



Chemotactile social recognition in the blue-ringed octopus, *Hapalochlaena maculosa*

Peter Morse¹ · Christine L. Huffard^{2,3}

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Abstract

Social recognition is the ability of individuals in a species to differentiate among conspecifics based on their identity or biologically meaningful demographic. Despite evidence that they have sophisticated brains, complex behavioural repertoires, and acute sensory processing, surprisingly little is known about mechanisms aiding social recognition in cephalopods. This class's unique chemotactile sense by the ventral arm surfaces gathers considerable information used in predator–prey interactions. Does it also help mediate social interactions? This study utilised 366 h of focal animal observations to assess the likelihood of *Hapalochlaena maculosa*, a nocturnal species, to retreat after physically contacting conspecifics based on their sex, familiarity and mating history. Females retreated from both sexes equally, while males were more likely to retreat after contacting female conspecifics. Most conspicuously, males were significantly more likely to retreat after contacting females with which they had already mated. These findings provide the first evidence for chemotactile sex discrimination and mate recognition within cephalopods, and supplement previous observations that male *H. maculosa* do not appear to detect the sex of conspecifics from a distance. The decision to retreat from or stay with an individual based on their sex or mating history, only after physical contact, emphasises the importance of chemotactile behaviour in octopus sensory ecology and behaviour. Furthermore, male octopuses have limited spermatophore production, and the use of chemotactile social recognition observed here may highlight the importance of reproduction, specifically sperm allocation and avoidance of sexual cannibalism, on the evolution of sensory ecology and cognition within this lineage.

Keywords Behaviour · Cephalopod · Chemosensory · Cognition · Sensory ecology · Sperm competition

Introduction

Social recognition is a generic term used to describe the capacity of individuals to use sensorial or contextual cues to distinguish among conspecifics or in some cases their socially relevant category (e.g. dominance, kinship, neighbour, sex etc.) (Colgan 1983). The overall complexity of social recognition and the underlying mechanisms driving

it vary greatly among the animal kingdom and are hypothesised to correlate directly to the life history and sociality of the species (Medvin et al. 1993; Ward et al. 2009). Social recognition is a necessary prerequisite for cooperative behaviours (Wilson 2000), and is thought to have evolved in various forms to facilitate social behaviours including anti-predator defence (Townsend et al. 2011), collaborative hunting (Gazda et al. 2005), resource competition (Jaeger 1981), mate choice (Cheetham et al. 2008), parental care (Medvin et al. 1993) and reciprocal altruism (Seyfarth and Cheney 1984), as well as many others.

Social recognition has been studied quite extensively within vertebrate groups (Colgan 1983; Mateo 2004), perhaps because their sensory ecology and mechanisms of social recognition are most relatable to our own as humans (Patullo and Macmillan 2015). However, where studied a diverse range of social recognition has also been reported within invertebrate taxa, leading to valuable insights to the link between social structure and cognitive evolution across

Responsible Editor: R. Villanueva.

✉ Peter Morse
Peter.Morse@my.jcu.edu.au

¹ College of Science and Engineering, James Cook University, Townsville, QLD, Australia

² Monterey Bay Aquarium Research Institute, 7700 Sandholdt Rd, Moss Landing, Monterey, CA 95039, USA

³ California Academy of Sciences, 55 Music Concourse Dr, San Francisco, CA 94118, USA

distinct phylogenetic lineages (Aquiloni and Tricarico 2015). One invertebrate group for which surprisingly little is still known about the dynamics of social recognition, despite substantial evidence for their relatively sophisticated brains and intricate social behaviours (Amodio et al. 2018; Shigeno et al. 2018), are the cephalopods (Mollusca: Cephalopoda) (Boal 2006). Within this class, the octopuses (Cephalopoda: Octopodidae) are often regarded as one of the most ‘asocial’ (Edsinger and Dölen 2018), and in some cases ‘antisocial’ (O’Brien et al. 2021), of the cephalopod clades, with the vast majority of their intraspecific interactions revolving around the necessary life stage of reproduction (Boal 2006; Huffard et al. 2008, 2010; Hanlon and Messenger 2018; Morse and Huffard 2019). As such, it might be hypothesised that social recognition in octopuses could be highly specialised from evolutionary pressures of sexual selection to help in facilitating reproductive behaviours such as mate choice and sperm competition.

