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Morphology and Developmental Plasticity of Reproductive Females in *Myrmecina nipponica* (Hymenoptera: Formicidae)

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ABSTRACT We examined the morphology and developmental plasticity of alate/dealate queens and permanently wingless reproductive females (hereafter referred to as “intermorphic queens”) in *Myrmecina nipponica* Wheeler. Alate/dealate queens and intermorphic queens had nearly equal reproductive capacities. The number of ovarioles was almost identical between virgin and inseminated alate/dealate queens, but inseminated intermorphic queens had significantly more ovarioles than virgin females. To determine if intermorphic queens in *M. nipponica* are ‘ergatoid queens’ or ‘intercaste,’ we compared seven external traits of each female caste. The external traits of intermorphic queens, in particular pronotal width and Weber’s length of the mesosoma, were more similar to workers than to alate/dealate queens. Data on ovarioles suggest that the intermorphic queens have a reproductive ability similar to alate/dealate queens. The absence of a reproductive female in a colony and low temperature stimulated the production of new intermorphic queens but not new alate queens. The plasticity afforded by the production of intermorphic queens is likely an adaptation to low food resources and patchy nest sites.

KEY WORDS *Myrmecina nipponica*, caste, ergatoid, intercaste, intermorphic queen

TWO FEMALE CASTES typically exist in ants: a queen caste that produces offspring and a worker caste that defends and maintains the nest. In addition, there are reports of females that have both queen and worker characteristics in some exceptional species (Wasmann 1890, Wheeler 1917, 1937, Ezhikov 1934, Passera 1984, Loiselle and Francoeur 1988, Peeters 1991, Heinze 1998). These females are permanently wingless, and in some species females have a spermatheca and can lay fertilized eggs; whereas in other species females have no spermatheca and only lay unfertilized eggs. A variety of terms have been used for these intermediate females (Buschinger and Winter 1976, Bolton 1986, see Table 1). Hölldobler and Wilson (1990) divided these females into two categories, ergatoid queen and intercaste. The ergatoid queens have spermathecae, function as reproductives, and their morphology is ontogenetically stable. In contrast, the intercastes lack spermathecae (except in several parasitic species such as *Formicoxenus* sp. and *Harpagoxenus sublaevis* Nylander), cannot lay diploid eggs, and therefore cannot function as true reproductives.

Typical ergatoid queens have been reported from some species of relatively primitive ant groups such as ponerines, *Myrmecia* (Haskins and Haskins 1955), cerapachyines and dorylines (Wilson 1958), and also from more derived ant groups, such as *Monomorium* (Tulloch 1930, Briesse 1983, Bolton 1986, DuBois 1986) and *Aphaenogaster phalangium* Emery in New Caledonia (Wilson 1971). Typically, intercastes have been found in social parasites, such as *Harpagoxenus* (Buschinger 1978, 1981; Winter and Buschinger 1986), *Formicoxenus* (Buschinger and Winter 1976, Buschinger 1981, Francoeur et al. 1985), *Protomognathus* (Hölldobler and Wilson 1990), and in some free-living species of *Leptothorax* and *Monomorium* (Plateaux 1981, Heinze and Buschinger 1987). According to Peeters (1991), intercastes have teratological morphological characters that arise sporadically under severe environmental conditions. Both ergatoid queens and intercaste females have a coordinated expression of various queen and worker characters (Heinze 1998), and these two castes have occasionally been confused as a result.

In *Myrmecina nipponica* Wheeler, two types of reproductive females exist, alate/dealate queens and permanently wingless reproductive females. These wingless reproductive females have been defined as intercastes, because they have continuous variation of morphological traits (Ohkawara et al. 1993). However, this classification is still controversial. The wingless females (hereafter referred to as intermorphic

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Table 1. List of various differences among ergatoid queen, intermorphic queen, and intercaste (See also Peeters 1991 and Heinze 1998)

