i>Brachygastra mellifica</i> (**)		398	.23	-.135	0	4	60	30°	M		Hastings et al. 1998
<i>Parachartergus colobopterus</i> (**)		45.8	.19	-.155	0	5	200	100°	M		Henshaw et al. 2000a
<i>Polybioides tabidus</i> (**)		34	.20	-.150	2.0	5	247	123.5°	M		Henshaw et al. 2002
<i>Polistes bellicosus</i>		1.6	.63	.065	1.0	10	46	23°	M		Arévalo et al. 1998
<i>Polistes chinensis</i> (*)		1	.75 ^a	.125	51.1	22	563	446.6	M		Tsuchida et al. 2003; Saigo and Tsuchida 2004; K. Tsuchida, personal communication
<i>Polistes dorsalis</i>		1	.75 ^a	.125	0	6	51	25.5°	M		Arévalo et al. 1998
<i>Polistes fuscatus variatus</i> (*)		1.5	.50	.020	0	4	53	26.5	A		Metcalf 1980
<i>Polistes gallicus</i>		1	.75 ^a	.125	0	5	31	15.5°	M		Strassmann et al. 2003
<i>Polistes metricus</i> (*)		1.03	.65	.076	1.3	6	152	76	A		Metcalf 1980
Vespinae wasps:											
<i>Dolichovespula arenaria</i> (*)		1	.71 ^a	.104	17.0	9	472	236	A		Foster and Ratnieks 2001b; F. L. W. Ratniek and J. J. Boomsma, personal communication
<i>Dolichovespula maculata</i>		1	.75 ^a	.125	20.9	7	202	153.3	M		Foster et al. 2001
<i>Dolichovespula media</i>		1	.71 ^a	.105	7.4	8	229	148	M		Foster et al. 2001
<i>Dolichovespula norvegica</i>		1	.71 ^a	.105	2.6	8	206	151.8	M		Foster et al. 2001
<i>Dolichovespula saxonica</i>	LP	1	.65 ^a	.075	40.0	8	205	143.2	M	$P = .004^b$	Foster and Ratnieks 2000
<i>D. saxonica</i>	HP	1	.46 ^a	-.020	0	1	30	15	M		Foster and Ratnieks 2000
<i>D. saxonica</i>	All	1	.62 ^a	.060	36.7	9	235	158.2	M		Foster and Ratnieks 2000
<i>Dolichovespula sylvestris</i>		1	.68 ^a	.090	9.8	10	2+20	153.5	M		Foster et al. 2001
<i>Vespa crabro flavofasciata</i> (*)		1	.72 ^a	.110	0	13	260	231	M		Takahashi et al. 2004b
<i>Vespa crabro gribodi</i>		1	.67 ^a	.085	0	14	282	176	M		Foster et al. 2000
<i>Vespa ducalis</i> (*)		1	.75 ^a	.125	0	20	400	257	M		Takahashi et al. 2002
<i>Vespa mandarinia</i> (*)		1	.70	.100	0	20	400	321	M		Takahashi et al. 2004a
<i>Vespula germanica</i> (**)		1	.45 ^a	-.024	0	4	255	190.1	M		Goodisman et al. 2002; T. Wenseleers, R. L. Hammond, K. Vuerinckx, J. Billen, and L. Keller, unpublished data; see “Note”
<i>Vespula maculifrons</i> (*)		1	.32	-.090	0	15	1,446	172	A		Ross 1986
<i>Vespula rufa</i>	LP	1	.61 ^a	.056	3.3	9	211	188.8	M	NS ^b	Wenseleers et al. 2005a
<i>V. rufa</i>	HP	1	.44 ^a	-.028	18.5	4	131	107.5	M		Wenseleers et al. 2005a
<i>V. rufa</i> (*)	All	1	.58 ^a	.040	11.1	13	342	296.3	M		Wenseleers et al. 2005a
<i>Vespula squamosa</i> (*)		1	.40	-.050	0	7	548	170	A		Ross 1986
<i>Vespula vulgaris</i>		1	.51	.005°	0	9	270	171	M		Foster and Ratnieks 2001a
Ants:											
<i>Acromyrmex echinator</i> (*)		1	.35	-.075	0	NA	232	116°	M		Bekkevold et al. 1999; number of males genotyped: M. B. Dijkstra, personal communication
<i>Acromyrmex octospinosus</i> (*)		1	.33	-.085	0	NA	122	66°	A		Boomsma et al. 1999; Villesen et al. 1999

