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Thelytokous Parthenogenesis in the Ant *Myrmecina nipponica* (Hymenoptera: Formicidae)

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Myrmecina nipponica **Wheeler is a terrestrial ant nesting chiefly in the soil in forest. It is a specialized predator of oribatid mites, but also scavenges on a broad spectrum of other arthropods. In the studied population at Cape Manazuru in central Japan, *M. nipponica* colonies are typically monogynous, and previous dissections of queens suggested that these individuals were not inseminated, thus suggesting these ants can reproduce via thelytokous parthenogenesis. To test for thelytokous parthenogenesis in *M. nipponica* the spermathecae of queens (dealate gynes) from worker-containing colonies were histologically examined in detail. All specimens examined (n = 5) had no spermatozoa in the spermatheca. In addition, a total of four colony-founding queens were reared in isolation in the laboratory to test whether non-inseminated females were capable of egg laying and to test whether female offspring emerged from this brood. In all of four culture replicates, only new workers were produced from the eggs those queens had laid and male offspring was absent. After the breeding experiment, the queens' spermathecae were histologically examined and no sperm were detected in their spermathecae. These results reveal that *M. nipponica* queens of the Manazuru population are capable of producing female offspring thelytokously. Sexual reproduction by typical gynes and also by intermorphs has been known from other local populations of *M. nipponica*; therefore, this species shows geographical polymorphism in sexuality.**

Key words: ant, *Myrmecina nipponica*, parthenogenesis, thelytoky, monogyny, forest

INTRODUCTION

Sex determination in the insect order Hymenoptera is haplo-diploid. Male individuals emerge from unfertilized haploid eggs, while female individuals emerge from fertilized diploid eggs. However, thelytoky, or thelytokous parthenogenesis, in which female offspring are produced asexually, is frequently observed in Hymenoptera (Mateo-Leach et al., 2009). In eusocial members of Hymenoptera, i.e., ants, bees, and wasps, since the first confirmation of thelytoky in the Cape honey bee (Jack, 1916), this kind of unusual reproduction has increasingly been reported, especially in ants (Rabeling and Kronauer, 2013). Presently, a total of thirteen ant species from four subfamilies have been reported to be thelytokous (Table 1). Most of them are members of the subfamily Myrmicinae. This is likely because, among 21 extant subfamilies of Formicidae, the Myrmicinae is the largest, containing nearly 6500 described species (Bolton, 2014).

Here I report that queens of another species of the Myrmicinae, *Myrmecina nipponica* Wheeler, are capable of thelytoky. This thelytoky is the only known to date from a population at Cape Manazuru in central Japan. Furthermore, the colony social structure of this species is curious, as polygyny involving mated and fertile intermorphs has been known from Hokkaido populations in Japan (Ohkawara et al., 1993; Murakami et al., 2000, 2002). The biology of such intermorphs in *Myrmecina* has been clarified for those northern populations of *M. nipponica* (Ohkawara et al., 1993; Murakami et al., 2000, 2002) and also for European *M. graminicola* (Buschinger and Schreiber, 2002; Buschinger et al., 2003; Buschinger, 2005). Intermorphs are wingless, morphologically intermediate individuals between the typical forms of queen and worker (Heinze, 1998). In the two species studied, the colony social structure is similar (Ohkawara et al., 1993; Buschinger and Schreiber, 2002): Monogynous colonies with a gynomorph (typical queen) and with an intermorph are both found in the field; but functionally polygynous colonies consist only of intermorphs. In both species, there has been no collection of colonies in which gynomorphs and intermorphs coexist and both morphs are fertile. However, colonies are strictly monogynous and intermorphs have not been collected in the Manazuru population. Therefore, data on colony structure are also given for this thelytokous population.

MATERIALS AND METHODS

Study area and ant sampling

In the present study, I report parthenogenetic reproduction for one population of *M. nipponica*, which is distributed in a small forest (c. 35 ha) at Cape Manazuru (35°08′N, 139°09′ E) in central Japan. The natural vegetation of this area is evergreen broadleaf forest dominated by *Castanopsis sieboldii* (Makino) Hatus. ex T. Yamaz. et Mashiba (Miyawaki et al., 1969). However, long-term human activities have produced a spatially patchy mosaic of mixed forests composed of natural vegetation and plantations of various crops (for the complex physiognomy, see Miyawaki et al., 1969; Masuko, 2010). In this forest, 90 nests of *M. nipponica* were excavated from

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Table 1. Species of ants (Hymenoptera: Formicidae) in which thelytoky has been confirmed.

