

## Male Ant-mimicking Salticid Spiders Discriminate Between Retreat Silks of Sympatric Females: Implications for Pre-mating Reproductive Isolation

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**Abstract** Mate recognition is essential to reproductive success especially under sympatry where encounters between the sexes of different species is likely. We examined the response of male ant-mimicking salticid spiders of the genus *Myrmarachne* and of five different color forms to retreat and dragline silks of sympatric females of six color forms to determine whether silk-based cues could be used as pre-mating isolation mechanisms and aid species determination. We found evidence for polymorphism within one species *Myrmarachne plataleoides*, a well-known mimic of the weaver ant *Oecophylla smaragdina*. Male color morphs of this species showed cross-interest in female silks of other color morphs of this species, but also exhibited greatest preference for the silk of their own color morph, providing evidence for assortative mating and the possibility of silk-based cues as mechanisms of incipient speciation via disruptive selection. Males of two other color forms exhibited unambiguous preference for the silk of their own color forms, suggesting that these two forms are distinct species. The silk-based findings were confirmed by no-choice mating experiments and opportunistic observations of natural matings.

**Keywords** Assortative mating · mimicry · polymorphism · reproductive isolation · speciation

Mechanisms involved in the reproductive isolation of forms occurring in sympatry are important to investigate because they provide insight into the process of sympatric speciation (Coyne and Orr 2004). Theoretical and empirical studies have recently focused on pre-mating isolation mechanisms that are relevant to the process of speciation in sympatry (Dieckmann and Doebeli 1999; van Doorn and Weissing 2001; Kirkpatrick and Ravigné 2002; Arnegard and Kondrashov 2004; Coyne and

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Orr 2004; Jiggins et al. 2005). Sympatric speciation is believed to be easier and faster when selection by local ecological conditions contributes to reproductive isolation and when mate choice and mating occurs in the environment that forms the selective habitat for the ecological trait (Kirkpatrick and Ravid 2002). The ecology of a mimetic species is linked with that of its syntopic model, and color mimicry of different sympatric models can lead to disruptive selection within a population resulting in color polymorphism and subsequently to reproductive isolation of the differently colored species (Mallet et al. 1998; Gray and McKinnon 2007). Therefore, the presence of differently colored models in sympatry can provide different targets for ecological selection of differently colored mimics and can thus set up conditions suitable for assortment by color (Jiggins et al. 2005). Although color may be used as a mating cue and assist in pre-mating isolation in such cases, chemical cues can also be important at short ranges (Vane-Wright and Boppré 1993; Jiggins et al. 2004).

We investigated pre-mating reproductive isolation mechanisms between various sympatric color forms in an ant-mimicking salticid spider community of the genus *Myrmarachne* (Araneae) that uses a variety of dominant sympatric and syntopic ant species as models. We wanted to determine whether these color forms are distinct species or morphs of a single species, and thus to understand the co-existence of these forms in sympatry especially since the problem of defining species is acute under mimicry if there is disruptive selection for polymorphism within a species. We used the potential cross-interest exhibited by males of different color forms to dragline and retreat silks of the variously colored females to examine pre-mating isolation mechanisms because silk-mediated sex recognition occurs in salticid spiders (Yoshida and Suzuki 1981; Jackson 1987; Clark and Jackson 1995). Furthermore, male salticid spiders often build retreats over and defend silken retreats of females in the penultimate molt. This enables mating with virgin, teneral (freshly molted) females (Jackson 1986). *Myrmarachne* males also regularly mate with previously mated females occupying silken retreats with or without egg clutches (S. Ahmed, pers. observ.). Thus, silk-based cues are important in salticid spider reproductive behavior. To determine whether the response to silk-based cues was sex-specific, we contrasted the response of males to female silks with that towards silks produced by males of the different color forms. Since males of some spider species are unable to discriminate between female silks of closely related sibling species (Roberts and Uetz 2004), suggesting that responses to silk alone may be insufficient as an index of reproductive isolation, we supplemented the male responses to female silk with opportunistic records of natural matings between the color forms, as well as no-choice mating experiments under natural conditions.