Table A2 (Continued)

Taxon and species	Colony class or study	N_e	r_{w-w}	r_{diff}	WPM	n_c	n_m	n_a	Met	SIV	References
<i>Aphaenogaster carolinensis</i> (*)		1	.75 ^a	.125	0	6	42	21	A		Crozier 1974
<i>Camponotus ocreatus</i> (*)		1	.75 ^a	.125	0	2	29	14.5	M		Goodisman and Hahn 2004
<i>Colobopsis nipponicus</i> (*)		1	.75 ^a	.125	0	6	60	30	A		Hasegawa 1994
<i>Crematogaster smithi</i>		1	.75 ^a	.125	11.0	4	55	27.5	M		Heinze et al. 2000
<i>Cyphomyrmex costatus</i>		1	.75 ^a	.125	0	3	17	8.5 ^c	M		Villesen et al. 2002; Villesen and Boomsma 2003
<i>Cyphomyrmex longiscapus</i>		1	.75 ^a	.125	0	3	18	9 ^c	M		Villesen et al. 2002; Villesen and Boomsma 2003
<i>Dinoponera quadriceps</i> (*)		1	.75 ^a	.125	8.5	15	73.5	73.5	B		Monnin and Peeters 1997
<i>Dorylus molestus</i> (*)		1.4	.24 ^a	-.103	0	8	176	126	M		Kronauer et al. 2006
<i>Epimyrma ravouxi</i>		1	.75 ^a	.125	0	7	47	27.5	M		Hammond and Keller 2004
<i>Formica exsecta</i> (*)	LP, study 1	1	.75 ^a	.125	10.0	2	20	10	A		Pamilo and Rosengren 1983
<i>F. exsecta</i>	LP, study 2	1	.62	.060	0	35	409	205	M		Sundström et al. 1996; Walin et al. 1998
<i>F. exsecta</i> (**)	LP, comb. est.	1	.63	.064	.5	37	429	215	M + A	NS	
<i>F. exsecta</i>	HP	1	.46	-.020	0	3	30	15	M		Sundström et al. 1996; Walin et al. 1998
<i>F. exsecta</i> (**)	All	1	.62	.060	.4	40	459	230	M + A		
<i>Formica fusca</i> (*)		3.3	.31	-.0008 ^a	0	30	600	300 ^c	A		Helanterä and Sundström 2005; L. Sundström, personal communication
<i>Formica rufa</i> (*)	LP	1	.75	.125	5.3	51	1020	510 ^c	A		Walin et al. 1998; L. Sundström, personal communication
<i>F. rufa</i> (*)	HP	1	.50	.000	3.9	28	560	280 ^c	A		Walin et al. 1998; L. Sundström, personal communication
<i>F. rufa</i> (*)	All	1	.59	.045	4.8	79	1580	790 ^c	A		Walin et al. 1998; L. Sundström, personal communication
<i>Formica sanguinea</i> (*)		1.2	.56	.030	3.2	5	63	31.5	A		Pamilo 1982; Pamilo and Rosengren 1983
<i>Formica truncorum</i> (*)		1	.60	.050	0	30	900	450 ^c	A		Sundström 1994; L. Sundström, personal communication
<i>Harpagoxenus sublaevis</i> (*)		1	.75 ^a	.125	0	2	58	29	A		Bourke et al. 1988
<i>Iridomyrmex purpureus</i> (*)		1	.75 ^a	.125	0	2	14	7	A		Halliday 1983
<i>Lasius niger</i> (*)	LP	1	.64	.070	9.4	16	307	153.5 ^c	A		van der Have et al. 1988
<i>L. niger</i>	LP	1	.69	.095	1.9	33	157	107.5	M		Fjerdingstad et al. 2002, 2003
<i>L. niger</i> (**)	LP, comb. est.	1	.67	.087	4.4	49	464	261	M + A	NS	
<i>L. niger</i>	HP	1	.45	-.025	2.1	13	65	46.75	M		Fjerdingstad et al. 2002, 2003
<i>L. niger</i> (**)	All	1	.63	.063	3.9	62	529	307.75	M + A		
<i>Leptothorax acervorum</i>	MON	1	.75 ^a	.125	2.3	11	242	220.3	M	NS	Chan and Bourke 1994; Hammond et al. 2003
<i>L. acervorum</i>	POL	3.6	.28	.005	4.6	8	86	65.9	M		Chan and Bourke 1994; Hammond et al. 2003
<i>L. acervorum</i>	All	2.1	.52	.083	2.8	20	328	286.2	M		Chan and Bourke 1994; Hammond et al. 2003
<i>Leptothorax allardycei</i> (*)		1	.75 ^a	.125	35.8	1	114	114	B		Cole 1981
<i>Leptothorax nylanderi</i>		1	.59	.045	2.5	33	163	81.5	M		Foitzik 1998; Foitzik and Heinze 2001
<i>Leptothorax unifasciatus</i>		1	.75 ^a	.125	2.7	10	80	73.4	M		Hammond and Keller 2004
<i>Myrmica punctiventris</i>		1	.73	.115	58.0	27	242	162.7	M		Herbers and Mouser 1998
<i>Myrmica ruginodis</i> (*)		1.7	.49	.060	0	30	289	144.5 ^c	A		Walin et al. 1998; P. Seppä, personal communication
<i>Myrmica tahoensis</i>	MON	1	.75 ^a	.125	65.1	9	35	21.5	M	NS	Evans 1998; J. Evans, personal communication