Subfamily	Species	Reference
Cerapachyinae	*Cerapachys biroi* Forel	Tsuji and Yamauchi, 1995
Ponerinae	*Platythyrea punctata* (F. Smith)	Heinze and Hölldobler, 1995; Schilder et al., 1999
Formicinae	*Cataglyphis cursor* (Fonscolombe)	Cagniant, 1973, 1979
	Cataglyphis hispanica (Emery)	Leniaud et al., 2012
	Paratrechina longicornis (Latreille)	Pearcy et al., 2011
Myrmicinae	*Messor capitatus* (Latreille)	Grasso et al., 2000
	Monomorium triviale Wheeler	Gotoh et al., 2011
	Mycocepurus smithii (Forel)	Fernández-Marín et al., 2005; Himler et al., 2009; Rabeling et al., 2009, 2011
	Pristomyrmex punctatus F. Smith	Teranishi, 1929; Itow et al., 1984; Tsuji and Dobata, 2011
	Strumigenys hexamera (Brown)	Masuko, 2013
	Strumigenys membranifera (Emery)	Ito et al., 2010
	Vollenhovia emeryi Wheeler	Ohkawara et al., 2006; Kobayashi et al., 2008
	Wasmannia auropunctata (Roger)	Fournier et al., 2005

the surface soil at a depth of approximately 10 cm. *Myrmecina nipponica* does not construct visible nest entrances, and there was no visible clue to locate *M. nipponica* nests on the ground surface that was covered with thick litter. Therefore, the nests were encountered serendipitously while digging in the ground. Using an aspirator, colony contents were collected as completely as possible. Ants were carried alive to the laboratory, where they were censused and preserved in fixatives or cultured, depending on the study goal. When the ants were collected in the field, the collection samples were classified as either complete, nearly complete, or partial. A colony was qualified as complete when it was certain from the collecting conditions that a whole colony was collected, and it was marked as nearly complete when only a few members were supposed to be lost. On the other hand, the sample was marked as partial when it was suspected that a significant portion of a colony had been lost. This classification of samples was necessary for later use of the collection data for examination of the population trend or the social structure.

Histology

To test whether queens were mated or unmated, the queens' gasters were kept in Kahle's solution (Barbosa, 1974) and then dehydrated in a series of ethanol dilutions and propylene oxide, before they were finally embedded in Agar Low Viscosity Resin™ (Agar Scientific, England). To enhance penetration of the resin into the whole gaster, the first gastric tergite (= tergite of the fourth abdominal segment) was removed in advance. Sections of 0.5–0.8 μm thicknesses were made using a diamond knife, stained in 1% methylene blue/1% borax solution. Sections spanned the entire spermatheca. The condition of spermatheca and ovary development was examined using a compound microscope (Olympus Vanox) and morphological details were photographed with a digital camera (Shimadzu Moticam-1000 and Moticam-2500).

Laboratory breeding experiment

To investigate whether the queens actually reproduce thelytokously, simple culture experiments were conducted in the laboratory. In 2011 and 2012, four foundresses were collected from the leaf litter that was brought to the laboratory from Manazuru forest. They were cultured separately in a polystyrene box ($63 \times 50 \times 25.7$ mm). The bottom of the nest box was covered with a mixture of gypsum and activated carbon powder. A brood chamber was excavated in the center of the gypsum floor (diameter 10 mm, depth 2 mm). The ceilings of brood chamber were covered with clear glass, which permitted observations of the ants inside the nest by use of a swing-arm stereomicroscope. The ants were reared at 22 ± 2°C in a constant temperature room. As prey, various soil arthropods or small-sized mealworms were offered near the nest entrance ad libitum. Masuko (1994) showed that *M. nipponica* is a specialized predator of oribatid mites, but also scavenges on a broad spectrum of arthropods.

