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Argentine Ant Affects Ant-Mimetic Arthropods: Does Argentine Ant Invasion Conserve Colouring Variation of Myrmecomorphic Jumping Spider?

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Abstract

Argentine ant invasion changed colour-polymorphic composition of ant-mimetic jumping spider *Myrmarachne* in southwestern Japan. In Argentine ant-free sites, most of *Myrmarachne* exhibited all-blackish colouration. In Argentine ant-infested sites, on the other hand, blackish morph decreased, and bicoloured (*i.e.* partly bright-coloured) morphs increased in dominance. Invasive Argentine ant drives away native blackish ants. Disappearance of blackish model ants supposedly led to malfunction of Batesian mimicry of *Myrmarachne*.

Keywords

Batesian Mimicry, Biological Invasion, *Linepithema humile*, Myrmecomorphy, *Myrmarachne*, Polymorphism

1. Introduction

It has attracted attention of biologists that many arthropods morphologically and/or behaviorally resemble ants [1]-[4]. Resemblance of non-ant arthropods to aggressive and/or unpalatable ants is called *myrmecomorphy* (ant-mimicry). Especially, spider myrmecomorphy has been described through many literatures [5]-[9]. Myrmecomorphy is considered to be an example of Batesian mimicry gaining protection from predators. Previous studies demonstrate that myrmecomorphic spiders are less likely to be preyed by predators [10]-[12]. In order to gain advantage through Batesian mimicry, ant-mimetic spiders must live in close proximity to model ants

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[13]-[15]. Disappearance of model species may consequently lead to malfunction of Batesian mimicry. Notwithstanding, few studies mentioned the effects of model ant disappearance on ant-mimics [16].

As for the causes of ant disappearance, it is notorious that invasion of exotic Argentine ant expels native ants [17]. Also in Japan, most of indigenous ants were driven away by Argentine ant [18] [19]. Ant is one of the most abundant organism in terrestrial ecosystem, and has various (hostile and symbiotic) relationships with other animals and plants [20]-[22]. Native ants' disappearance caused by Argentine ant, therefore, variously and widely affects other animals and plants [23]. In Japan, previous studies showed that Argentine ant had various relationships with non-ant animals [24]-[27]. However, little has been studied about indirect effects of Argentine ant, via the disappearance of native ants, on some predators, competitors, symbionts and *myrmecomorphs*. So, in present paper, we are concerned with the response of ant-mimicking jumping spider *Myrmarachne* against Argentine ant invasion.

2. Materials and Methods

2.1. Study Taxa

Myrmarachne (Araneae: Salticidae) is a speciose genus of jumping spiders and the most striking examples of myrmecomorphy. Spiders of *Myrmarachne* morphologically and behaviorally mimic ants. Some *Myrmarachne* species exhibit variation of dermal colouration within species (colour-polymorphic mimicry), possibly each mimicking different ant species [6] [28]-[35]. Moreover, some species of *Myrmarachne* show transformational mimicry, mimicking different ant species at each instar [6] [32]. In addition, many species of *Myrmarachne* are sexually dimorphic [36]. Such colour-polymorphism, transformational mimicry and sexual dimorphism all contribute to the difficulty of visual identification of *Myrmarachne* spp. on site. Furthermore, since the same-coloured "morphs" of whatever species supposedly mimic the same ant species, such "morphs", not "species", should similarly respond to myrmecofaunal change. In this study, from the viewpoint of ant-resemblance, we tentatively grouped *Myrmarachne* spp. by colour-morphs, regardless of sex and instar, as mentioned below.

Blackish morph. *Colouration*: All black, or black with blackish brown posterior cephalothorax and/or anterior abdomen (**Figure 1(a)** and **Figure 1(b)**). Posterior abdomen of some individuals grayish; *Species*: Typical types of *M. japonica* (Karsch) and *M. inermichelis* Bösenberg & Strand, and blackish type of *M. elongata* Szombathy; *Possible model ants in lowland of Hiroshima Prefecture*: *Camponotus japonicus* Mayr (*M. japonica* is especially mimics this ant), *Formica japonica* Motschoulsky, *Tetramorium tsushimae* Emery, *Nylanderia amia* (Forel), and *Ochetellus glaber* (Mayr). The latter three species are candidate models of juvenile mimics. Besides, *Pachycondyla chinensis* (Emery) morphologically resembles *M. inermichelis*, but it is rarely seen on plants.