Table A2 (Continued)

Taxon and species	Colony class or study	N_e	r_{w-w}	r_{diff}	WPM	n_c	n_m	n_a	Met	SIV	References
<i>M. tahoensis</i>	POL	1.7	.57	-.025	84.8	2	13	8.25	M		Evans 1998; J. Evans, personal communication
<i>M. tahoensis</i>	All	1.1	.72	.098	70.6	11	48	29.75	M		Evans 1998; J. Evans, personal communication
<i>Nothomyrmecia macrops</i>		1	.61	.055	0	6	21	18.6	M		Sanetra and Crozier 2001
<i>Pogonomyrmex rugosus</i> (*)		1	.32	-.090	0	19	198	155	M		Hammond et al. 2004; R. L. Hammond, personal communication
<i>Polyergus rufescens</i> (*)		1	.75 ^a	.125	100	4	170	127.5	M		Brunner et al. 2005
<i>Protomognathus americanus</i>		1	.68	.090	41.0	4	13	6.5 ^c	M		Foitzik and Herbers 2001
<i>Rhytidoponera chalybaea</i> (*)	Queen cols.	1	.75 ^a	.125	0	16	453	226.5 ^c	A		Ward 1983
<i>Rhytidoponera confusa</i> (*)	Queen cols.	1	.75 ^a	.125	0	16	213	106.5 ^c	A		Ward 1983
<i>Sericomyrmex amabilis</i>		1	.75 ^a	.125	0	2	19	9.5 ^c	M		Villesen et al. 2002; Villesen and Boomsma 2003
<i>Trachymyrmex cornetzi</i> sp.1		1	.75 ^a	.125	0	3	20	10 ^c	M		Villesen et al. 2002; Villesen and Boomsma 2003
<i>Trachymyrmex</i> cf. <i>zeteki</i>		1	.75 ^a	.125	0	4	30	15 ^c	M		Villesen et al. 2002; Villesen and Boomsma 2003

Note: Data on 50 species are largely based on the review of Hammond and Keller (2004); data from a further 40 species, indicated by an asterisk, are newly added. Double asterisks indicate cases where the Hammond and Keller (2004) estimate was altered due to the inclusion of additional studies or reanalysis of the original data. Colony class: LP = low paternity; HP = high paternity; MON = monogynous; POL = polygynous; cols. = colonies; comb. est. = combined estimate; N_e = effective number of queens; r_{w-w} = worker-worker relatedness; r_{diff} = difference in relatedness between workers' sons and queen's sons; WPM = percentage of worker-produced males; n_c , n_m , and n_a = number of colonies and absolute and assignable number of males assayed for male parentage; Met = method used to estimate WPM: M (microsatellites), A (allozymes), D (DNA fingerprinting), P (recessive phenotypic marker) or B (behavioral observation); SIV = significance of intraspecific variation in male parentage; NA = not available.