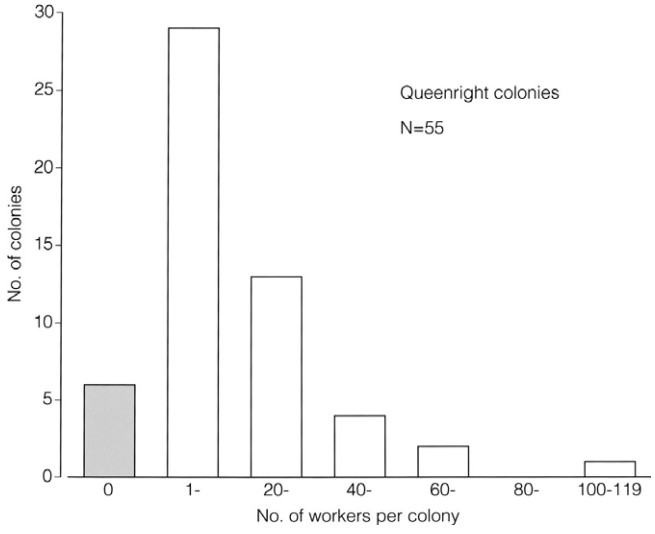

Fig. 1. Frequency distribution of colony worker population in *Myrmecina nipponica*, based on 55 complete or nearly complete collections made between 1978 and 1999. Founding colonies, which contained only the queen and her immature brood, are shaded.

RESULTS

Colony structure

During a 12-year period, from 1978 to 1990, a total of 90 *M. nipponica* nests were collected from Manazuru forest. Most of these (n = 88) were directly excavated from the soil at a depth ranging between 2 and 15 centimeters, and most nests were encountered at approximately 10 cm depth. Fifty-five nests were complete or nearly complete collections and contained a queen. All of these queenright colonies were monogynous, i.e., each containing a single dealate gyne (queen). All these queens were typical gynomorphs; no intermorphs were discovered. Figure 1 shows the frequency distribution of colony worker population based on the 55 colonies. With the exception of six founding colonies that had not yet produced workers, the mean number of workers per colony was 21 (SD = 20.5; range = 1–103; n = 49). During the same study period, however, no males were

collected in Manazuru forest, whereas a total of 53 alate gynes were found in three colonies and a total of 28 gyne pupae in three colonies. All six colonies were collected in the months of July and August in 1981 and 1982.

Dissections

The dissections of three queens in 1982 (colonies 82-109, 82-274 and 82-442) first suggested that *M. nipponica* is capable of parthenogenesis. Each dissected queen was a single dealate gyne found in separate colonies that contained adult workers and immature brood. Two of these (82-109 and 82-274) had corpora lutea (yellow bodies) in their ovarioles. The corpora lutea are remnants of follicle cells and their presence indicates that the insect had laid eggs (Torre-Bueno, 1989). Despite these facts, the presence of spermatozoa in the spermathecae could not be confirmed in two queens of 82-274 and 82-442. The dissection record on the queen of 82-109 indicates that spermatozoa were present in her spermatheca, but later reexamination of the dissected organs revealed that the spermatheca was empty (see below). Concurrently, the total number of ovarioles was examined for dissected specimens. This ranged from seven to 11 (mean = 8.9; SD = 1.3; n = 7) for gynes and from 2 to 6 (mean = 3.2; SD = 1.2; n = 30) for workers. Of 30 dissected workers (12 collected in March, 10 in May, and eight in December), none had developed ovaries.

