Monogyny and regulation of worker mating in the queenless ant *Dinoponera quadriceps*

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Abstract. The morphologically specialized queen caste has been lost in various ponerine ants, and mated workers ('gamergates') reproduce instead of queens. Unlike previous reports in the literature, we found only one gamergate in each colony of *Dinoponera quadriceps*. We documented monogyny by dissecting ovaries and spermathecae in 914 workers from 15 colonies, and by observing mating in the laboratory. In colonies without a gamergate, aggressive interactions among some of the unmated nestmates led to the behavioural differentiation of a top-ranking worker ('alpha'), which laid almost all the eggs. Only the alpha went outside the nest at night, and mated if foreign males were present ($N=11$ tests), thus becoming a gamergate. The alpha was sexually attractive even when her ovaries were not yet active. After intromission, the male remained linked to the alpha while she severed the end of his abdomen. Pieces of the male genitalia remained attached to her genital tract, and she removed them after 30 ± 18 min ($\bar{X} \pm$ SD; $N=9$). We interpret this to be a mating plug, preventing other males from fathering her offspring. None of these newly inseminated gamergates continued to go outside the nest, and, when tested, they never re-mated ($N=4$). Thus, gamergates of *D. quadriceps* probably mate only once. In queenless ant species, comparative evidence indicates that worker mating is often regulated in monogynous species, while unrestricted mating of young individuals is typical of polygynous species (oviposition is regulated subsequently). Furthermore, the occurrence of either monogyny or polygyny influences the mating strategies of males, and mating plugs have been reported only in some monogynous species.

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The absence of a morphologically specialized queen caste in some ants is now well documented, occurring in about 100 species belonging to 10 genera (all in the subfamily Ponerinae; Peeters 1993, 1997). Comparative data, particularly the existence of species with and without queens within the same genera, indicate that this is a secondary evolutionary modification. The loss of the queen caste is possible in species with little queen–worker dimorphism, because the spermatheca of these workers is functional (unlike most ants). Every worker has the ability to mate and lay diploid eggs. Only a few workers reproduce sexually in each colony, however; these

are called 'gamergates' to emphasize that they differ in several characteristics from queens. As far as we know, ponerine ants are the only group of social Hymenopterans in which morphologically specialized workers remain able to mate (in some species only). Reproductive conflict is characteristically intense in queenless ant societies because all members are totipotent. Consequently, behavioural interactions among adult workers regulate their ovarian activity and access to foreign mates. This contrasts with social insects that have morphologically specialized breeders and helpers.

In many ants, winged queens and males disperse and mate away from their natal nests (Hölldobler & Wilson 1990). In contrast, the males of queenless ants fly away and search for foreign nests, where they copulate with workers near the entrance or underground (Peeters 1991). Newly mated workers do not establish new colonies independently of nestmates; they reproduce in the natal nest and colony fission occurs (a

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mother colony becomes divided into two auton-
omous groups). Mating of workers is regulated
either by individual age or by aggressive inter-
actions among workers (reviewed by Peeters
1993). An association between dominance rela-
tionships and mating was first shown in a colony
of the monogynous *Pachycondyla sublaevis*, where
a male was attracted only to the top-ranking
worker (Ito & Higashi 1991). In contrast, all
young workers can be inseminated during the
limited period of male activity in the polygynous
Pachycondyla (=*Ophthalmopone*) *berthoudi* and
Harpegnathos saltator (Peeters & Crewe 1985;
Peeters & Hölldobler 1995). In ants with flying
queens, regulation of mating is not adaptive since
queens failing to copulate represent a waste of
reproductive investment (only mated queens can
found new colonies). In contrast, workers of
queenless ant species function as either reproduc-
tives or sterile labourers, and regulation of mating
is one of the behavioural mechanisms controlling
the number of gamergates in each colony.