	Morphological traits	Spermatheca	Functional egg-layer	Examples
Ergatoid queen	Ontogenetically stable morphology	Yes	Yes	<i>Onychomyrmex</i> (Brown 1960) <i>Leptogenys</i> (Bolton 1975)
Intermorphic queen	Unstable changes from winged queen and workers	Yes	Yes	<i>Harpagoxenus sublaevis</i> Nyl. (Buschinger & Winter 1975) <i>Formicoxenus</i> spp. (Francoeur et al. 1985) <i>Leptothorax</i> (s. str) sp. A (Heinze & Buschinger 1987)
Intercaste	Teratological morphology	Yes/no	No	<i>Harpagoxenus americanus</i> M. R. Smith (Buschinger & Alloway 1977) <i>H. canadensis</i> M. R. Smith (Buschinger & Alloway 1978) <i>Myrmica rubra</i> L. (Brian 1955)

queens) regularly replace normal queens, and this replacement is thought to occur mainly in ergatoid queens, not in intercastes (Peeters 1991). Although Ohkawara et al. (1993) reported that intermorphic queens in *M. nipponica* occasionally coexist with alate/dealate queens in a single colony, such coexistence has been observed in only $\approx 5\%$ of all alate/dealate queen-right colonies (T.M., unpublished data). Thus, the emergence of intermorphic queens in alate/dealate queen right colonies is a rare event in this ant species, and the origin of intermorphic queens is unknown.

Alate/dealate queen right colonies and colonies that have intermorphic queens are part of the same interbreeding population, sometimes occurring adjacent to one another. Males can mate with either type of female, and therefore they maintain gene flow between the two types of colonies (L. Wang, personal communication). Both females are produced in early to mid August. Winged queens have mating flights in late August, and inseminated alate/dealate queens found new colonies in the manner of independent colony founding typical of most ants. In contrast, newly produced intermorphic queens are already wingless and therefore cannot swarm and release a sex pheromone from the pygidial gland and attract males (R. Yoshioka, personal communication). The inseminated intermorphic queens overwinter in natal colonies and disperse in the following spring to found new colonies in the manner of colony budding.

In the current study, we compared the numbers of ovarioles and oocytes among alate/dealate queens, intermorphic queens, and workers of *M. nipponica* to examine the fecundity and mating status of each female caste. Next, we examined the differences in external traits between each female caste and the development of last instar larvae. The adaptive value of each reproductive female in this ant species is discussed. In addition, we examined whether the intermorphic queens are "ergatoid queens" or "intercastes" based on the data collected.

Materials and Methods

Dissection and Measurement of Traits. In August 1993, two 10 by 10-m quadrats were chosen in a broad-

leaved deciduous forest near Tomakomai Experiment Forest of Hokkaido University (42° 50' north, 141° 40' east) in the northern part of Japan. All of the *M. nipponica* colonies were collected from these quadrats. Of 122 colonies collected, 26 were orphan colonies (without a functional reproductive female), which were eliminated from the present analysis. The remaining 96 colonies yielded a total of 1,180 workers, 48 inseminated intermorphic queens, 159 virgin intermorphic queens, 48 inseminated alate/dealate queens, and 60 virgin alate/dealate queens. All the collected individuals were dissected under a microscope to count the number of ovarioles. The number of immature oocytes was counted in inseminated females.

All of the alate/dealate queens and intermorphic queens and 200 of the workers were chosen for the following measurements to the nearest 0.01 mm under a dissecting microscope: head width, pronotal width, Weber's length of mesomoma, compound eye width, gastral width, gastral length, and body length (Ogata 1991).

Tests of Developmental Plasticity of Last Instar Larvae. In June 1994, 11 alate/dealate queen colonies and 10 intermorphic queen colonies were collected in the Tomakomai Experiment Forest. Colonies contained one inseminated female (either an alate/dealate queen or intermorphic queen), 30–40 workers, 15–20 larvae, and 0–5 eggs. Each field-collected colony was subdivided into two subcolonies of nearly equal colony size. One subcolony retained the alate/dealate queen or the intermorphic queen, but the other subcolony was orphaned. Subcolonies were reared for about 2 mo in the laboratory until all of the last instar larvae developed into new adults. After 2 mo, the number of newly eclosed workers, intermorphic queens, and alate/dealate queens was counted in each subcolony.

From June to August in 1998, 38 mature colonies were collected in the Tomakomai Experiment Forest. Of these, alate/dealate queens functioned as reproductive females in 14 colonies, and intermorphic queens functioned as reproductive females in the other 24 colonies. To test whether the production of alate/dealate queens versus intermorphic queens is temperature dependent, seven of the alate/dealate

queen colonies and 12 of the intermorphic queen colonies were reared at 5°C for 90 d from 24 December 1998, to 28 March 1999, and thereafter at 20°C until all of the last instar larvae developed into new adults for 92 d. The other seven alate/dealate queen colonies and 12 intermorphic queen colonies were reared at 20°C throughout the entire experiment. At the end of the experiment, the number of newly eclosed workers, intermorphic queens, and alate/dealate queens was counted in each colony.