## Materials and Methods

We studied sympatric ant and spider communities within the campus of the Jawaharlal Nehru Centre for Advanced Scientific Research (JNCASR) and the Indian Institute of Science (IISc), Bangalore, India. The principal ants in this community are the red weaver ant *Oecophylla smaragdina*, *Myrmicaria brunnea*, *Camponotus compressus*, and *C. sericeus* (Table 1). Of these, *O. smaragdina* is the

most abundant and, although an arboreal nester, forages in both arboreal and terrestrial strata. The other ant species are largely terrestrial, building underground nests. Ant-mimicking spiders (genus *Myrmarachne*) were found in or near foraging trails or near loose formations of the terrestrial nesting ants, close to or away from their nest entrances. Only *Myrmarachne plataleoides* was positively identified to the species level (Talwar et al. 2001). The range of this species overlaps that of its ant-model *O. smaragdina* in south and south-east Asia (Pollard 1994). Other ant-mimicking spiders are currently designated as morphospecies and voucher specimens are being maintained at the Centre for Ecological Sciences, Indian Institute of Science, pending the systematic treatment of this group. Based on morphological and color pattern similarity between ants and spiders, we designated ant model and spider mimic pairs (Table 1, Figs. 1a-e and 2a-c). For two forms, the ant model is unknown, and for one form (M5), only females have been found. Therefore, in this paper we report on five male forms and six female forms in this sympatric *Myrmarachne* community.

Adult males and females were collected from the wild, individually housed in plastic containers and maintained on a diet of laboratory-reared *Drosophila* and honey for the duration of the experiments at a 12L:12D photoperiod and temperature of  $25 \pm 1^\circ\text{C}$ . Seven days before an experiment, female spiders were introduced into individual glass vials (Fig. 3) where they built silken retreats at the far end of the vials.

### Mate Choice Experiments

For each experiment, using small glass vials, males of each of five color forms (MP, M1–M4; Table 1;  $N=10$  per form) were individually released gently into the small circular space (the neutral area) of the choice apparatus into which opened the mouths of the vials containing retreats of the six female color forms (Fig. 3). An individual male was employed only once. The vials were placed in a circular array around the rim of the neutral area and their relative order was randomized for each trial. The angular spaces between the vial mouths were blocked with opaque ground glass and the whole apparatus was enclosed within two circular halves of petridish-

**Table 1** Sympatric Ant Model and Spider Mimic Pairs in the Community

| Ant model   | Spider mimic                    | Remarks  |
|---|---------------------------------|--|
| <i>Oecophylla smaragdina</i> (Fabricius); Formicinae; major and minor workers | <i>Myrmarachne plataleoides</i> | All red  |
| <i>Camponotus compressus</i> (Fabricius); Formicinae; major worker            | <i>Myrmarachne</i> sp. 1 (M1)   | All black, resembles <i>M. plataleoides</i> except for color                                   |
| <i>Camponotus sericeus</i> (Fabricius); Formicinae                            | <i>Myrmarachne</i> sp. 2 (M2)   | Black and gold   |
| <i>Myrmicaria brunnea</i> Saunders; Myrmicinae                                | <i>Myrmarachne</i> sp. 3 (M3)   | Black and red-brown, abdomen characteristically curved as in ant-model                         |
| ? <i>Camponotus angusticollis</i> (Jerdon); Formicinae; major worker          | <i>Myrmarachne</i> sp. 4 (M4)   | Black and red, intermediate between <i>M. plataleoides</i> and M1                              |
| ?   | <i>Myrmarachne</i> sp. 5 (M5)   | Black and gold with characteristic V-shaped mark on abdomen; females only; no males ever found |

like glass plates such that the movements of the test male spider were confined to the neutral area, the opening of each vial, or the vials themselves. Females were removed from their vials 10 min prior to each experiment; males were thus presented with only silk and other chemical cues left by the females. A vial containing retreat silk of a common lycosid spider was used as control (dummy silk). The amount of dummy silk employed approximated that of the salticid retreats and was balled up to resemble retreat silk. We measured the time spent by each test male in the following three regions: (1) neutral area, (2) near vial, i.e. at the entrance of each vial, (3) inside each vial, performing the following activities: touching each retreat, or inside each retreat, during each 10-min trial. Since females could also have deposited dragline silk at the mouth of the vials besides the retreat silks at the far end of the vials, spiders may have entered vials on encountering appropriate dragline silks at the vial mouths and then performed additional behaviors at the retreats. Touching and entering retreats were considered behaviors that demonstrated maximum response, i.e. maximum interest exhibited by the males to the silk. All experiments were conducted between 1000 and 1500 h. The entire apparatus was cleaned with acetone and neutral detergent after each trial. The data for each trial were converted into percentages (out of 10 min), arcsine transformed and analysed using one-way ANOVAs, followed by pair-wise Student–Newman–Keuls tests and Bonferroni's correction for multiple tests, using an initial  $\alpha$  value of 0.05. All statistical analyses were performed using the software package STATISTICA.