   We studied the linkage between mating behav-
iour and reproductive dominance in *Dinoponera
quadriceps*. *Dinoponera* is a South American genus
of queenless ants with six species. The workers are
the largest known in ants, roughly 3 cm long
(Kempf 1971). In *D. australis*, colonies are very
small ($\bar{X} \pm$ SD$=13 \pm 6$ workers; range 7–31), and
have a single gamergate (Paiva & Brandão 1995).
In contrast, *D. quadriceps* has larger colonies
which sometimes exceed 100 workers. Araujo
et al. (1990a, b) reported the occurrence of up to
10 gamergates in some nests of *D. quadriceps* but
we demonstrate here that this species is monogy-
nous, and that only the top-ranking worker can
mate in each colony. We also present clear behav-
ioural evidence of single mating by females. These
data on mating biology give important infor-
mation about colony kin structure, which is nec-
essary to understand the patterns of reproductive
conflict in this queenless ant.

METHODS

We excavated 17 nests of *D. quadriceps* in Bahia
state (road between Sambaiba and Tobias
Barreto), Brazil, in October 1994 and January
1996 (Table I) and collected all adults and brood.
The mean colony size $\pm$ SD was 82 ± 29 workers
(range 39–141). Ants were kept in plaster nests

consisting of various chambers with a glass
roof allowing observations (total surface$=756$ or
912 cm^2 according to colony size), and connected
to a foraging arena (2068 cm^2) where live insects
were deposited daily as food. Laboratory con-
ditions were 23–27°C, 70% relative humidity and a
12:12 h light:dark cycle.

   All workers in 15 colonies were identified with
numbers glued on to the thorax, and we recorded
agonistic interactions. Each colony was observed
for 59 ± 11 h during 86 ± 8 days ($\bar{X} \pm$ SD; 885 h in
total); daily observation periods lasted a minimum
of 30 min. Two behaviours (biting of antennae,
and standing still with outstretched antennae on
either side of subordinate's head ('blocking')) are
highly characteristic of the top-ranking (alpha)
worker, and are mostly directed at the second-
ranking worker (beta) (unpublished data). We
classed alphas as virgin when they made nocturnal
visits outside the nests, and when there was no
diploid brood in the colonies. We dissected all the
ants immediately after their death or at the end of
the observations, to check ovarian activity and
spermathecal content. Dissections were done at
$\times 55$ magnification to record the occurrence of
developing yolky oocytes (including large mature
ones with a chorion) and yellow bodies (remains
of nurse cells deposited at the base of the ovarioles
whenever an egg is laid). These indicate the
capacity to lay eggs (at the present time or very
soon), and past oviposition, respectively. We
checked the spermathecae of all workers from
colonies 1–7 at $\times 400$ magnification, while in
colonies 8–17 we checked only the opaque
spermathecae at this magnification; this allowed
for the unambiguous determination of the
presence of sperm.

   We tested workers for sexual activity in the
laboratory, using foreign males seen walking or
flying in the foraging arena of their parental
colonies (this behaviour indicates that they were
looking for females). We conducted three series
of tests at night under red light (Table II). In
the first series we introduced a foreign male
into the foraging arena of a colony, when the
virgin alpha worker was outside the nest ($N=7$),
to test whether males mate with the alpha
worker. In the second series, two foreign males
were placed with a beta worker in a neutral
plastic box ($20 \times 15 \times 4$ cm), to test whether
males were attracted to beta workers ($N=2$).
After 15 min the beta was replaced by the

Table I. Adult census of 17 colonies of *Dinoponera quadriceps* immediately after field collection, and occurrence of gamergates based on the dissection of 914 workers

Colony code	Number of workers	Number of males (adults+pupae)	Number of workers dissected
1	40	1+2	39
2	86	1+6	86
3	68	0+1	38
4	98	5+5	87
5	95	3+6	0
6	141	6+8	50
7	56	0+1	40
8	129	15+1	96
9	59	3+0	59
10	105	9+1	71
11	39	0+1	39
12	76	4+5	67
13	85	6+1	51
14	112	2+0	81
15	50	0+0	40
16	86	8+1	0
17	72	9+0	70
A	13		12
B	7		7
C	17		17

All colonies examined had one gamergate, except colonies 1, 3 and 14 which had none. Colonies 1–7 and 8–17 were collected in October 1994 and January 1996, respectively. Groups A–C were created experimentally (see Methods).