Results

Number of Ovarioles and Oocytes. Alate/dealate queens had 6–12 ovarioles, with an average of 8.9 ± 0.8 ($n = 108$, mean \pm SD) and intermorphic queens had 4–13 ovarioles ($n = 207$, 9.0 ± 1.5). There was no significant difference in the number of ovarioles between alate/dealate queens and intermorphic queens (t -test; $t = 0.57$, $df = 313$, $P = 0.57$). The mean number of immature oocytes was 21.4 ± 12.9 for inseminated alate/dealate queens and 23.5 ± 12.5 for inseminated intermorphic queens. This difference was not significantly different ($t = 0.78$, $df = 94$, $P = 0.44$). In intermorphic queens, there was a significant difference in the number of ovarioles between virgin ($n = 159$) and inseminated ($n = 48$) intermorphic queens. Inseminated intermorphic queens had an average of 10.0 ± 1.6 ovarioles, which was significantly more than the 8.7 ± 1.3 ovarioles of virgin intermorphic queens ($t = 2.48$, $df = 205$, $P = 0.01$) (Fig. 1). However, there was no significant difference in ovariole number between inseminated queens and virgin queens ($d.f. = 106$, $t = 0.53$, $P = 0.60$). To examine oviposition by workers, we compared the ovarioles and oocytes of workers. Workers ($n = 1,180$) had 2–10 ovarioles, with an average of 2.2 ± 0.8 , which was significantly less than the average in intermorphic queens ($t = 55.6$, $df = 629$, $P < 0.001$) and alate/dealate queens ($t = 52.6$, $df = 802$, $P < 0.001$). The mean number of immature oocytes was 0.04 ± 0.01 , indicating that oviposition by workers was a rare event in this ant species.

Size of External Traits. Measurements of seven external traits are presented in Table 2 for the three female types. Although the compound eye widths of alate/dealate queens were significantly larger than the intermorphic queens ($t = 3.41$, $df = 88$, $P = 0.01$), the size distributions overlapped in these females and were easily distinguished from workers ($t = 34.91$, $df = 88$, $P < 0.001$ between alate/dealate queens and workers, $t = 41.59$, $df = 208$, $P < 0.001$ between intermorphic queens and workers) (Fig. 2). In contrast, the size of Weber's length of mesosoma of intermorphic queens was larger than workers ($t = 14.29$, $df = 208$, $P < 0.001$), but the distributions overlapped in these female types and were distinguishable from alate/dealate queens ($t = 33.73$, $df = 88$, $P < 0.001$ between alate/dealate queens and intermorphic queens, $t = 36.7$, $df = 88$, $P < 0.001$ between alate/dealate queens and workers) (Fig. 2). Thus, intermorphic queens could be easily distinguished their mor-

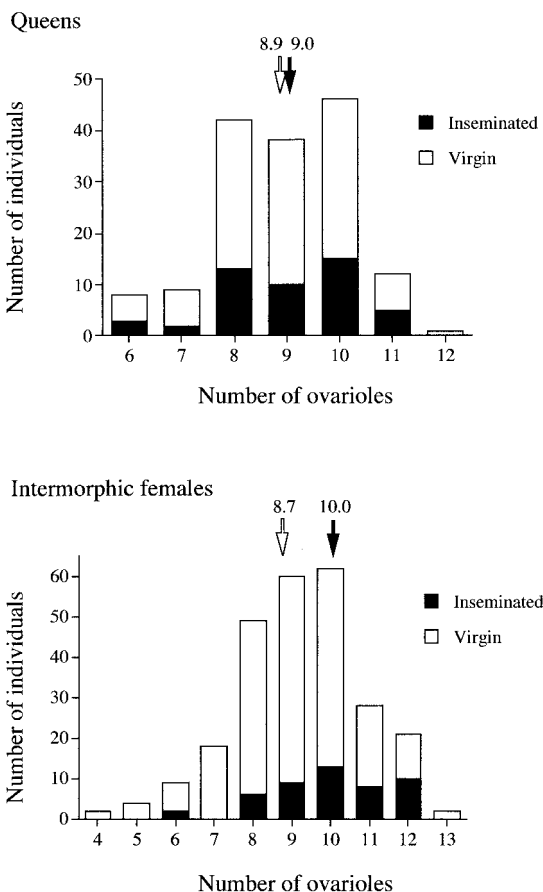


Fig. 1. Frequency distribution of the number of ovarioles in alate/dealate queens and intermorphic queens in *M. nipponica*. Black and white arrows show averages for virgin and inseminated females, respectively.

phological traits from alate/dealate queens and workers.