Bicoloured morphs. Partially bright coloured. Including three subtypes as mentioned below.

Front-brightened morph. *Colouration*: Cephalothorax and anterior abdomen bright, posterior abdomen blackish (**Figure 1(c)**). Bright colour varied among individuals: light brown (leather brown), strong brown (raw

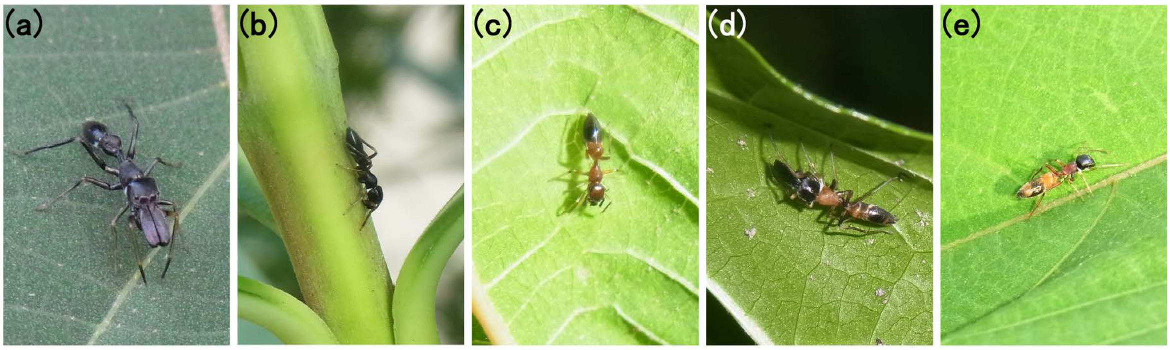

Figure 1. Typical colour-morphs of genus *Myrmarachne* in lowland of southwestern Japan. (a) Blackish morph (typical type of *M. inermichelis*, male); (b) Blackish morph (typical type of *M. inermichelis*, female); (c) Front-brightened morph (supposedly reddish type of *M. inermichelis*, juvenile); (d) Mid-brightened morph (typical type of *M. elongata*, male); (e) Mid-brightened morph (typical type of *M. elongata*, female).

sienna), strong yellowish brown (khaki), moderate yellow, and so on. Bright parts do not always exhibit the same colour; *Species*: Reddish type of juvenile *M. inermichelis* [34]; *Possible model ants*: *Monomorium intrudens* F. Smith, *Tetramorium bicaritatum* (Nylander), and some of *Camponotus vitiosus* F. Smith. Although typical *C. vitiosus* exhibit mid-brightened colouration as mentioned below, some of *C. vitiosus* exhibit front-brightened colouration.

Mid-brightened morph. *Colouration*: Anterior cephalothorax and posterior abdomen blackish, posterior cephalothorax and/or anterior abdomen bright-coloured (**Figure 1(d)** and **Figure 1(e)**). Bright colour varied among individuals: light brown (leather brown), strong brown (raw sienna), strong yellowish brown (khaki), deep yellow (yellow ocher), moderate yellow, moderate red (brick red), deep red (ruby), brownish orange, and so on. Posterior cephalothorax and anterior abdomen do not always exhibit the same colour; *Species*: Typical type of *M. elongata*; *Possible model ants*: Typical *C. vitiosus* and *Pheidole noda* F. Smith. Although *Polyrhachis lamellidens* F. Smith and *Camponotus hemichlaena* Yasumatsu & Brown also exhibit mid-brightened colouration, these ants are rarely seen in lowland urban/residential area of Hiroshima.

Rear-brightened morph. *Colouration and species*: Some of this morph have blackish cephalothorax and bright abdomen, others have bright abdomen with blackish belt at middle abdomen. The former is bright type of *M. japonica*, the latter may be *M. elongata* with blackish posterior cephalothorax and bright-coloured posterior abdomen. Bright colour varied among individuals: strong yellowish brown (khaki), moderate yellowish brown (buff), deep yellow (yellow ocher), and so on; *Model ant*: unknown.