To date there is conflicting and enigmatic evidence for and against various forms of social recognition among octopuses. The common octopus (*Octopus vulgaris*) has been observed to recognise familiar conspecifics in the laboratory based on visual cues (Tricarico et al. 2011), and the California two-spot octopus (*O. bimaculoides*) appears capable of discriminating the sex of conspecifics from a distance based on chemical signals in the water (Walderon et al. 2011). Distance sex discrimination has also been observed in wild *Abdopus aculeatus*, and is presumably mediated by sex-specific chromatophore patterning (Huffard et al. 2010). Additionally, the males of two species of octopus, an unidentified pygmy octopus and the southern blue-ringed octopus (*Hapalochlaena maculosa*), have been observed to adjust their copulation time with females depending on whether or not they were the last male to have mated with them (Cigliano 1995; Morse et al. 2015), suggesting that some octopuses might be capable of mate recognition. However, the prevalence of male-male copulation attempts in the laboratory (*Hapalochlaena* spp.: Cheng and Caldwell 2000; Morse et al. 2015) suggests some octopuses cannot recognise the sex of their conspecifics accurately, and an interspecific male-male copulation attempt observed in the deep sea demonstrates the inability of some male octopuses to ascertain even their own species (Lutz and Voight 1994). Furthermore, recent behavioural studies of *H. maculosa* indicate that females of this species are likely to discriminate the sex, and possibly identity, of conspecifics via distance chemoreception using chemical cues in the seawater, but the males do not appear able to do this (Morse et al. 2017). In laboratory focal animal observations with the same species, both males and females approached either sex indiscriminately, leading to either mating attempts, grappling or retreat behaviours (Morse et al. 2015).

It seems plausible that there could be a missing piece of the puzzle in our understanding of octopus social recognition and its link to their unique sensory ecology. A distinct aspect of cephalopod morphology is that they possess specialised chemosensory and mechanosensory cells on the suckers lining the undersides of each of their arms that separately convey information to the brain about both chemical profiles and texture (Budelman 1996; Mollo et al. 2014, 2017; Di Cosmo and Polese 2017; Di Cosmo et al. 2018; van Giesen et al. 2020). Octopuses possess many more of these chemosensory receptors (~ 10,000 cells per sucker in *O. vulgaris*: Graziadei 1964a) compared to their decapod (Cephalopoda: Decapodiformes) sister taxa (~ 100 cells per sucker in cuttlefish: Graziadei 1964b), and this has been thought to relate to the way in which octopuses reach their arms into holes and crevices while foraging for food (Budelman 1996). It is also pertinent to note that a chemotactile phase leading up to copulation has been observed in several octopus species (Wells and Wells 1972; Voight 1991; Morse 2008; Morse et al. 2018a), and the chemosensory lobes of octopuses, which are responsible for processing chemical stimuli, are integrated with the parts of the brain that regulate signal molecules involved in both feeding and reproductive behaviours (Polese et al. 2015). It therefore appears straightforward that chemotactile (mechanical and/or chemical) information is a very important tool used by octopuses to interact with their environment (Mollo et al. 2014, 2017; Di Cosmo et al. 2018; van Giesen et al. 2020) and possibly each other (Di Cosmo and Polese 2017). However, to the best of the authors’ knowledge, the role of chemotactile cues in octopus social behaviour or any cephalopod mating system has never been investigated.

The present study aims to provide new context for the interpretation of octopus interactions by evaluating evidence for and against chemotactile-based social recognition in the relatively well-studied *H. maculosa*. Specifically, this study aims to determine whether *H. maculosa* of different sex and size are more or less likely to retreat after contacting conspecifics depending on the following three socially-relevant criteria: (i) conspecific sex; (ii) conspecific novelty; and (iii) shared mating history. Evidence for chemotactile recognition at these levels may reveal previously unexplored links among sensory ecology, sexual selection and cognition in cephalopods.

Methods

Animal acquisition and maintenance

The method of obtaining the animals used in this study, and their care within the laboratory has been previously reported for coinciding studies (Morse et al. 2015, 2017).

To summarise, twelve female and twelve male *H. maculosa* were obtained from either false shelter traps (Morse et al. 2015) or the by-catch of commercial fishermen between Mandurah and Cockburn Sound in Western Australia (WA). Female size ranged from 1 to 12 g, and male size from 2 to 9 g (Appendix 1). Each animal had a minimum mantle length of 20 mm, which was revealed during pilot studies as the minimum size for this species to be observed in copulation (Morse et al. 2015). However, three females (1, 3 and 8 g respectively) were unreceptive to all male copulation attempts and did not copulate during this study, indicating they may not yet have reached sexual maturity. All males engaged in copulation during the present study. Focal animal size (wet weight) was included in analyses to account for, and quantify, variation in behaviour arising from potentially different life-stages of individuals (see below).