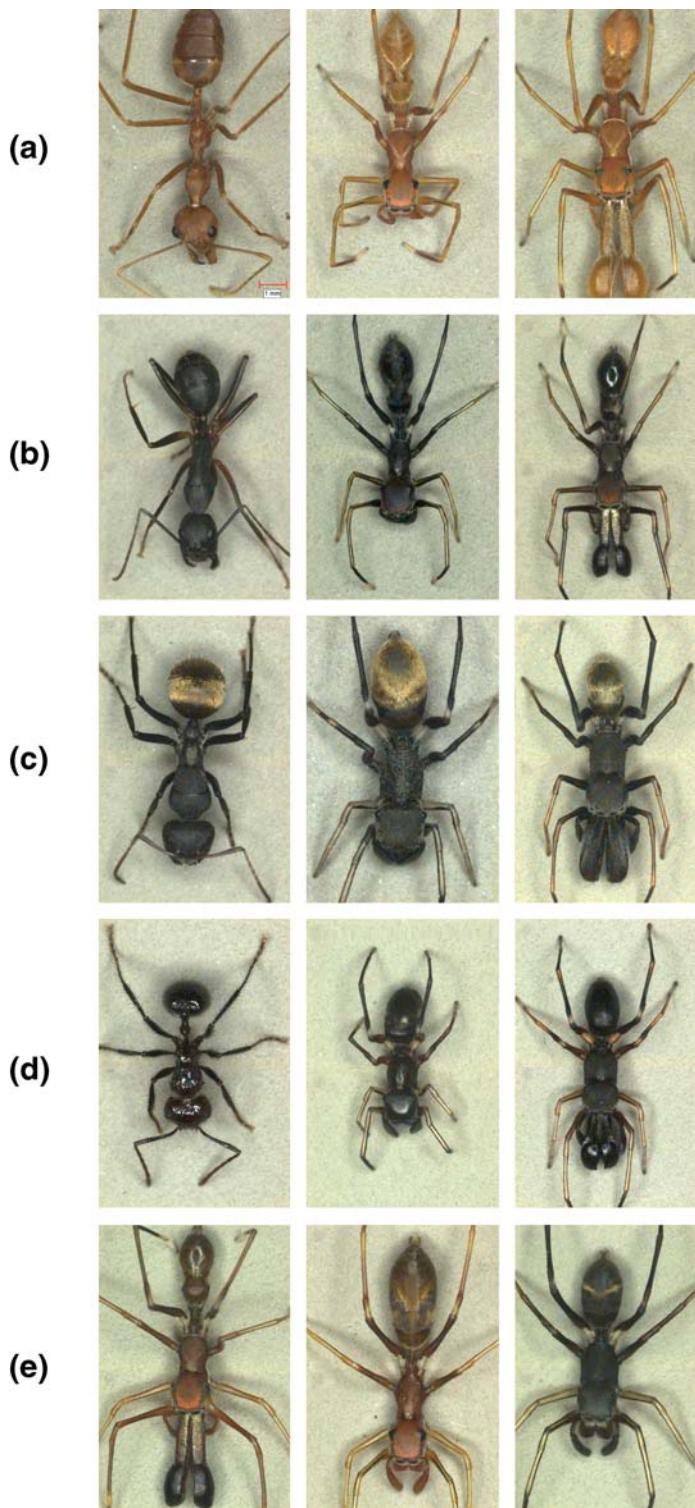
### Response of Males to Male Silks

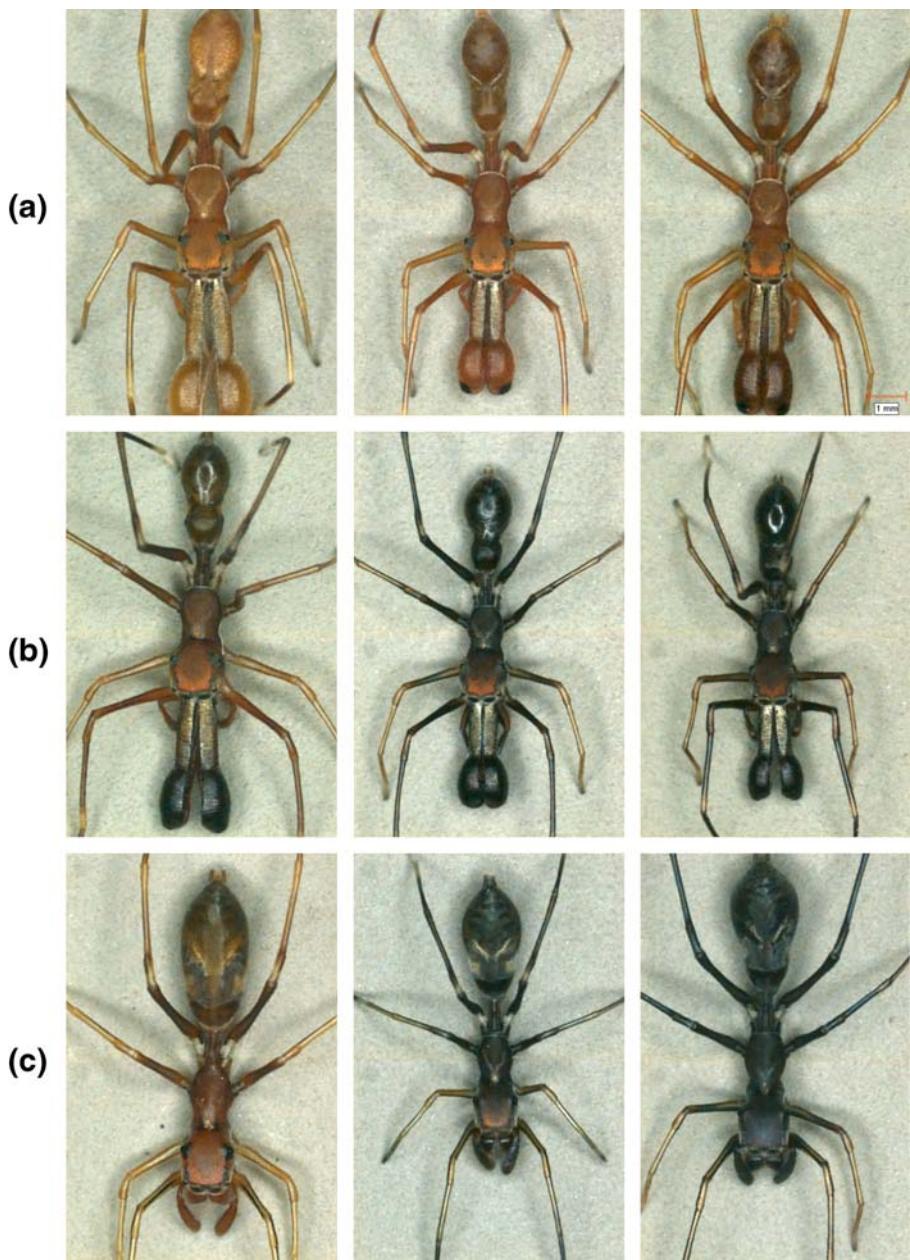
To determine whether male response to silks was sex-specific, we allowed males of the five color forms to leave chemical cues, possibly via dragline silks, in clean glass vials overnight (12 h). We did not use silken retreats in this experiment as males do not always construct retreats in vials; moreover, their retreats are usually very sparsely built and thus difficult to standardize between males. Using the same choice apparatus as before, we recorded the response of five males of each of the five color forms to an array of vials containing cues of the other male forms as well as a blank, clean vial (control) for a 10-min period, and recorded the amount of time spent near (at the mouth of) and within the test vials. All test vials contained male dragline silk. The data were analysed as in the male–female interaction experiment.