2.2. Study Sites and Methods

Spider survey was conducted in lowland suburbs of Hiroshima and Fukuoka Prefectures in 2012-2013 (**Figure 2**): urban greenery space, roadside, vacant lot, and so on. Argentine ant-infested sites were similar to free sites in their landscape. As for ant fauna, however, indigenous ants almost disappeared from Argentine ant-infested sites. Spiders of genus *Myrmarachne* were visually searched on herb, shrub, tree trunk, fence, and so on. Each *Myrmarachne* spider seen was recorded on site, and photographed as much as possible. In 2012 survey, *Myrmarachne* were searched in various places in order to confirm whether Argentine ant invasion affected colour-polymorphic composition of *Myrmarachne* (**Figure 2**): five Argentine ant-free sites in Fukuoka Prefecture (August); eight free sites in Hiroshima Prefecture (August-October); and five Argentine ant-infested sites, sepa-

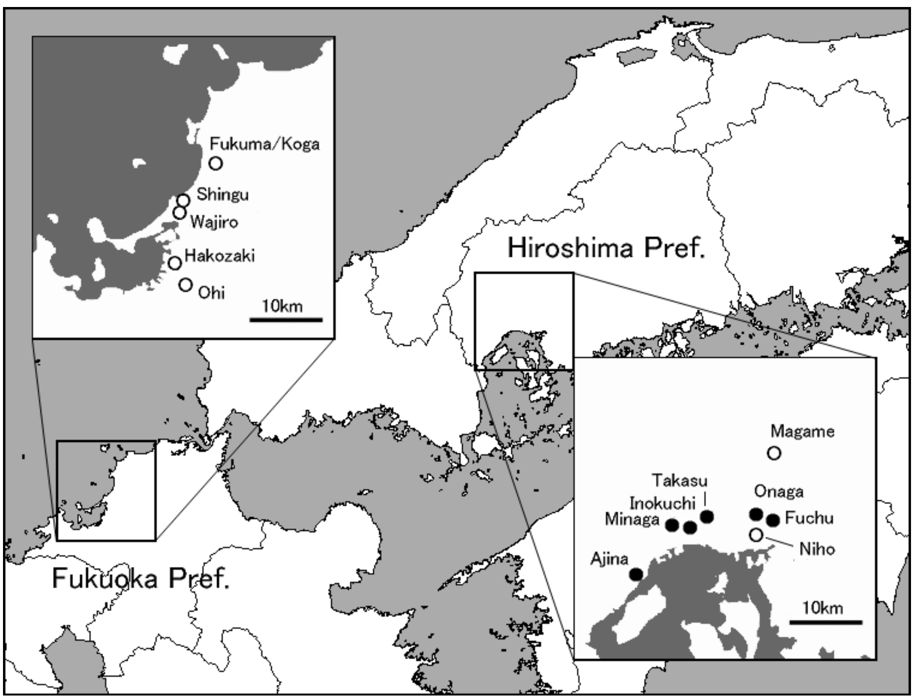

Figure 2. Location of study sites in 2012 survey. Each open circle shows Argentine ant-free site. Every closed circle includes both Argentine ant-free and infested sites.

rately located each other, in Hiroshima Prefecture (August-October). These infested sites were already reported [37] [38]. In 2013 survey, colour-polymorphic composition was seasonally surveyed in the four successive sites of Hiroshima Prefecture: Ajina, Minaga, Inokuchi and Onaga. In November 2013, however, we could not survey in Ajina for lack of time.

3. Results

3.1. Colour-Polymorphic Composition: 2012 Survey

In the most of Argentine ant-free sites, colour-polymorphic composition showed common pattern irrespective of locality (Table 1). That is, blackish morph overwhelmingly dominated (median 85.0%), and bicoloured morphs generally occupied less than a fifth (median 15.0%). Among the bicoloured morphs in Argentine ant-free sites,

Table 1. Comparison of polymorphic composition of *Myrmarachne* spiders Across Argentine ant infestation. Figures in parenthesis show the percentages.