Table II. Protocols and results of the laboratory mating tests

Test series	N	Experimental context	Mating within 15 min?
1	7	Virgin alpha in foraging arena	Yes (virgin alpha only)
2	2	Beta in a neutral box;	No
	2	Beta replaced by virgin alpha	Yes
3	4	Gamergate in a neutral box	No

In series 1, one male was introduced. In series 2 and 3, two males were put into a neutral box with the tested worker. In series 2, beta and virgin alpha workers were successively tested with the same males. All observed matings were confirmed by dissections of the spermatheca. Only the alphas mated (virgin alpha versus beta: Yates' corrected chi-square test: $\chi^2_1 = 11.0$, $P < 0.05$), and mated alphas did not re-mate (virgin alpha versus mated alpha: Yates' corrected chi-square test: $\chi^2_1 = 13.0$, $P < 0.01$).

virgin alpha from the same colony, to check that these males were sexually active. Finally, in the third series, we tested an already mated worker with two foreign males in a neutral box ($N=4$), to test whether a gamergate re-mates. Two of these gamergates had copulated in the laboratory, respectively 1 and 2 nights before being tested for re-mating. The other two had mated in the field at an undetermined date. We also introduced a foreign male directly into a nest entrance, when the virgin alpha was inside the nest ($N=2$), to test whether the male was accepted in the nest and mated with the alpha. Three small groups (7–17 young workers) were created from other colonies, and an alpha and a beta differentiated in each, which enabled us to increase the number of alpha workers that could be tested with males.

RESULTS

Dissections ($N=914$ individuals) revealed that all workers had a spermatheca and ovaries with 10 ovarioles. Therefore they all had the ability to reproduce sexually. However, only one worker was mated at any one time in each colony (Table I). Behavioural observations showed that this worker always had the alpha rank in a linear dominance hierarchy involving a small subset of nestmates (unpublished data). The alpha laid the majority of eggs as well as having fully developed ovaries. In some colonies lacking a gamergate (missing naturally or removed experimentally; $N=14$), the virgin alpha worker laid haploid eggs giving rise to males, and her ovarian development was similar to that of gamergates. We observed 129 ovipositions, and either virgin alpha workers or gamergates were involved in 111 of these. In six colonies, one to three workers with high ranks in the hierarchy were also able to oviposit, but their ovaries were much less developed than the alphas' and they laid only 18 of 129 eggs, the majority of which were destroyed by the alpha (12 of 18).

In colonies lacking a gamergate, the virgin alpha was frequently observed outside the nest entrance at night. She went out several times each night, and remained outside for only a few minutes. No other high-ranking workers were ever observed outside the nest. In colonies with a gamergate ($N=12$), the beta never walked outside. The virgin alpha was the only worker able to mate (Table II); the beta never mated, even when placed alone with foreign males. These same males mated afterwards with virgin alphas and therefore did not find the beta sexually attractive. Foreign males experimentally introduced inside two nests mated with the virgin alpha on both occasions, although their presence disturbed many workers. All the copulations observed in the laboratory were successful, as shown by the presence of sperm in the workers' spermathecae.

Figure 1 illustrates the stereotyped sequence of interactions during copulation. Virgin alphas did not behave in any conspicuous manner (in some species, the abdomen is raised during the release of sex pheromones, e.g. Hölldobler & Haskins 1977), but males easily discriminated them from other workers. Immediately after touching the alpha with his antennae, a male changed his behaviour radically: he followed her while
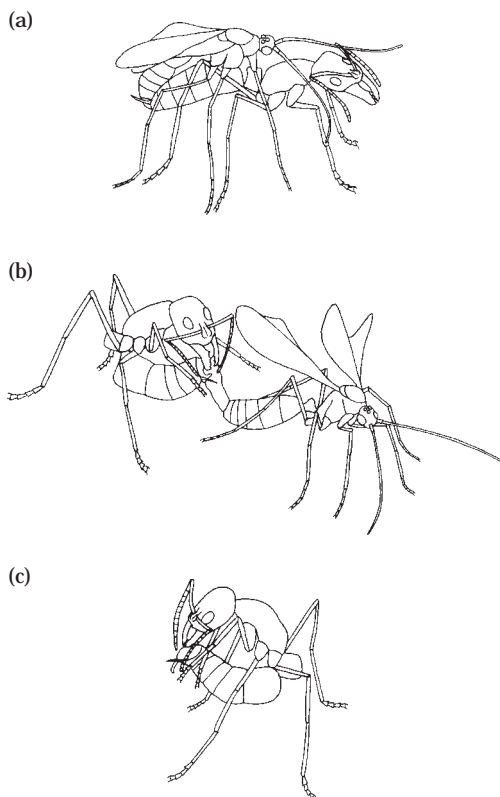
(a)