### Reproductive History of Experimental Animals and Natural Mating Experiments

Despite considerable effort, we have not been able to rear all these color forms successfully in the laboratory and hence were forced to use only wild-caught adults.

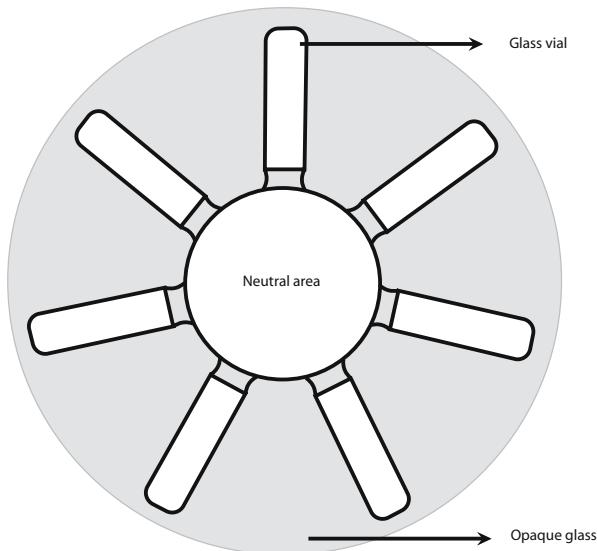
**Fig. 1** The sympatric ant models and salticid spider mimics of the genus *Myrmarachne*. In all rows except the last, the ant model is on the extreme left, the female spider mimic is in the center, and male spider mimic is on the extreme right. a, left to right: *Oecophylla smaragdina*, female and male *Myrmarachne plataleoides* (MP); b, left to right: *Camponotus compressus*, female and male *Myrmarachne* morphospecies 1 (M1); c, left to right: *Camponotus sericeus*, female and male *Myrmarachne* morphospecies 2 (M2); d, left to right: *Myrmicaria brunnea*, female and male *Myrmarachne* morphospecies 3 (M3); e, left to right: male and female *Myrmarachne* morphospecies 4 (M4), and female *Myrmarachne* morphospecies 5 (M5). Scale bar=1 mm.