	Blackish		Bicoloured						Total	
			Front		Mid		Rear			
Argentine ant-free										
Fukuoka Prefecture										
Ohi	4	(66.7)			2	(33.3)			6	(100.0)
Hakozaki	7	(87.5)			1	(12.5)			8	(100.0)
Wajiro	6	(37.5)			9	(56.3)	1	(6.3)	16	(100.0)
Shingu	6	(100.0)							6	(100.0)
Fukuma/Koga	7	(77.8)			2	(22.2)			9	(100.0)
Hiroshima Prefecture										
Ajina	17	(85.0)			3	(15.0)			20	(100.0)
Minaga	13	(72.2)			4	(22.2)	1	(5.6)	18	(100.0)
Inokuchi	29	(82.9)	1	(2.9)	4	(11.4)	1	(2.9)	35	(100.0)
Takasu	18	(100.0)							18	(100.0)
Magame	10	(90.9)			1	(9.1)			11	(100.0)
Onaga	17	(68.0)			7	(28.0)	1	(4.0)	25	(100.0)
Niho	17	(89.5)			2	(10.5)			19	(100.0)
Fuchu	12	(92.3)			1	(7.7)			13	(100.0)
Argentine ant-infested										
Hiroshima Prefecture										
Ajina	10	(43.5)	2	(8.7)	10	(43.5)	1	(4.3)	23	(100.0)
Minaga	8	(44.4)	1	(5.6)	9	(50.0)			18	(100.0)
Inokuchi	6	(26.1)			16	(69.6)	1	(4.3)	23	(100.0)
Takasu	10	(55.6)	2	(11.1)	6	(33.3)			18	(100.0)
Onaga	10	(55.6)	2	(11.1)	6	(33.3)			18	(100.0)
Fuchu	6	(46.2)	1	(7.7)	4	(30.8)	2	(15.4)	13	(100.0)

mid-brightened morph was almost ubiquitous, but generally less than a fifth yet (median 12.5%). In Argentine ant-infested sites, on the other hand, blackish morph decreased in dominance than in free sites (median, from 85.0% to 45.3%), and bicoloured morphs increased to the majority in return (median, from 15.0% to 54.8%); especially mid-brightened morph conspicuously increased than in free sites (median, from 12.5% to 38.4%). Besides, front-brightened morph was almost limited in Argentine ant-infested sites. Mann-Whitney U-test showed that morphic dominance were significantly different between Argentine ant-free and infested sites (blackish morph, $p = 0.0029$; front-brightened morph, $p = 0.0050$; mid-brightened morph, $p = 0.0050$), excluding rear-brightened morph ($p = 0.4048$). Across the prefectures in Argentine ant-free sites, on the other hand, there were no differences of colour-polymorphic dominance (blackish morph, $p = 0.3414$; front-brightened morph, $p = 0.7144$; mid-brightened morph, $p = 0.2416$; rear-brightened morph, $p = 0.7697$; Mann-Whitney U-test).

3.2. Seasonal Change: 2012-2013 Survey

Morphic composition in 2013 survey generally showed the same pattern as in 2012 (**Table 2**). Wilcoxon signed-ranks tests, by matching of simultaneous data between Argentine ant-free and infested sites (Ajina, Minaga, Inokuchi and Onaga), also showed that morphic dominance (%) were significantly different between free and infested sites (blackish morph, $p = 0.0003$; front-brightened morph, $p = 0.0455$; mid-brightened morph, $p = 0.0005$), excluding rear-brightened morph ($p = 0.4497$). However, there were common patterns in seasonal fluctuation of colour-polymorphic composition to Argentine ant-free and infested sites. That is, bicoloured morphs increased in summer regardless of Argentine ant infestation; blackish morph accordingly decreased in dominance then. In Argentine ant-free sites after summer, blackish morph always recovered and gained the overwhelming majority (median 85.0%), but bicoloured morphs almost disappeared. In Argentine ant-infested sites, on the contrary, bicoloured morphs had always stated on, in spite of decrease after summer; and blackish morph repeatedly lost the majority (median 50.0%), despite of dominating just before summer.

Table 2. Comparison of seasonal change of polymorphic composition of Myrmarachne spiders across Argentine ant infestation. Figures in parenthesis show the percentages.