All animals were housed in individual 1 L plastic containers connected to a closed flow-through system with a 1000 L sump at Fremantle Octopus Company facilities in O'Connor, WA. Seawater was obtained from Cockburn Sound and maintained at 22 °C with a salinity of 34–35 ppt. Each animal was given an appropriately sized shell for use as a shelter and was fed ad libitum with pieces of thawed, frozen prawns and occasional live crabs. ReefOne™ biOrb LED aquarium lights were used to simulate daylight for 14 h per day, which corresponded to local daylight hours when focal animal observations began. Activated carbon was used to neutralise potential odours in the seawater entering individual containers in order to limit the exposure of each animal to the conspecifics around them, and all animals were maintained in this manner for a minimum of two weeks prior to entering focal animal observations. Animals were obtained under the WA Department of Parks and Wildlife permit SF00963. The use and treatment of the animals were approved by the James Cook University Ethics Committee (approval no. A1850).

Focal animal observations

The 24 animals were split into four separate trials, each containing six animals. As a coinciding study aimed to address differences in behaviour based on operational sex ratio (OSR), the numbers of males and females differed among the trials (Morse et al. 2015). The first trial had four females and two males, the second had two females and four males, and the third and fourth trials each had three females and three males (Appendix 1).

All trials took place in a 1 m² observation tank, with a water depth of 50 cm. The bottom of the tank was lined with sandy rubble, and 12 shells of varying shapes and sizes were haphazardly placed in the tank for animals to shelter in. Water conditions were maintained at 22 °C and 34–35 ppt. A ReefOne™ biOrb LED aquarium light was used to

provide 14 h of daylight per 24 h period and animals were fed ad libitum with pieces of prawn throughout the trials. The six animals in each trial were allowed to interact freely, as they were observed using CCTV with infrared-recording capability for nocturnal hours. The first two trials each ran for 5 days. However, the third trial (with equal OSR) was terminated after 3.28 days as one of the males became inactive after excessive copulation. Therefore, a fourth trial was run for an additional two days in order to gain a total of 5.28 days of observation with equal OSR (Appendix 1).

The resulting 15.28 days of focal animal video observations were reviewed to record all intraspecific interactions. Specifically, an 'interaction' between individuals was defined in this study as any time an animal contacted another with the undersides of at least one of their arms. This typically led to either one of the animals retreating, a copulation attempt, grappling or a prolonged chemotactile phase (longer than 30 s). For the sake of this study a 'retreat after contact' was defined as when the focal animal subsequently crawled or swam away from the conspecific that they contacted. Most retreats occurred immediately after contact, however for consistency, this behaviour was scored as a retreat if it happened within 30 s of making contact. The focal animal was considered to 'stay after contact' if they did anything other than move away from the conspecific for 30 s, or if they held their ground while the animal they had contacted retreated. Conspecifics were considered 'novel' in this study if it was the first time that pair interacted within the trial. Conspecifics were considered 'familiar' if they had previously had an interaction where either one was observed to contact the other. This definition was chosen because contact often instigated the other animal to reciprocate the contact, but this could not always be verified or refuted in every interaction depending on the angle of the interaction in relation to the camera. Similarly, it was not possible in every case to observe hectocotylus insertion due to the fixed camera angle. Therefore, male and female pairs were considered to have copulated if the male was observed mounting the female for a minimum of 1 min, as hectocotylus insertion immediately followed mounting behaviour in all observable interactions during this study and in other studies with the same species (Morse et al. 2018a).

Analysis of contact and retreat behaviour

The probability of individuals to retreat after contacting conspecifics in trials was analysed using mixed-effect logistic regressions (MELR) with the 'glmer' function in the 'lme4' package in R software (version 3.3.2) (R Core Team 2016). The generalised linear model family was set to 'binomial' with a 'logit' link. Because there were multiple observations for each focal animal and the conspecifics they contacted, both 'focal ID' and

'conspecific ID' were set as random-effects. In order to ensure model convergence while accounting for a long list of variables, five MELR models were constructed to analyse the binomial response variable, 'retreat' or 'stay', among focal animals. The first MELR analysed the effect on all interactions from the following fixed-effects: 'trial', 'focal animal sex', 'focal animal size' and 'conspecific size'. The following two MELRs analysed retreat rates of female and male focal animals separately, investigating the fixed-effects: 'trial', 'conspecific sex', 'focal animal size', 'conspecific size' and 'conspecific novelty'. Two final MELR models were used to specifically analyse male–female and female–male interactions, investigating the fixed-effects: 'trial', 'focal animal size', 'conspecific size' and 'shared mating history' (whether or not the pair had mated previously). Conspecific size was not specifically addressed in this study as it is not likely to be detected through chemotactile sensory. However, it was included in models as it was likely to be an additional factor influencing animals' decisions whether to stay or retreat. All figures were constructed using the 'networkD3', 'plot' and 'barplot' functions in R software (version 3.3.2: R Core Team 2016).