Notes on the procedures used to estimate relatedness and male parentage. Below we give some technical details on the procedures used to estimate relatedness and the percentage of males that are workers' sons (WPM). For species that are not explicitly mentioned, estimates were taken directly from the review of Hammond and Keller (2004) or from the original published source. A worker's son can be identified using genetic markers whenever it contains an allele that could only be inherited from the queen's mate. If a single informative locus is available, this results in a detection power of 50%. Unless otherwise noted, all estimates of WPM take into account detection power. **Sweat bees: *A. striata*.** We only included data from colonies headed by a primary queen ("eusocial colonies") where no evidence for worker reproduction was found (Mueller et al. 1994). In colonies that had lost the primary queen ("parasocial colonies") and where a mated worker had taken over reproduction, an estimated 9.3% of the males were the workers' sons (Mueller et al. 1994). Nevertheless, because such colonies experience a short period of queenlessness during which males could have been produced, data from parasocial colonies were not included. ***L. laevisissimum*.** The regression relatedness of workers to the males reared was $r_{w-m} = 0.63$ and was significantly higher than the value of 0.5 expected if all males were the queen's sons (Packer and Owen 1994). The proportion of males that were the workers' sons ψ was estimated from the equation $r_{w-m} = \psi(3/4) + (1 - \psi) \times (1/2)$, which gave $\psi = 0.52$; that is, WPM = 52%. **Bumblebees: *B. melanopygus*.** Estimate of WPM is based on the screening of 1,125 males using the Mendelianly inherited abdominal pile-coloration marker (Owen and Plowright 1980). Since the power to detect workers' sons differed among colonies, WPM was estimated using a maximum likelihood approach (Owen and Plowright 1982). ***B. terrestris*.** Estimate of WPM is based on two microsatellite studies (Lopez-Vaamonde et al. 2004; Alaux et al. 2004) and one study that used a heritable body-color marker, created by crossing two *Bombus terrestris* subspecies, *B. terrestris terrestris*, and *B. terrestris sassaricus* (Velthuis et al. 2002). All three studies used a maximum likelihood approach to estimate WPM and gave good agreement, with 2.3%–4.8% of the males being workers' sons. **Stingless bees: *M. fava*.** Behavioral studies show that 94.5% of the males are workers' sons (Sommeijer et al. 1999; Chinh et al. 2003). The colony kin structure of this species has not been studied using genetic methods. However, since single mating is the rule in stingless bees (Peters et al. 1999; Strassmann 2001), we set $r_{w-w} = 0.75$. ***M. subnitida*.** Male parentage has been investigated using allozymes (Contel and Kerr 1976) and behavioral study (Koedam et al. 1999, 2005). The estimate of WPM for the behavioral studies was taken directly from the published sources. For the allozyme study, we calculated the average WPM based on 14 colonies with parental genotypes AB \times A and 4 colonies with parental genotypes AA \times B (or BB \times A; Contel and Kerr 1976). Two colonies that had fewer than 10 males genotyped were excluded. For the four colonies where all workers were heterozygous, the parental genotypes were reconstructed in such a way that it resulted in the most conservative estimate of WPM (e.g., if nine males were A and one male B, the parental genotypes were assumed to be an AA queen mated to a B male as opposed to a BB queen mated to an A male). Out of these four colonies, three had both A and B males present, showing that worker reproduction was definitely present. For the remaining 14 colonies, WPM was estimated based on statistical deviations from the 1 : 1 ratio expected under exclusive queen production of males. ***P. droryana*.** A microsatellite study based on the analysis of 19 males from one colony was unable to detect male production by workers (Tóth et al. 2002b). However, a larger allozyme study, based on the analysis of 281 males from 14 colonies, implies that 16.2% of the males were workers' sons (Machado et al. 1984). This conclusion was based on statistically significant deviations from a 1 : 1 ratio expected under exclusive queen production of males in AB \times A crosses. Note that the putative evidence for multiple mating in a few species of stingless bees has since been overturned and has been shown to be due to the accidental inclusion of drifted workers (Paxton et al. 2001a; Palmer et al. 2002). **Honeybees: *A. mellifera*.** The estimate of WPM was based on the screening of 57,960 males using the cordovan marker (Rothenbuhler et al. 1968). This marker could positively identify 50% of the workers' sons. The study colonies all had the genotype cc(queen) \times C,C,C ... C(males). As a result, all the workers were Cc and half of their male offspring had wild-type body color (C) and were detectable. All queen's sons and half the workers' sons had cordovan body color (c). **Polistine wasps: *B. mellifica*, *P. colobopterus*, *P. tabidus*** (Epiponini). Hammond and Keller (2004, pp. 2–4) mention that “likelihood analysis showed that almost all males were queen produced, although there was a possibility of a small amount of worker reproduction. In view of this, we set the proportion of worker-produced males to 5% for each species.” Here we used a more exact approach and used the overall population-wide maximum likelihood estimates of the proportion of males that were workers' sons, which were 2% (Henshaw et al. 2000b), 0% (Hastings et al. 1998), and 0% (Henshaw et al. 2000a), respectively. Individual colony-level maximum likelihood estimates could not be used, as these were too uncertain for some colonies (Hastings et al. 1998; Henshaw et al. 2000a, 2002). In the Epiponini, worker policing remains to be directly shown, although oophagy of worker-laid eggs has been observed in *Protopolybia acutiscutis* (Naumann 1970) and *P. exigua* (Simões 1977). ***P. chinensis*.** The published value for WPM of 39.1% (Tsuchida et al. 2003) had not been corrected for the power to detect workers' sons, 79.3% (K. Tsuchida, personal communication). The corrected value for WPM is 51.1%. **Vespine wasps: *V. germanica*.** Based on the analysis of 255 males from four colonies using ~2 informative microsatellite markers, all males were found to be queen's sons (T. Wenseleers, R. L. Hammond, K. Vuerinckx, J. Billen, and L. Keller, unpublished data; $n_a = 190.1$). All four colonies had an effective paternity >2, and the harmonic mean effective paternity was 2.93. Another less extensive study ($n_a = 62.2$) also supported queen production of males for 11 out of 12 colonies (Goodisman et al. 2002). For the 12th