		Argentine ant-free					Argentine ant-infested				
		Blackish	Bicoloured			Total	Blackish	Bicoloured			Total
			Front	Mid	Rear			Front	Mid	Rear	
Ajina	Aug-Oct 2012	17 (85.0)		3 (15.0)		20 (100.0)	10 (43.5)	2 (8.7)	10 (43.5)	1 (4.3)	23 (100.0)
	May/Jun 2013	6 (85.7)			1 (14.3)	7 (100.0)	3 (50.0)		2 (33.3)	1 (16.7)	6 (100.0)
	Aug 2013	10 (83.3)	1 (8.3)	1 (8.3)		12 (100.0)	3 (27.3)	2 (18.2)	6 (54.5)		11 (100.0)
Minaga	Aug/Sep 2012	13 (72.2)		4 (22.2)	1 (5.6)	18 (100.0)	8 (44.4)	1 (5.6)	9 (50.0)		18 (100.0)
	May 2013	15 (100.0)				15 (100.0)	8 (88.9)			1 (11.1)	9 (100.0)
	Aug 2013	13 (72.2)		5 (27.8)		18 (100.0)	2 (22.2)		7 (77.8)		9 (100.0)
	Nov 2013	9 (100.0)				9 (100.0)	4 (57.1)	2 (28.6)	1 (14.3)		7 (100.0)
Inokuchi	Aug-Oct 2012	29 (82.9)	1 (2.9)	4 (11.4)	1 (2.9)	35 (100.0)	6 (26.1)		16 (69.6)	1 (4.3)	23 (100.0)
	May 2013	9 (100.0)				9 (100.0)	10 (76.9)	1 (7.7)	2 (15.4)		13 (100.0)
	Jul 2013	9 (75.0)		3 (25.0)		12 (100.0)	3 (30.0)	1 (10.0)	6 (60.0)		10 (100.0)
	Nov 2013	6 (85.7)		1 (14.3)		7 (100.0)	4 (50.0)	2 (25.0)	2 (25.0)		8 (100.0)
Onaga	Aug 2012	17 (68.0)		7 (28.0)	1 (4.0)	25 (100.0)	10 (55.6)	2 (11.1)	6 (33.3)		18 (100.0)
	May 2013	7 (100.0)				7 (100.0)	5 (83.3)		1 (16.7)		6 (100.0)
	Jul 2013	9 (81.8)		2 (18.2)		11 (100.0)	3 (37.5)		4 (50.0)	1 (12.5)	8 (100.0)
	Nov 2013	4 (100.0)				4 (100.0)	2 (50.0)		2 (50.0)		4 (100.0)

4. Discussion

In lowland urban/residential area of Hiroshima Prefecture, blackish ants (e.g. *F. japonica* and *C. japonicus*) are more prevailing in dominance than bicoloured ant *C. vitiosus* [18] [19]. It may be the reason why blackish morph gains the majority in Argentine ant-free sites. However, such oligopoly of blackish morph was weakened, *i.e.* bicoloured morphs increased, in summer. What caused summer increase and afterward decrease of bicoloured morphs in dominance? Those that *M. elongata* (*i.e.* the majority of bicoloured morphs) hatched earlier and *M. inermichelis* (the majority of blackish morph) did later can account for this pattern. Instead of later hatching of *M. inermichelis*, after-summer increase of predator of bicoloured *Myrmarachne* may lead similar pattern. Whatever led such seasonal fluctuation, this pattern was common to Argentine ant-infested and free sites. That is, Argentine ant invasion did not affect the occurrence of such fluctuation itself. Here, we would like to emphasize the difference of the polymorphic dominance between infested and free sites. What kept the dominance of bicoloured morphs higher in infested sites than free sites? In other words, what prevented blackish morph to gain the majority in Argentine ant-infested sites after summer?

Precondition for Batesian mimicry is that mimic lives in close proximity to model. Disappearance of model species should consequently cause malfunction of Batesian mimicry. Piñol *et al.* (2012) showed that long-term exclusion of ant led decrease of ant-mimetic mirid bug [16]. Disappearance of indigenous ants caused by Argentine ant may similarly work on myrmecomorphic *Myrmarachne* spiders. Correspondingly, ant-mimetic mirid bugs decreased in Argentine ant-infested sites in Japan (Touyama & Ito, in preparation).