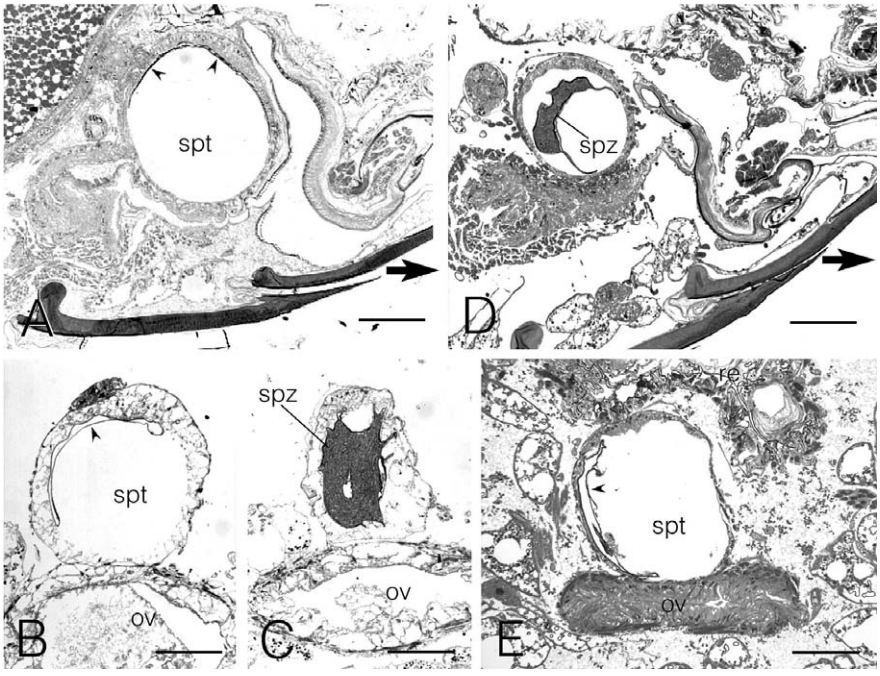

Fig. 2. Semithin sections of the spermathecae of queens of *M. nipponica* and *M. flava*. **(A)** Longitudinal section through the gaster of a queen of *M. nipponica* (colony 83–119). Lateral view. Spermatheca (spt) is swollen but empty. Arrowheads indicate a bag-like structure. Arrow points posteriorly. **(B)** Cross-section of the spermatheca previously dissected and preserved of a queen of *M. nipponica* (colony 82–109). ov, common oviduct. **(C)** Cross-section of the spermatheca previously dissected and preserved of a queen of *M. flava*. The spermatheca is filled with spermatozoa (spz). **(D)** Longitudinal section through the gaster of a queen of an *M. nipponica* colony collected from Izu-Oshima Island in 1981. Spermatheca contains spermatozoa (spz), but fixation in ethanol caused tissue shrinkage. Lateral view. Arrow points posteriorly. **(E)** Cross-section showing the empty spermatheca (spt) of a cultured queen (F2) of *M. nipponica*. re, rectum. Scale bars 50 μm.

Histology

The reproductive organs dissected out from two queens (82-109 and 82-274) were preserved in 80% ethanol. In the present study, histological sections were made from this preserved material. In addition, three queens, which had been collected in 1983 or 1984, were investigated histologically. The colonies of these queens (83-119, 84-84, and 84-119) contained workers and immature brood (eggs, larvae and/or pupae) when collected in the field. The histological examination of the queens' gasters showed that the spermathecae of these five queens were empty (Fig. 2A, B). To add a positive control of a spermatheca filled with spermatozoa, sections were made from the spermathecae of queens of a sexually reproducing *Myrmecina* species, *M. flava* Terayama (Fig. 2C). Furthermore, a complete colony of *M. nipponica* was collected at Nomashi (34°44′N, 139°21′ E) on Izu-Oshima Island in 1981. It contained a queen, 10 workers, and 11 larvae, and histological sectioning revealed that the queen was mated (Fig. 2D).

The results indicate that dealate gynes (= queens) of *M. nipponica* collected from Manazuru forest were not inseminated, that they were reproductively active, and that they were found in colonies containing other adult and immature individuals.

Laboratory breeding experiments

Given the results of the histological study, thelytokous parthenogenesis was strongly suggested for the Manazuru population of *M. nipponica*. Next, we tested in the laboratory if unmated gynes actually laid eggs that produce female offspring. Table 2 summarizes the result of the culture of four founding queens. All four queens produced adult workers in 3.5–7 months after the beginning of culture. One queen, F1, died approximately one month after the first worker had emerged. When discovered, her body had already decayed, so the spermatheca could not be examined. Two other queens, F2 and F3, were killed after the experiment for histological study by placing them in a freezer. At that time, colony of F2 contained 28 workers, 24 larvae, and 19 eggs, and that of F3 contained 12 workers, 16 larvae, and eight eggs. Their gasters were sectioned and the results showed that both queens had empty spermathecae (Fig. 2E). The culture of another queen, F4, is still ongoing for other study purposes.