Results

Description of chemotactile interactions

This study is based on a total of 434 chemotactile interactions observed among *H. maculosa* in the laboratory (Fig. 1; Appendix 1). Of these interactions, physical contact was made 128 times by female focal animals and 306 times by males. Females retreated after making contact in 61 of these interactions (Fig. 1). Among the 67 interactions where the female stayed after contact, the conspecific that had been contacted either retreated ($N=56$) or was a male that subsequently attempted to mount the female ($N=11$). Of these copulation attempts, nine were successful. Males only retreated in 72 interactions after they had made contact with another conspecific (Fig. 1). Of the 234 interactions where the male stayed after contact, the conspecific they had contacted retreated from them in 127 instances. In the other 107 cases, the male either stayed in the vicinity of the conspecific they had contacted for more than 30 s before moving slowly away ($N=3$) or attempted to mount the conspecific they had contacted ($N=104$). Male focal animals were observed here to attempt mounting both other males ($N=81$) and females ($N=23$). Twenty of these male–female mount attempts proceeding male contact resulted in successful copulation.

Effects of sex and size

Among all 434 interactions observed in this study there was no effect of trial number or OSR on the likelihood of individuals to retreat from conspecifics after contact (mixed-effects logistic regression: $\chi^2_3 = 1.246$, $p = 0.742$). Females were significantly more likely to retreat after contacting a conspecific than were males in this study (MELR: $\chi^2_1 = 13.276$, $p < 0.001$; Fig. 2). Females retreated at similar rates after contacting both males and females (MELR: $\chi^2_1 = 1.032$, $p = 0.310$; Fig. 2), and larger females were significantly less likely to retreat than smaller females (MELR: $\chi^2_1 = 4.535$, $p = 0.033$). Female retreat rates were not affected by the size of the conspecific they contacted (MELR: $\chi^2_1 = 1.238$, $p = 0.266$).

Males were significantly more likely to retreat after contacting females than after contacting males (MELR: $\chi^2_1 = 3.960$, $p = 0.047$; Fig. 2), especially as female size increased (MELR: $\chi^2_1 = 7.870$, $p = 0.005$). Focal male size had no effect on his likelihood of retreating after contacting another conspecific (MELR: $\chi^2_1 = 0.148$, $p = 0.700$). However, males were paradoxically more likely to retreat from smaller male conspecifics rather than large male conspecifics (MELR: $\chi^2_1 = 6.636$, $p = 0.010$).