Effect of the Presence of Reproductive Females on Caste Production. In the 10 alate/dealate queen-right subcolonies, 14 alate queens and six males were produced in three subcolonies. In queenless subcolonies, three of the 10 and five of the 10 subcolonies produced a total of 10 alate queens and five males, respectively. Intermorphic queens were not produced in any queen-right or queenless subcolonies. All of the sub-

Table 2. Mean \pm SD (mm) of seven external traits in *Myrmecina nipponica*

<i>n</i>	Queen 108	Intermorphic queen 217	Worker 200
Head width	0.93 ± 0.02	0.88 ± 0.03	0.86 ± 0.03
Pronotal width	0.65 ± 0.02	0.59 ± 0.02	0.57 ± 0.02
Weber's length of mesosoma	1.24 ± 0.04	1.05 ± 0.04	0.99 ± 0.04
Gastral width	1.13 ± 0.03	1.04 ± 0.04	0.95 ± 0.04
Gastral length	1.25 ± 0.04	1.14 ± 0.06	1.03 ± 0.06
Ocellus width	0.17 ± 0.01	0.16 ± 0.01	0.11 ± 0.01
Body length	3.84 ± 0.12	3.50 ± 0.12	3.33 ± 0.12

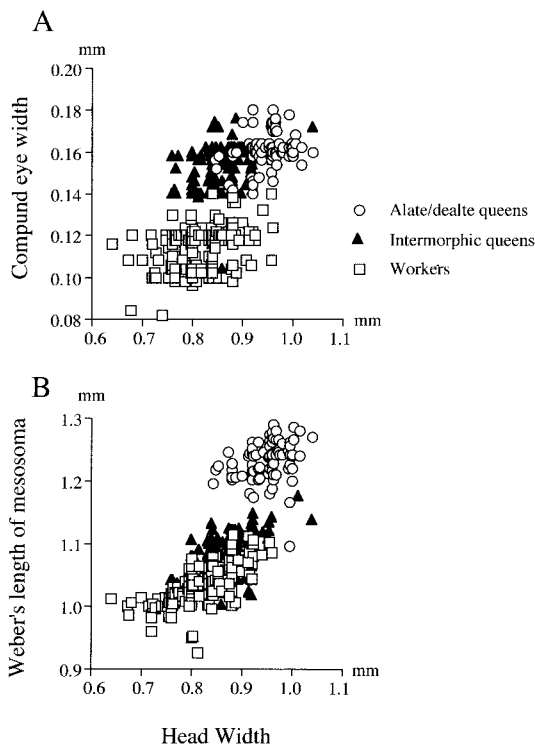


Fig. 2. Body size of alate/dealate queens (open circles), intermorphic queens (closed triangles), and workers (open squares) of *M. nipponica*.

colonies produced workers (Table 3). There was no significant difference in the production of each caste between alate/dealate queen-right and queenless subcolonies (chi-squared test; $\chi^2 = 0.306$, $df = 2$, $P = 0.858$). In the 10 intermorphic queen-right subcolonies, no intermorphic queens were produced. In contrast, nine new intermorphic queens were produced in five of the 10 intermorphic queenless subcolonies. This difference was significant ($\chi^2 = 10.87$, $df = 2$, $P = 0.004$).

Effects of Temperature on Caste Production. In alate/dealate queen colonies kept at 5°C, four alate queens and 10 intermorphic queens were produced in three of the seven colonies and one of the seven colonies, respectively (Table 4). In colonies reared at 20°C, six alate queens (two of the 12 colonies) but no intermorphic queens were produced. The difference

between two temperature conditions was statistically significant (chi-squared test; $\chi^2 = 17.05$, $df = 3$, $P = 0.007$). For intermorphic queen colonies, there was a significant difference in the production between the groups rearing at 5 and 20°C ($\chi^2 = 22.22$, $df = 2$, $P < 0.001$). A total of 49 intermorphic queens were produced in 11 of the 12 intermorphic queen colonies kept at 5°C, and 10 intermorphic queens were produced in six of 12 colonies kept at 20°C. Cold temperature conditions may lead to teratological intercastes without reproductive function. However, in this experiment all intermorphic queens had a spermatheca and were potentially functional reproductive females.