**Fig. 2** Color gradation between the typical *Myrmecarachne plataleoides* (MP) and *Myrmecarachne* morphospecies 1 (M1). a and b: color gradation in males; c: color gradation in females. Intermediate (M4) males and females lie between the all-red (MP) and the all-black (M1) forms. *Scale bar*=1 mm.

**Fig. 3** The choice apparatus indicating the central neutral area and the vials containing the female spider retreat silks or male cues. Dimensions: vials=5.7×2.4 cm; circular glass dish=18.6 cm (diameter).

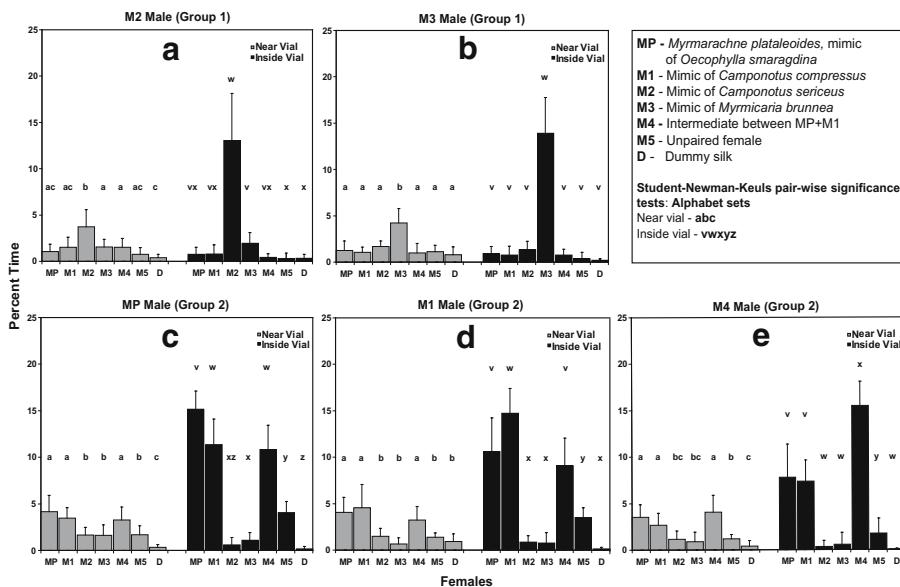


Furthermore, some of the color forms are rare. Also, because of transformational mimicry during development in these spiders, especially in *M. plataleoides*, in which each instar changes color, mimicking a different ant (Bhattacharya 1939), it is not possible for us to predict the phenotype of the adult by collecting immature spiders from the wild. We, therefore, did not know the reproductive history of the test animals. However, all experimental females produced egg clutches and were, therefore, previously mated. Consequently, although we could not use virgin females for practical reasons, our interpretations are not affected since male spiders of various groups including salticids are known to mate with previously mated females as our own data (unpublished) and others have shown (Elgar 1998; Bukowski et al. 2001; Schäfer and Uhl 2002). To substantiate our results, we also conducted no-choice mating experiments in the wild wherein we presented single males to single females of the various forms. We also made opportunistic records of the colors of males guarding the retreats of the various female forms in the wild. Our current inability to rear all color forms successfully also precluded the investigation of polymorphism using conventional methods such as examination of the production, viability and fertility of hybrids, and constrained us to use surrogate methods such as silk-based cues to investigate reproductive isolation.

## Results

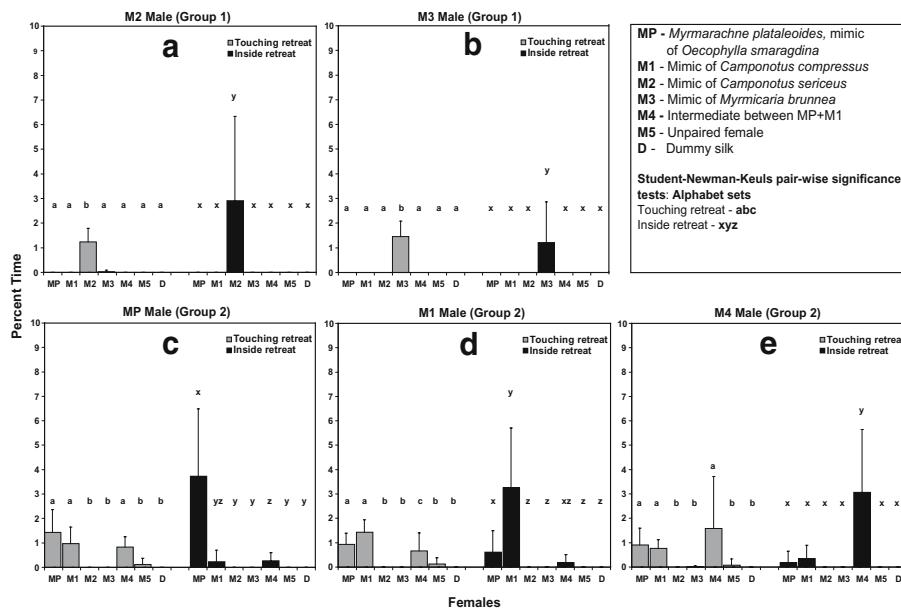
### Silk Choice Experiment

All male color forms showed significant variation in the type of behaviors and the time spent performing them when given a simultaneous choice of different female silks (Figs. 4 and 5) indicating that they perceived and responded to differences in the silks. Males visited each vial in the choice apparatus at least once, thus indicating