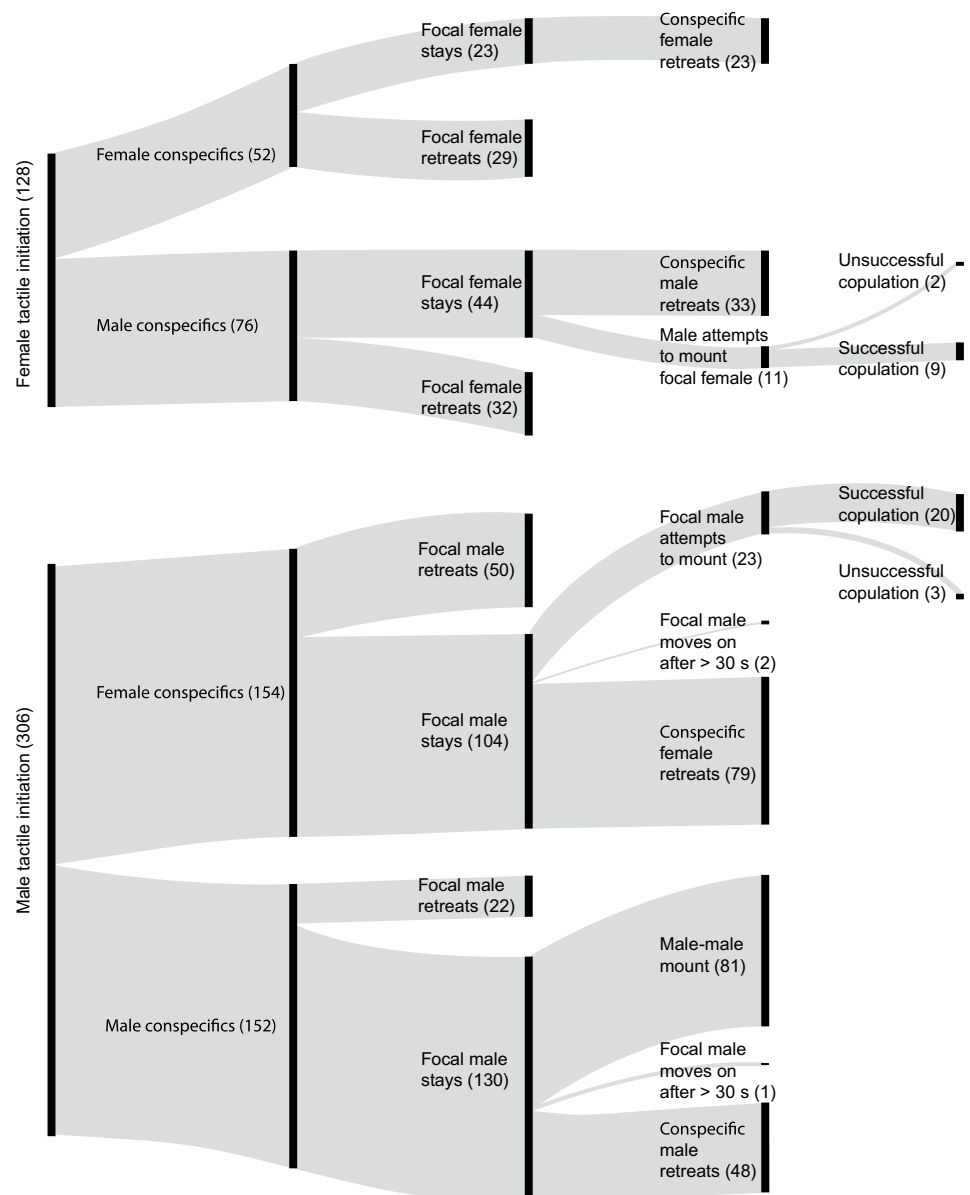
Effects of novelty and mating history

Conspecific novelty had no overall effect on the likelihood of an individual to retreat after contacting a conspecific during trials (MELR: $\chi^2_1 = 1.607$, $p = 0.205$; Fig. 3). However, there was a non-significant trend for males to retreat more frequently from females they had previously interacted with (MELR: $\chi^2_1 = 2.440$, $p = 0.118$; Fig. 3). Additionally, males were significantly more likely to retreat after contacting a female with which he had already mated previously (MELR: $\chi^2_1 = 4.685$, $p = 0.030$; Fig. 4). Mating history among pairs had no effect on the likelihood of the female to retreat after subsequently contacting males during trials (MELR: $\chi^2_1 = 0.148$, $p = 0.701$).

Discussion

Haplochlaena maculosa in this study appeared capable of utilising chemotactile cues to discriminate among socially and biologically relevant traits in the conspecifics they physically contacted. The likelihood of an individual to retreat after contacting a conspecific was associated with the sex (Fig. 2), size, and shared mating history (Fig. 4) of the conspecific being contacted. This likelihood also varied by the sex and size of individual initiating the physical contact. Males fled from female conspecifics more often than they did male conspecifics, demonstrating chemotactile sex recognition.

Fig. 1 A sankey diagram illustrating the frequency of different ‘stay’ or ‘retreat’ behaviours observed among the 434 chemotactile interactions of *H. maculosa* during the present study