(b)

(c)

Figure 1. Behavioural sequence during mating in *D. quadriceps*. (a) The male antennates the alpha's head and antennae, and attempts to introduce his aedeagus into her genital opening. (b) The alpha bends her gaster underneath the thorax, moving the male in front of her, and cuts the end of his abdomen. (c) The alpha removes the pieces of the male's genitalia. (All sketches drawn from photographs.)

vibrating his antennae and boxing her head and antennae, and tried to mount her. When the alpha was willing, intromission occurred very soon after the first antennal contact. The alpha soon went back into the nest, dragging the male with her. Then she bent her abdomen forward, placing the male in front of her, and cut off the end of his abdomen within 1–2 min. Parts of the male's sexual apparatus (aedeagal lobes and valves, volsella and parameres) always remained attached to her genital tract, and she proceeded to remove these in 30 ± 18 min ($\bar{X} \pm$ SD; $N=9$; range 15–73). No other worker was observed either grooming her or trying to remove the male genitalia.

When two males were placed with a virgin alpha both attempted to copulate (test series 2, Table II). After one had succeeded, the second did not try to remove the genitalia of the first, and was thus unable to mate. The genitalia of the male thus served as a mating plug, effectively preventing a subsequent mating. Furthermore, once the alpha had removed the genitalia of the first male, she refused to mate again: she moved her abdomen away from the second male, extruded her sting and ran away. None of the 11 newly mated workers was again observed outside the nest, and the gamergates tested did not re-mate (test series 3), suggesting that *D. quadriceps* is monandrous.

After experimental removal of the alpha worker (N=16), she was replaced by the beta, which was generally the youngest worker of the colony (unpublished data). About 2 weeks later, the new alpha started going outside the nest to encounter foreign males. Mating was observed as early as 14 days after the removal of the previous alpha. The youngest alpha mated in the laboratory was 37 days old while the oldest was 145 days old (she was nevertheless the youngest individual in her colony). Since mating was possible only when we introduced a foreign male, these values are only indicative: mating could have occurred earlier if there had been opportunities.

In one colony without a gamergate, the virgin alpha worker was sometimes followed by one or two excited males from her own colony, while she was in the foraging arena at night. She did not mate with them, however (dissection confirmed that her spermatheca was empty). Furthermore, males emerged in several colonies without gamergates (Table I), but they never mated with the virgin alpha of their own colonies. Some of these same males and virgin alphas were later tested with foreign mates and copulated. These observations suggest that the virgin alpha can discriminate nestmate males and avoids inbreeding.

Of six newly inseminated workers dissected 1 day after they had mated in the laboratory, four had fully active ovaries with mature oocytes and yellow bodies, indicating that they were already laying unfertilized eggs before they had mated. The remaining two had few or no active ovarioles, with two and no yolky oocytes, respectively, and they lacked yellow bodies. These had thus not started to lay eggs yet, but they had been ranked alpha for only 18 and 20 days. In three colonies an old gamergate was replaced by the beta and died soon afterwards. She had regressed ovaries (few or no yolky oocytes), but her yellow bodies were conspicuous which reveals that she had previously laid many eggs. Therefore the only inseminated workers lacking active ovaries were either recently mated or old and dying. In all other cases the mated worker reproduced.

DISCUSSION

In our study only one mated individual occurred per colony of *D. quadriceps*. She had fully developed ovaries with yellow bodies, and was observed laying eggs, revealing that she was the gamergate. Only recently differentiated, or old, gamergates had undeveloped and regressed ovaries, respectively. Sterile mated workers were thus never found. The laboratory experiments (Table II) confirm that *D. quadriceps* is monogynous, because beta workers were not attractive to males. Our results contrast with those of Araujo et al. (1990a, b), who studied *D. quadriceps* from the same geographical region and concluded that they were polygynous. They further reported that various mated workers are sterile. We do not know why our results differ from those of Araujo et al.; there is no evidence for between-population polymorphism in the social system of this species (personal observation).