Finally, a bag-like structure was observed in all empty spermathecae that were histologically examined in the present study. This structure flattens against the inner wall when the spermatheca is empty (Fig. 2A, B, E, arrowheads), but

Table 2. Dates of events in culture experiments using *M. nipponica* founding queens.

	Code of founding queen			
	F1	F2	F3	F4
Start of culture	20 June 2011	20 June 2011	2 Oct. 2011	11 May 2012
Eggs first confirmed	6 July 2011	6 July 2011	5 Oct. 2011	13 May 2012
Emergence of first worker confirmed	31 Oct. 2011	2 Oct. 2011	29 April 2012	24 Aug. 2012
Queen found dead	25 Nov. 2011			
Total no. of workers on 31 Dec. 2012 when the queen F3 was killed		9	12	2
Total no. of workers on 13 Feb. 2014 when the queen F2 was killed		28		13

comparison with the appearance of the sperm-filled spermathecae (Fig. 2C, D) suggests that it functions as an inner receptacle for sperm.

DISCUSSION

The results of the present study led to the conclusion that female offspring are produced asexually in the Manazuru population of *M. nipponica*. The first evidence for thelytoky was obtained from specimens collected in 1982, and the culture experiments using recently collected queens also showed that they can reproduce thelytokously. Thus, thelytoky is not an accidental, but rather a regular phenomenon for the Manazuru population.

Including this result, thelytoky in Formicidae has become known from 14 species. The modes of thelytoky vary among these species (Rabeling and Kronauer, 2013). In some species, e.g., *Monomorium triviale*, *Strumigenys hexamera*, and *S. membranifera*, workers lack ovaries and are completely sterile (Ito et al., 2010; Gotoh et al., 2011; Masuko, 2013); *M. nipponica* workers in contrast possess ovaries. It remains to be determined whether they produce viable offspring via thelytokous parthenogenesis or whether *M. nipponica* workers produce trophic eggs. On the other hand, thelytoky also prevails in the queenless ants, *Cerapachys biroi* and *Pristomyrmex punctatus*, which are unique among thelytokous ants, due to the absence of typically winged queens and the fact that workers (wingless females) produce themselves thelytokously (Tsuji and Yamauchi, 1995; Tsuji and Dobata, 2011).

For sexual reproduction in *M. nipponica*, reproduction both by mated gynomorphs and by mated intermorphs, which was first reported from the Hokkaido population (Ohkawara et al., 1993), has now been discovered also on Shikoku Island in western Japan (Ito, personal communication). The presence of sperm in the spermatheca of a queen from Izu-Oshima further indicates that males exist in a population only 50 km distant from the thelytokous population at Manazuru. Therefore, *M. nipponica* in Japan may consist of a mosaic of sexual and asexual populations, similar to the asexual fungus-growing ant *Mycocepurus smithii* in South and Central America (Rabeling et al., 2011) and *Platythyrea punctata* in Florida and West Indies (Schilder et al., 1999). Future studies are needed to determine the geographic distribution of thelytoky in *M. nipponica*.

Many species in which thelytoky has been reported are, empirically or potentially, either invasive ants or ants inhabiting open, disturbed places (Ito et al., 2010; Rabeling and Kronauer, 2013). Moreover, many of them are polygynous and their colonies proliferate by fission. Arguably these traits, combined with thelytoky, would increase their potential to successfully invade new habitats. In contrast, *M. nipponica* is a forest dwelling ant and strictly monogynous in Manazuru. Some other thelytokous ants are also monogynous, e.g., *Cataglyphis cursor* (Eyer et al., 2013), *C. hispanica* (Leniaud et al., 2012) and *Messor capitatus* (Arnan et al., 2012), but these species inhabit open areas. Thus, *M. nipponica* is at present unique among thelytokous ants.

In conclusion, an increasing number of cases of thelytoky have been discovered in invasive ants while only a few cases of thelytoky are known in forest ants. However, it should be noted that invasive ants are generally conspicuous and well-studied, and thus unusual reproductive systems, if present, can be more promptly detected. Therefore, additional cases of thelytoky may be discovered from forest ants in the future when more studies are extended over such hypogaeic or cryptobiotic species.

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