**Fig. 4** Percent time spent by five male color forms (MP, M1–M4) in various regions of the choice apparatus and performing various behaviors in response to retreat silks of six females (MP, M1–M5) and a dummy silk (D) (means and standard deviations of ten trials per male form). Percent time in neutral area is not shown, although percentages are calculated taking time in this area into account. For each behavior or position within the choice apparatus, a different alphabet set is used to indicate values that are significantly different from each other via post-hoc Student–Newman–Keuls tests following a one-way ANOVA and Bonferroni's correction for multiple tests. All  $F$ -statistics of the ANOVAs were highly significant ( $p < 0.0001$ ). Within an alphabet set, bars with same letters above them are not significantly different from each other at Bonferroni-corrected  $\alpha = 0.007$ . The alphabet sets are: near vial, abc; inside vial: vxxyz.

no positional bias in the apparatus. All males showed an extremely low response to the silk of M5 females and to the dummy (control) silk. Of the female silks to which males responded, two patterns emerged resulting in two groups of spiders: a) Group 1—consisting of M2 and M3 (Figs. 4a–b and 5a–b), and b) Group 2—consisting of MP, M1, and M4 (Figs. 4c–e and 5c–e). a) Group 1: In this group, the male mimics of the ants *C. serecius* (M2) and *M. brunnea* (M3) showed a significantly higher response to the silk of only the female form which matched them in color pattern (M2 and M3, respectively) and not to any other form; these males touched and entered the retreats of only this corresponding female form (M2 or M3). b) Group 2: In this group, the males (MP, M1, and M4) showed cross-interest in the silks of all three females in the group: MP, M1, and M4 (Figs. 4 and 5). Furthermore, *Myrmachne plataleoides* (MP) males showed a significantly greater response to the silks of *M. plataleoides* (MP) females, that also included touching and entering their retreats (Fig. 5c). Although MP males showed high levels of cross-interest in the silks of M1 females and M4 females, by spending considerable amounts of time inside the vials of these females and even touching and entering their retreats (Fig. 5c), yet they spent a significantly greater amount of time inside the vials and inside the retreats of MP females only. MP males responded minimally to the silks of Group 1 females (M2 and M3) and did not enter or touch their retreats (Fig. 5c).



**Fig. 5** Percent time spent by five male color forms (MP, M1–M4) in various regions of the choice apparatus and performing various behaviors in response to retreat silks of six females (MP, M1–M5) and a dummy silk (D) (means and standard deviations of ten trials per male form). Percent time in the neutral area is not shown, although percentages are calculated taking time in this area into account. For each behavior or position within the choice apparatus, a different alphabet set is used to indicate values that are significantly different from each other via post-hoc Student–Newman–Keuls tests following a one-way ANOVA and Bonferroni's correction for multiple tests. All  $F$  statistics of the ANOVAs were highly significant ( $p < 0.0001$ ). Within an alphabet set, bars with same letters above them are not significantly different from each other at Bonferroni-corrected  $\alpha = 0.007$ . The alphabet sets are: Touching retreat: abc. Inside retreat: xyz.

Results similar to that for MP males were obtained for the all-black (M1) and red-black males (M4) that showed the greatest response to the silks of their corresponding females (M1 and M4, respectively) in terms of touching and entering retreats, but also exhibited high levels of cross-interest in those of *M. plataleoides* (MP) females (Fig. 5d–e). M1 and M4 males similarly showed little interest in Group 1 (M2 and M3) silks (Fig. 5d–e). Thus, there was unambiguous choice of female silks in members of Group 1 (M2 and M3) with each male preferentially selecting the silk of its corresponding female (M2 or M3), and cross-interest between silks in members of Group 2 (MP, M1 and M4). Moreover, members of Group 2 also showed significantly greater interest in female silks of their own corresponding color form, thus indicating the possibility of a silk-based assortative mating between color forms within this group.