Our tests demonstrated that the sexual activity of workers is regulated by their rank in the hierarchy. Mating was possible only in orphaned colonies, and the virgin alpha was the only high-ranking individual to go outside the nest and copulate: betas never mated and gamergates never re-mated (Table II). Thus, the presence of a sexually attractive worker in *D. quadriceps* colonies is not seasonally regulated: the beta attains the alpha rank after the death of the previous gamergate or after colony fission, and is then able to mate. Colonies can become orphaned at any time of the year, and thus the presence of a sexually receptive worker is unpredictable. This lack of seasonality may be the rule for monogynous queenless ants, and seems to affect the temporal pattern of male production. Araujo & Jaisson (1994) have found *D. quadriceps* male adults and/or pupae throughout the year (except in January, February, May, July and December), and we have collected males in January and October (Table I). Males are thus produced for

most of the year, and can individually search for foreign nests where a virgin alpha may be present. More comparative data are needed to determine whether continuous breeding is related to the life-history characteristics of monogynous species without queens, or simply to their tropical distribution. Unlike temperate ants, male activity in tropical species may not be seasonally restricted (Bourke & Franks 1995). However, in *Pachycondyla* (=*Ophthalmopone*) *berthoudi*, a polygynous queenless ant occurring in tropical regions, males are active for only 2 months of the year (Peeters & Crewe 1986).

Sibling mating seems not to occur in *D. quadriceps*. None of the males produced in colonies without gamergates ever mated with the resident virgin alpha. Since mating takes place near the nests, the sexually receptive worker suffers little predation, and could attempt to mate over several nights. This is unlike many ant species with queens in which the queens mate during a single nuptial flight, and suffer heavy predation (Hölldobler & Wilson 1990; Bourke & Franks 1995). Since males of *D. quadriceps* are present for most of the year, an alpha worker can presumably find a mate relatively quickly.

Sexual calling by workers has been observed in several queenless ants and is always associated with the release of olfactory attractants. Unlike other species, the virgin alpha in *D. quadriceps* does not exhibit any sexual calling posture. Since she is the only worker attractive to males, however, she probably also releases sexual pheromones. The delay of 2 weeks between accession to the alpha rank and the first time this worker searches for males outside the nest may correspond to developmental changes related to the biosynthesis of these pheromones, and/or with a modification of her behaviour. Sexual attractiveness is not related to ovarian activity: four out of six newly mated workers were already laying eggs, while the other two were not. Furthermore, beta egg-layers had slightly developed ovaries but they were not attractive to males and never mated.

Worker mating in other monogynous ants without queens is also regulated through agonistic relationships among adults. An exceptional mechanism occurs in *Diacamma australe*, *Diacamma* sp. from Japan and *Diacamma* sp. from Malaysia, where all eclosing workers have tiny innervated thoracic appendages (unique to this genus). These are soon bitten off by the single gamergate who is the only worker to retain them. Such mutilation permanently prevents workers from mating: even when the gamergate is removed, egg-laying mutilated workers remain virgin. The first worker to eclose in orphaned colonies is not mutilated, however, and so can mate (Fukumoto et al. 1989; Peeters & Higashi 1989; Gronenberg & Peeters 1993; Sommer et al. 1993). In *Pachycondyla sublaevis*, a hierarchy is established, and males are attracted only to the alpha worker (one colony studied; Ito & Higashi 1991). In contrast, in *Pachycondyla* sp. from west Java, several workers mate but become inhibited after subsequent aggressive interactions (Ito 1993a). In *Streblognathus aethiopicus*, a few workers (all having active ovaries) in an orphaned colony showed sexual calling (Ware et al. 1990).