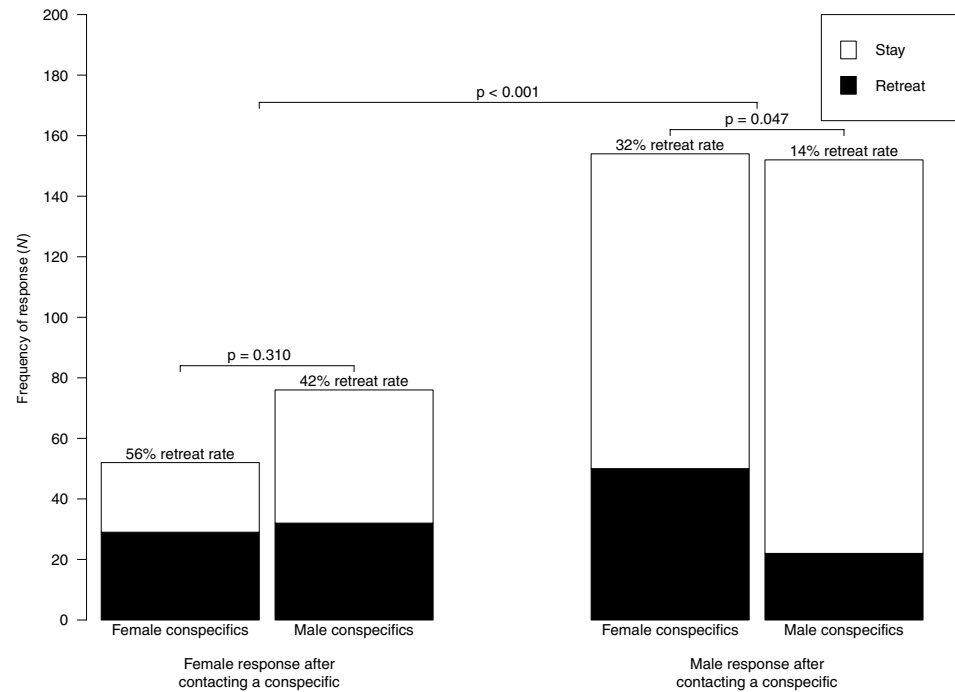


They also appeared able to discriminate females with whom they had previously mated from those they had not. By contrast, females showed no indication of using chemotactile information to determine whether to retreat. Intriguingly, a prior study of this species indicated that females are able to identify the sex and possibly the identity of conspecifics from chemical signatures in the water, however males have not been observed to be able to do this (Morse et al. 2017). The novelty or familiarity of conspecifics did not influence the probability of an individual to retreat after contact in this study. Therefore, shared mating history rather than familiarity itself was more likely to influence a male's decision whether to retreat from a conspecific female. Together these results suggest octopuses, particularly male *H. maculosa*, may use chemotactile information gathered

by chemosensory cells on the arms to recognise socially-relevant categories of conspecifics.

Male *H. maculosa* were able to assess the prior mating history of females by touch, but without necessarily inserting the hectocotylus. Male mate recognition may occur in cephalopods that adjust copulation time based on prior mating history of females (Cigliano 1995; Wada et al. 2010; Morse et al. 2015). In all of these cases known previously, males had already initiated copulation, presumably allowing the hectocotylus to assess the presence and potentially the identity of existing sperm. By contrast, *H. maculosa* males in this study appeared able to assess whether they had already mated with a female prior to mounting her—presumably via tactile chemosense, though mechanosense cannot be discounted. It is unknown whether males remember the

Fig. 2 Retreat rates of male and female *H. maculosa* after initiating contact with conspecifics of either sex during laboratory trials. The p-values represent statistical differences in the proportion of response behaviours (stay vs retreat) as derived from a mixed-effects logistic regression model



scent of their former mates, impart their chemical signature onto females' skin while mounting to mate (i.e., scent marking), or whether females emit the chemical signature of their stored sperm. While all of these possibilities merit further exploration, scent-marking, despite being widespread among terrestrial animals (Hurst 2005), is not known to occur in marine systems and therefore seems unlikely. It is more probable in this case that males can remember characteristics about the phenotype or possibly the identity of the females with which they have mated, as occurs broadly across social animals (Mateo 2004). The use of chemotactile cues in social recognition may be widespread among male cephalopods. In numerous reported observations of squids, cuttlefishes, and octopuses, including *H. maculosa* (Morse et al. 2018a), males make physical contact with females prior to mating (e.g. *O. vulgaris*, Wells and Wells 1972; *O. digueti*, Voight 1991; *Sepia pharoanis*, Nabhitabhata and Nilaphat 1999; *Sepioteuthis lessoniana*, Wada et al. 2005; and *O. tehuilchus*, Berrueta et al. 2020). This behaviour is performed by both guarding (*S. officinalis*, Allen et al. 2017) and sneaker males (*Doryteuthis opalescens*, Zeidberg 2009). Chemotactile behaviour has long been suspected to play a role in sex recognition in *O. vulgaris* (Wells and Wells 1972), a possibility that is supported here for this and the other species listed above.