colony, however, data were either consistent with two matrilineal lines being present as a result of queen takeover (Wenseleers et al. 2005a) or with worker parentage of some of the males (Hammond and Keller 2004). Because of this ambiguity, the Goodisman et al. (2002) study was excluded. The worker-worker relatedness that is given is a weighted average of the relatedness in 17 colonies analyzed by Goodisman et al. (2002; $r_{w-w} = 0.46$) and in four colonies analyzed by Hammond et al. (in preparation; $r_{w-w} = 0.42$), giving $r_{w-w} = 0.45$ and $r_{diff} = -0.024$. *V. rufa*. Colonies were split into those with effective paternity ≤ 2 and > 2 , and WPM was estimated for these two colony classes based on the original microsatellite data (Wenseleers et al. 2005a). *V. vulgaris*. r_{diff} was 0.005, and not significantly different from 0 (95% confidence limits: $[-0.015, 0.025]$, Foster and Ratnieks 2001a). *Ants: D. quadricaps*. Colonies of this species are headed by a single queen (who is actually a mated worker or “gamergate”; Monnin and Peeters 1997). Behavioral study showed that the percentage of eggs laid by workers p is 14.0% (18/129; Monnin and Peeters 1997). The probability that queen-laid eggs were reared into adulthood was $s_q = 0.975$, since 39 out of 40 of her eggs were added to the egg pile without being eaten. The probability that worker-laid eggs were reared into adulthood, however, was lower, $s_w = 0.28$, since only five out of the 18 worker-laid eggs escaped being policed by the queen (see table A1 note). The five eggs, however, did develop, since they remained in the egg pile until they darkened, and darkened eggs were never observed to be eaten (Monnin and Peeters 1997). Assuming that the gamergate laid male and female eggs in approximately an equal ratio $WPM = p \times s_w / (p \times s_w + (1-p) \times (1/2) \times s_q) = 8.5\%$. This is a conservative estimate, since the gamergate’s eggs would mostly have been female and destined to be reared into more workers. Behavioral observation has shown that gamergates in this species are single mated, since after mating, the genitals of the male and part of its abdomen remain attached to the female. This acts as a mating plug and prevents further matings (Monnin and Peeters 1997). Note that worker policing via egg-eating in this species is also absent (table A1). *F. exsecta*. In an allozyme-based study, one out of 20 males collected from two colonies with informative genotypes was the son of a worker (Pamilo and Rosengren 1983). Another microsatellite-based study found no evidence for worker reproduction in this species (Sundström et al. 1996; Walin et al. 1998). Based on the two studies combined, the estimate of WPM is 0.4%. A low level of worker reproduction is also supported by a forthcoming microsatellite-based study (C. Liautard, E. Vitikainen, and L. Sundström, personal communication). *F. fusca*. Absence of worker reproduction was inferred based on allozyme genotyping of 30 monogynous colonies (L. Sundström, personal communication). Based on microsatellite analysis, however, the mean effective queen number N_e and queen-queen relatedness G across two study populations has been measured at 3.25 and 0.455 (Hannonen et al. 2004). This gives a mean $r_{w-w} = [3 + G(N_e - 1)]/4N_e = 0.31$ and $r_{diff} = r_{w-wm} - r_{w-qn} = r_{w-w}/2 - [1 + G(N_e - 1)]/4N_e = -0.0008$ (Pamilo 1991). Because r_{diff} was actually slightly > 0 in one of the study populations and slightly < 0 in the other, we considered r_{diff} to be not significantly different from 0 (Hannonen et al. 2004; Helanterä and Sundström 2005). *F. rufa*. Colonies were divided in those headed by multiple-mated and single-mated queens (Walin et al. 1998; L. Sundström, personal communication). Out of 28 colonies headed by multiple-mated queens, two had evidence for worker reproduction, and 11 out of 560 males were workers’ sons. Out of 51 colonies headed by single-mated queens, six had evidence for worker reproduction, and 