#### Response of Males to Male Silks

Males of all color forms, when exposed to cues left by other males in the experimental apparatus, spent equal amounts of time near and within all the choice vials including the control vial (non-significant ANOVAs,  $p > 0.05$  in all cases), thus

**Table 2** No-choice Mating Tests (% Mating Success, *N*) and Opportunistic Observations of Males Co-habiting with Virgin Females {*N*}

|              |                | Females        |         |         |                |        |
|--------------|----------------|----------------|---------|---------|----------------|--------|
|              | MP             | M1             | M2      | M3      | M4             | M5     |
| <b>Males</b> |                |                |         |         |                |        |
| MP           | (29.2, 24) {9} | (28.6, 7)      | (0, 10) | (0, 10) | – <sup>a</sup> | (0, 4) |
| M1           | (47.6, 21) {1} | (41.7, 12) {5} | (0, 10) | (0, 10) | –              | (0, 5) |
| M2           | –              | –              | (0, 10) | (0, 10) | –              | (0, 4) |
| M3           | –              | –              | (0, 10) | (0, 10) | –              | –      |
| M4           | (87.5, 8)      | (85.7, 7) {7}  | (0, 10) | (0, 10) | {4}            | (0, 4) |

<sup>a</sup> – = test not conducted

indicating that, when only male cues are available, they explored all vials equally. This also reaffirmed that the apparatus itself did not generate any movement bias.

#### No-choice Mating Tests and Opportunistic Mating Records

Owing to the cross-interest shown by males of Group 2 (MP, M1 and M4) males to the silks of MP, M1 and M4 females, and the low response of all males (Group 1 and Group 2) to M5 female silks, we conducted no-choice mating experiments in the wild whenever possible between these forms (Table 2). M5 females were exposed to males of all types except M3 (Table 2). The results confirmed those of the silk choice experiments. No males from either Group 1 or Group 2 mated with M5 females. Multiple no-choice mating experiments (ten in each case) conducted between males and females of Group 1 (M2, M3) and Group 2 (MP, M1, M4) showed that no mating or interest was exhibited between members of the two groups (Table 2). Within Group 1, males and females of M2 and M3 were reciprocally exposed to each other in no-choice experiments (ten in each case) and no mating or interest was exhibited between these forms, indicating that M2 and M3 mate exclusively with their respective females (Table 2). We found co-habitation (males building retreats above those of virgin females) between MP, M1 and M4 color forms in the wild indicating that natural cross-mating occurs between members of Group 2 (Table 2).

#### Discussion

The problem of defining species is a difficult one; species definitions are being constantly debated, and species are beginning to be regarded less as reproductively isolated types or populations and more as gene pools under selection for or against exchanging genes (Mallet 1995). The problem of delimiting species is even more acute in mimetic species when there may be ecological and thus natural selection

pressure towards polymorphism wherein individuals of a species could be advantaged by mimicking two or more models in sympatry (van Doorn and Weissing 2001; Kirkpatrick and Ravigné 2002). In such a situation, the adaptive response favoured by disruptive selection could be assortative mating leading to speciation (Jiggins et al. 2004; Gray and McKinnon 2007). This could result in the evolution of pre-mating isolation mechanisms that favor such non-random mating and an evolutionary trajectory via incipient species towards established species (Seehausen et al. 1999; Rueffler et al. 2006).

We demonstrated that the chemical and/or the tactile cues laid down by salticid ant-mimicking females in draglines and retreat silks were sufficient to elicit responses from males in the absence of any visual cues. Males had been earlier recorded performing courtship dances to empty retreats in a few instances, thus justifying our choice of these sensory modalities. The fact that males showed no differential response to cues left by other males and responded equivalently to them as to a blank vial, indicates that the response of males to these silk-based cues is sex-specific and thus relevant to the mating process. Chemosensory modalities should also be particularly important in the mating process of these spiders because males develop exaggerated chelicerae only in the last molt before which they are superficially indistinguishable from females. Furthermore, salticid males often locate females using silk, and thus silk-based cues should be important as mating cues (Yoshida and Suzuki 1981).

We showed that there was significant cross-interest between males of three color forms within Group 2 [the well-known red *M. plataleoides* (MP), an all-black form (M1), and an intermediate red-black form (M4)] towards the silk of the three corresponding female forms. Males within Group 2 entered the retreats of all three corresponding female forms, indicating a maximal response to their cues. Yet, each of the male forms within Group 2 spent the most time inside vials and within the retreats of only the female form that it corresponded to in color and thus appeared to be exhibiting assortative mating between color forms within this group using silk-based cues. The members of Group 2 (MP, M1 and M4) were also found to naturally interbreed. How can this intra-group color polymorphism be explained? Two hypotheses suggest themselves. 1) *Myrmarachne plataleoides* (MP) could be under disruptive selection pressure to mimic the sympatric and syntopic black ant *C. compressus*, the black and red *C. angusticollis* besides its usual model the red *O. smaragdina*, and is thus exhibiting intraspecific color polymorphism. Under this hypothesis, the red-black M4 and the all-black M1 are color morphs of the well-known red *M. plataleoides*, a wide-spread mimic of the red weaver ant *O. smaragdina* (Bhattacharya 1939; Pollard 1994). 2) There is an all-black *Myrmarachne* species (M1) that mimics the black *C. compressus* ant and that resembles the red *M. plataleoides* (MP) in all aspects except for color and behavior, and hybridization between this species and *M. plataleoides* in the region of contact is resulting in the red-black form (M4).