Discussion

Typically, instead of alate/dealate queens, ergatoid queens have been found in all army ants, and they are morphologically specialized, e.g., large gaster and expanded postpetiole. This indicates that the ergatoid queen is a female caste with a specialized life cycle (Peeters and Ito 2001). In contrast, intercastes are rare in natural habitats and have no reproductive function in a colony (Buschinger and Alloway 1978, Heinze 1998). Furthermore, intercastes are produced by teratogenesis of the development of thoracic structure, ocelli number, body size, and number of ovarioles (Peeters 1991). According to Heinze (1998), intermorphic queens seem to resemble intercastes. However, they are more likely ergatoid queens, because they regularly occur in a colony, have morphological features, stable anatomy of their ovaries, and specialized reproductive function (see also Table 1). In the current study we indicate that the reproductive wingless females of *M. nipponica* had most characters of intermorphic queens, such as stable morphological features (Table 2; Fig. 2) and stable anatomy of ovaries (Fig. 1) rather than intercastes. Therefore, we use the term of *intermorphic queens* as the reproductive wingless females of this ant.

The difference in ovariole number between inseminated and virgin females in each reproductive female of *M. nipponica* may be caused by the different reproductive strategies. Alate/dealate queens can fly away from their natal nests and mate randomly with males. In contrast, intermorphic queens cannot fly away from their natal nests and usually secrete sex pheromones from pygidial gland to attract males from other nests

Table 3. Total number of individuals produced in each caste for subcolonies of *M. nipponica* with or without a reproductive female

	No. colonies	Alate/dealate queens	Intermorphic queens	Workers	Males
Alate/dealate queen colonies					
With	10	14 (3)	0	104 (10)	7 (3)
Without	10	10 (3)	0	91 (10)	5 (5)
Intermorphic queen colonies					
With	10	0	0	90 (10)	5 (3)
Without	10	0	9 (5)	79 (10)	2 (2)

Number of colonies that produced a given caste is shown in parentheses.

Table 4. Total production of each caste under the conditions of 5 and 20°C in *M. nipponica*

Temp, °C	No. colonies	Alate/dealate queens	Intermorphic queens	Workers	Males
		Alate/dealate queen colonies			
5	7	4 (3)	10 (1)	143 (7)	32 (5)
20	7	6 (2)	0	141 (7)	12 (3)
		Intermorphic queen colonies			
5	12	0	49 (11)	167 (12)	29 (7)
20	12	0	13 (6)	183 (12)	18 (7)

Number of colonies that produced a given caste is shown in parentheses.

(R. Yoshioka, personal communication). Normally in ants, larger females have a greater number of ovarioles and can secrete more sex pheromone. Larger intermorphic queens could thus attract more males than smaller intermorphic queens (F. Ito, personal communication). One other possibility could also explain the difference in the ovariole number between virgin and inseminated intermorphic queens. In the primitive ant subfamily Ponerinae, some researchers reported several types of competition to determine the reproductive female (Peeters and Crewe 1984, 1985; Peeters 1987; Peeters and Higashi 1989; Ito and Higashi 1991; Fukumoto et al. 1989; Peeters and Billen 1991). For instance, in the ponerine ants *Diacamma rugosum* Le Guillou and *D. australe* F. all workers can mate and lay eggs. In fact, only individuals that have special thoracic structures called ‘gemmae’ can reproduce. All workers of these ants have gemmae until eclosing, but almost all workers have their gemmae removed by older workers, and removal of the gemmae switches an individual from a reproductive female to a worker caste (Peeters and Higashi 1989, Fukumoto et al. 1989, Peeters and Billen 1991). Although this phenomenon is unreported in higher Myrmecine ants, there may be specialized behaviors or structures to select reproductive females in intermorphic queen colonies of *M. nipponica*.

Winged queens can fly away from their natal nests and establish new nests in new habitats (Markin et al. 1971). The existence of permanently wingless queens is believed to have evolved as an adaptation for dispersal by colony fission or budding. That is, it has been suggested that these queens are able to occupy an area around their natal nests and are more adapted to limited and patchy nest habitat than alate/dealate queens (Briese 1983, Bolton 1986, Heinze and Buschinger 1989, Heinze et al. 1992, Tinaut and Heinze 1992, Bourke and Franks 1995). In *M. nipponica*, intermorphic queens are only 55% of the size of alate/dealate queens (dry weight ratio, Murakami et al. 2000). This suggests that the production of intermorphic queens may be more economical under conditions of low food resources. In fact, intermorphic queens of *M. nipponica* only exist in low-temperature zones or high altitude zones in Japan (F. Ito, personal communication; T.M., unpublished data). Therefore, intermorphic queens may represent an adaptation to low food resources and a heterogeneous environment with an uneven distribution of nest sites. In addition, because

intermorphic queens can emerge under conditions of low temperature and from late instar larvae (Tables 3 and 4), they can be facultatively generated under variable environmental conditions that impose occasional stress.

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