27 out of 1,020 males were workers’ sons. The exact power to detect workers’ sons across all colonies was unknown, but we conservatively assumed it was 50%. This gave an estimate of WPM for the single-paternity and multiple-paternity colonies of 5.3% and 3.9% and 4.8% overall. *H. sublaevis*. For this species, we only included two colonies for which all workers were heterozygous and which were actually informative (Bourke et al. 1988). *L. niger*. WPM was estimated based on a microsatellite (Fjerdingstad et al. 2002, 2003) and an allozyme study (van der Have et al. 1988). For the latter study, van der Have et al. (1988) inferred that worker-produced male pupae were present in two out of 16 queenright colonies for which loci were informative. The maximum likelihood estimates of WPM for those two colonies were that 70% and 100% of all males were workers’ sons, giving an overall estimate of WPM = 9.44%. The effective paternity estimates were below 2 for all colonies. Estimates were combined with those of Fjerdingstad et al. (2002, 2003) using weighted averages. *L. allardycei*. Using a color dye, it was shown that the percentage of eggs laid by workers p is 21.8% (41/187; Cole 1981). Given that these eggs underwent normal development, and assuming that the queen laid male and female eggs in an equal ratio, $WPM = p/[p + (1-p) \times (1/2)] = 35.8\%$. This is a conservative estimate since the queen’s eggs probably contained a majority of female worker-produced eggs. The colony kin structure of this species has not been studied using genetic methods. However, colonies are always headed by a single queen, and queens of other leptoanthracine ants have generally been shown to be single mated (Heinze et al. 1997; table A2). Hence, we set $r_{w-w} = 0.75$ and $r_{diff} = 0.125$. *L. unifasciatus*. The percentage of worker-produced males WPM was estimated based on the genotyping of eggs rather than adult males (Hammond and Keller 2004). Nevertheless, because both worker and queen policing has been shown to be absent in this species (N. Stroeymeyt, E. Brunner, and J. Heinze, personal communication), the percentage of adult worker-produced males is probably the same. In addition, the genotyped eggs likely contained mostly older eggs. *M. tahoensis*. In Hammond and Keller (2004), the overall relatedness of the monogynous and polygynous colony classes combined was lower than that of each class individually, which is impossible. Here, the correct overall relatedness estimate is given. *R. chalybaea* and *R. confusa*. We only included data from colonies headed by a primary queen, where no evidence for worker reproduction was found (Ward 1983). In colonies that had lost the primary queen, and where one or several mated workers had taken over reproduction, a small percentage of the males were inferred to be the workers’ sons (Ward 1983). Nevertheless, because such colonies experience a short period of queenlessness during which males could have been produced, data from the latter type of colonies were not included.

^a Pedigree relatedness estimate. A value of 0.75 was used for all species where colonies were headed by a single queen and genetic evidence for multiple mating or frequent queen turnover were absent. This avoided spurious contrasts being introduced as a result of sampling error on regression relatedness estimates. However, using regression relatedness throughout led to the same overall conclusions.

^b Based on published correlations between relatedness and the percentage of males that were workers’ sons.

^c Maximum likelihood method used or number of assignable males not reported; it was conservatively assumed that there was only one informative locus and that the power to detect workers’ sons was 50%, giving $n_s = n_w/2$.

^d Some of these males were the offspring of workers that had drifted from other colonies (Lopez-Vaamonde et al. 2004).

^e r_{diff} was not significantly different from 0.

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