Female *H. maculosa* did not appear to use chemotactile cues in this study. This finding is consistent with previous observations that females of this species can already achieve some degree of social recognition from a distance

via chemical cues in the water (Morse et al. 2017). Instead, physical contact initiated by female *H. maculosa* may align with the suspected use of chemotactile behaviour in other female cephalopods: communicating mate choice to males prior to mating (*O. vulgaris*, Wells and Wells 1972; *H. lunulata*, Cheng and Caldwell 2000; *Idiosepius* spp., Nabhitabhata and Suwanamala 2008; and the larger Pacific striped octopus, Caldwell et al. 2015). Copulation by *H. maculosa* is often preceded by a chemotactile phase, which is sometimes initiated by females (Morse et al. 2015, 2018a). However, only nine of the 129 female-initiated chemotactile interactions observed in the current study resulted in copulation (Fig. 1), and females retreated from 42% of the males they contacted (Fig. 2), suggesting that female chemotactile behaviour likely serves more functions in this species than just signalling honest mate choice.

Hapalochlaena maculosa joins the long list of invertebrates that use multiple sensory inputs to facilitate social recognition (e.g. annelids, Lorenzi et al. 2015; and crayfish, Patullo and Macmillan 2015). Multi-modal social recognition may be particularly important for nocturnal (e.g. *H. maculosa*) or eyeless animals (e.g. annelids) for which visual recognition may be difficult or impossible (Aquiloni and Tricarico 2015). Data collection for this study occurred at night, and visual cues were assumed to be limited. Octopuses' sucker-lined arms sense both textures (Wells and Wells 1957) and chemical signatures (Wells et al. 1965; Di Cosmo and Polese 2017; Di Cosmo et al. 2018; van Giesen et al. 2020); either of those inputs, or both, may have been