In contrast with monogynous ants, mating is generally not regulated by dominance relationships in species with multiple gamergates. In *P. berthoudi* and *Harpegnathos saltator*, all young workers are sexually attractive, and up to 66 and 70% of workers become inseminated in each colony, respectively (Peeters & Crewe 1985; Peeters & Hölldobler 1995). The operational sex ratio is thus female-biased, and males should be selected to mate more than once (Bourke & Franks 1995). Individual males of *P. berthoudi* and *H. saltator* indeed seem to mate with several workers (Peeters & Crewe 1986; J. Liebig & C. Peeters, unpublished data). Mating is also unlikely to be regulated in *P. tridentata*, where 80–100% of the workers mate (Sommer et al. 1994). All mated workers oviposit in *P. berthoudi* (Peeters & Crewe 1985), but not in *H. saltator* and *P. tridentata*, where egg production is controlled by dominance interactions, with the result that many mated workers are sterile (Sommer et al. 1994; Peeters & Hölldobler 1995). Male polygamy thus increases the probability that at least a few of a male's sexual partners will be dominant and reproduce. In *Rhytidoponera confusa* and *Amblyopone* sp., both polygynous species, only a proportion of young workers mate during the period of male activity, but this regulation is not understood (Ward 1983; Ito 1993b). In *Polistes* wasps (which lack dimorphic queens and workers), many females mate away from nests, but subsequent dominance interactions on the comb can lead to functional monogyny; males also mate multiply (see Reeve 1991).

In various insects, males prevent females from re-mating by blocking their genital tracts

(Eberhard 1996; Simmons & Siva-Jothy, in press). In ants, males have an elaborate genital structure which allows them to clasp the female's cloaca during copulation (frequently while flying), and mating plugs are expected in species with a male-biased sex ratio and single mating by males (Bourke & Franks 1995). Ant females (workers or queens) mate during just one episode at the start of their life, and mating plugs need only have a short-term blocking effect after the first mating (unlike in solitary insects). At a proximate level, the neuroendocrine effects of insemination may cause a rapid behavioural change making further copulation impossible. When only one female per colony is sexually receptive, any morphological variations in the male genitalia that increase the likelihood of 'locking' the male on to her genital tract would be selected for. The female response must then be to remove it rapidly so that eggs can be laid.

In *D. quadriceps* the genitalia of the male remain attached to the worker's abdomen and block access by potential rivals. In *Diacamma* sp. from Japan, the copulating male is dismembered by workers, until only his abdomen remains locked on to the mated worker for at least 12 h (Fukumoto et al. 1989; C. Peeters, unpublished data). In *Diacamma australe*, intact males also remained attached to the worker for over 12 h (C. Peeters, unpublished data), and such prolonged copulation seems to be another strategy to block access by rivals (Sillén-Tullberg 1981). In both *D. quadriceps* and *Diacamma*, the males outnumber sexually receptive workers, and a male has little chance of finding a second nest where he could mate again. Similarly, in army ants (e.g. *Eciton hamatum* and *E. burchelli*), the sex ratio is strongly male-biased (fission occurs and only a few permanently wingless queens are produced), and thus mating opportunities are rare. Males shed their wings prior to mating, losing the ability to find another colony. In the laboratory, males remained in copula with a queen for up to 10 h (see Gotwald 1995). In *Pogonomyrmex* ants (subfamily Formicinae), winged queens and males meet in mating aggregations away from nests; male competition for females is intense, and males tend to stay in copula as long as possible, and sometimes leave their copulatory organs on the queens, although these do not prevent re-mating (Hölldobler 1976). Honey bee, *Apis mellifera*, drones leave their detached genitalia in the queen after mating, thereby killing themselves. This does not prevent further matings by the queen, however, and apparently functions to stop sperm leaking from her genital tract (Woyciechowski et al. 1994). Thus, male 'suicide' does not always prevent further copulation of the female. An alternative type of mating plug occurs when reactive components in the seminal fluid harden upon contact with air, for example *Atrophaneura alcinous* butterflies (Matsumoto & Suzuki 1992). Such plugs have limited usefulness as mechanical obstacles, but the males stay alive and are able to re-mate.

In conclusion, the mating strategies of males differ between queenless ants that have a single or multiple gamergates. In monogynous species, mating is generally regulated by aggressive interactions, and only one worker may be receptive in orphaned nests. This female represents a safe investment for males, since she is the dominant individual and often already lays unfertilized eggs. Furthermore, the small likelihood of finding a receptive worker in another nest leads males to mate suicidally, leaving a mating plug which prevents the worker from re-mating. In contrast, unrestricted mating by young workers occurs in some polygynous species (oviposition is regulated later), and mating plugs have not been reported. Indeed, males need to mate several times to increase the probability that at least one of their partners will become dominant and reproduce.

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