Hypothesis 1 appears to be the most plausible for the following reasons. Firstly, preliminary unpublished data (over two seasons) indicate that the M1 and M4 forms are available only in the wet season. It is, therefore, possible that these two forms are the result of a seasonal color polyphenism in *M. plataleoides* as has been found in insects such as orthopterans (Sword 1999). Secondly, it appears that the M1 and M4

forms are extremely localised in distribution, occurring in considerable numbers only on the JNCASR campus, and M4 occurs only occasionally at IISc. Despite regular sampling, these forms have not been recorded elsewhere in Bangalore although *M. plataleoides* is common in many areas throughout the city wherever *O. smaragdina* is present. *Camponotus compressus* (the model for M1) is a ground nesting ant and is, therefore, not abundant in an urban setting; large populations of this ant are available in JNCASR and very few nests occur at IISc (our own observations). The density of *O. smaragdina* is also much higher at JNCASR which contains bamboo groves and semi-natural areas. Thus, the abundance of the black ant model *C. compressus* and of the red model *O. smaragdina* at JNCASR may explain the localized occurrence of the various color forms at JNCASR and, thus, disruptive selection for color polymorphism at JNCASR, which is assisted by the assortative mating between color forms that was observed. Such localized areas of disruptive selection have been found in other taxa such as *Drosophila* (Korol et al. 2000). Thirdly, *M. plataleoides* may be predisposed to color polymorphism because it exhibits transformational mimicry (Bhattacharya 1939) wherein different instars mimic different ants of a variety of colors and sizes ranging from red *Pheidole* to black *Crematogaster*. This suggests that the genetic architecture for production of different colors is already present in *M. plataleoides* and could, therefore, be selected for in the adult stage to produce color polymorphic adults that could be targets for disruptive selection. Unfortunately, the genetic control of color polymorphisms is known only for some butterflies (Naisbit et al. 2003) and spiders (Maelfait et al. 1990; Oxford and Gillespie 1998). The above arguments, the gradation in color between MP, M4, and M1 (Fig. 2), and the cross-mating observed between these forms, suggest that M1 and M4 are color forms of the same species, i.e. *Myrmecarne plataleoides* (MP). The assortative mating observed between these color forms suggests the possibility of progression towards incipient speciation in sympatry as has been observed in cichlids (Seehausen et al. 1999), *Rhagoletis* (Linn et al. 2003), *Drosophila* (Singh et al. 2005), larch budmoths and butterflies (Jiggins et al. 2005). However, mechanisms for the maintenance of polymorphism in mimicry are still unclear as is also whether mimicry alone could be a cause for disruptive selection leading to speciation (Joron and Mallet 1998; Mallet and Joron 1999). Yet, ant-mimicking spiders are known to exhibit color polymorphism (Reiskind 1965; Cutler 1980) and multiple mimetic forms within a species have been found in other spider families such as Clubionidae (Reiskind 1970).

The clear preference shown by the mimics of *Camponotus sericeus* (M2) and *Myrmicaria brunnea* (M3) (spiders of Group 1) for the female silk of only their own corresponding form indicates that these are two distinct sympatric species which also use silk-based cues as pre-mating mechanisms for mate recognition which in this case also facilitates mating with the corresponding color form. The complete lack of interest exhibited by all males in M5 females as well as the failure of natural mating experiments with M5 indicate that this is a form whose chemical and morphological phenotype is not recognized by the other forms and is not acceptable to them. Furthermore, male M5 forms have never been found. It is possible that this form is produced in such low frequency that we have been unable to find these rare males despite our sampling efforts. The relationship of this form is, therefore, unclear and awaits further investigation which will also include molecular genetic analysis.

Although visual cues are important in assortative mating and pre-mating reproductive isolation in sympatric color mimetic morphs and species (Jiggins et al. 2004), chemical cues are also likely to be significant (Jiggins et al. 2005), as our study has also shown. Empirical evidence for chemical cues is scarcely available for mimetic systems, and much more basic research is needed to understand the mechanisms involved in mating decisions as well as the type of selective forces driving speciation and maintaining polymorphism in sympatry (Etges 2002; Kirkpatrick and Ravigné 2002; Arnegard and Kondrashov 2004; Gray and McKinnon 2007). Communities of ant-mimicking salticid spiders that occur in sympatry and syntopy with a diverse community of terrestrial and arboreal ants offer excellent opportunities to examine the proximate cues and processes that contribute to the reproductive isolation of mimetic forms.

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