Blackish morph of Japanese *Myrmarachne*, dominating in Argentine ant-free sites, mainly resembles native ants *F. japonica* and *C. japonicus*. Such ant species disappear from Argentine ant-infested sites, in spite of ubiquity and dominating in Argentine ant-free sites [18] [19]. Disappearance of model ants (*F. japonica* and *C. japonicus*) supposedly led to decrease of their mimics, *i.e.* blackish morph of *Myrmarachne* spiders, in infested sites via invalidation of Batesian mimicry. Bicoloured morphs of *Myrmarachne* spiders, on the other hand, resemble some bicoloured ant species. Front-brightened morph resembles *C. vitiosus* (with non-typical colouration), *T. bicarinatum*, and *M. intrudens* (candidate model of juvenile mimics). Mid-brightened morph may mimic *C. vitiosus* (with typical colouration) and/or *P. noda* in urban/residential area of lowland Hiroshima. Among such potential model ants, *C. vitiosus* is ubiquitous through urban/residential area of lowland Hiroshima, and relatively resistant against Argentine ant invasion [18] [19]. The existence of bicoloured *C. vitiosus* in infested sites possibly provides some advantage for bicoloured morphs of *Myrmarachne*.

It seems plausible to suppose that Argentine ant-inducing myrmecofaunal change caused the change of colour-polymorphic composition of ant-mimetic *Myrmarachne*. As for ant-mimicking bug (Hemiptera: Alydidae), Oliveira (1985) pointed out that colour-polymorphic composition was changed with myrmecofaunal composition [39]. Regrettably, present study was not concerned with quantitative comparison of *Myrmarachne* across Argentine ant infestation. But our previous study suggested that there were no difference of density and incidence of total *Myrmarachne* on shrub *Mallotus japonicus* between Argentine ant-free and infested sites (Touyama & Ito, in preparation).

Unidentified predators of *Myrmarachne* (*i.e.* operator of ant-mimicry) should suffer little effect by Argentine ant infestation, if the change of colour-polymorphic composition was due to the invalidation of Batesian mimicry. We did not regrettably come across any scenes of *Myrmarachne* preyed by whatever predator throughout the present study. We have repeatedly, but not quantitatively, observed some predatory arthropods in Argentine ant-infested sites as well as free sites (Touyama unpublished data, 2012-2013): crab spider (Araneae: Thomisidae), lynx spider (Araneae: Oxyopidae), jumping spider, and mantises (Mantodea: Mantidae). Among them, mantis [11], Salticidae and Philodromidae spiders [10] were suggested to be important predators of non-mimetic spiders, and be deceived by Batesian mimicry. We have not seen Philodromid spider during present study, but repeatedly observed crab spiders (Araneae: Thomisidae) which have similar life form (sit-and-wait predator) as Philodromidae. But we doubt whether crab spiders is deceived by myrmecomorphy, based on the following two circumstantial evidences. First, McIver (1987) pointed out that crab spider could properly discriminate between model ants and mimicking mirid bug [40]. Secondly, some crab spiders preferingly predate, rather than evade, ants [41]: we have observed some crab spider preying native black ant *F. japonica* in three cases (Ajina in 8 October 2012 and 25 May 2013; Inokuchi in 16 May 2013: all in free sites). Incidentally, we have come across no scenes of Argentine ant preyed by whatever predator. Besides the Batesian mimicry, there is a little ironical hypothesis that *myrmecophagic* Thomicid spider (and/or other predator) may become prey on blackish morph of

Myrmarachne, instead of the disappeared black ants. But we have no data concerning this story. This problem needs further study.

In examination of ecological problems caused by Argentine ant, we are likely to be attracted to direct charge and/or harassment, rather than indirect effects via native ant disappearance, by Argentine ant. Although it may be less attractive, indirect effects of Argentine ants invasion are ecologically worth consideration. Taking the indirect effects into account, Argentine ant may harmfully affect more organism than our awareness. It needs further investigations for right understanding of the effects of Argentine ant invasion.

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