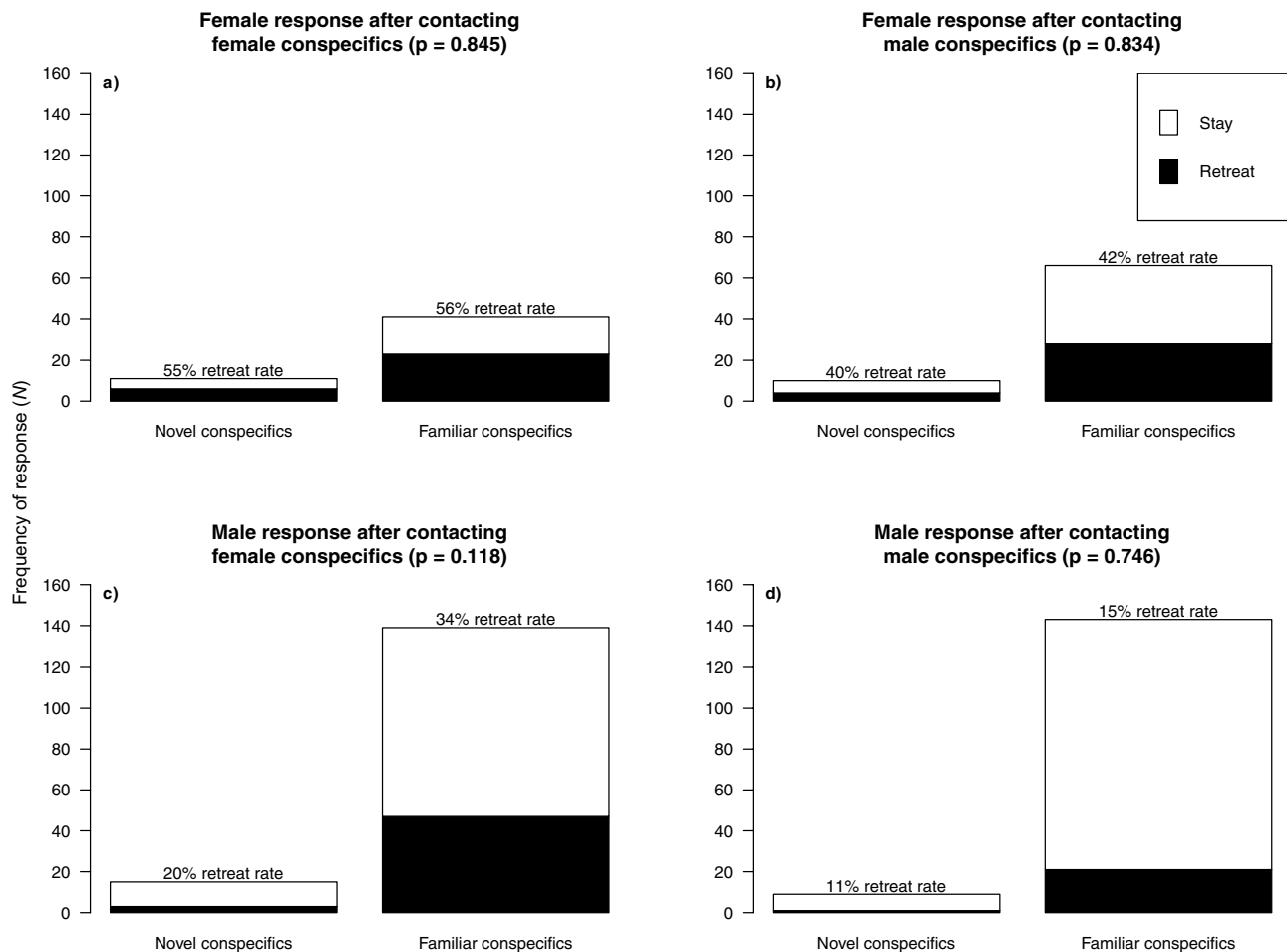


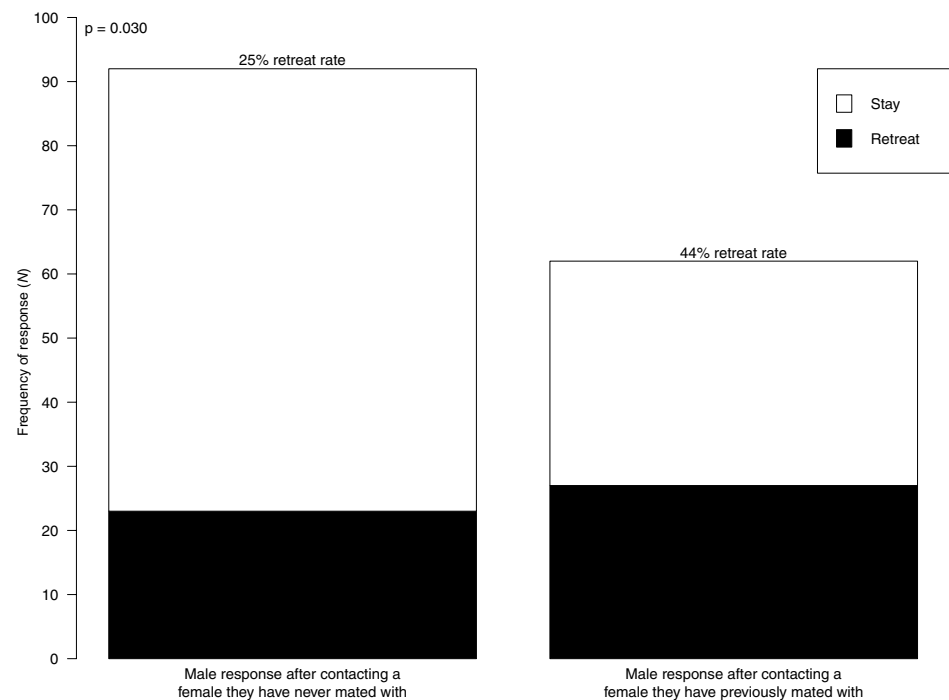
Fig. 3 The response of *H. maculosa* after initiating contact with novel and familiar conspecifics during laboratory trials. The p-values represent statistical differences in the proportion of response behaviours (stay vs retreat) as derived from a mixed-effects logistic regression model

used here. It is suspected in this case that dermal hormones, which can vary by both sex and reproductive status (e.g. *O. bimaculoides*, Chancellor et al. 2021), may be the most likely chemicals assessed and utilised in social recognition here. These chemotactile cues would have complemented other cues (e.g. chemical or possibly visual) sensed from a distance. A prior study of combined visual and chemotactile learning in *O. vulgaris* found these modalities operated largely without interaction (Allen et al. 1986), and the neural underpinnings of visual and chemotactile learning are reported to take place separately within the octopus brain (Wells 1961). *Octopus vulgaris* uses multiple sensory cues to recognize and discriminate between prey types (Maselli et al. 2020). Individuals offered simultaneous access to both visual and chemical recognition cues in prey discrimination tests performed only slightly, or no better, than those offered either chemical cues only, or conflicting sensory inputs (ibid). In these experiments, individual *O. vulgaris* were given up to an hour to make those decisions. By contrast,

H. maculosa in this study only took seconds to sense, process, and prioritise multiple information channels, and make decisions about retreat based on social recognition. While all individuals in this study had access to the same sensory channels, males (this study) and females (Morse et al. 2017) appeared to use different cues in social recognition, suggesting sex differences in this prioritisation of sensory information in decision-making.

In addition to revealing social recognition, patterns of retreat following touch in *H. maculosa* align with previous assessments of its mating system, and may provide insights into prosocial mechanisms that maintain it. Larger females were less likely than smaller females to retreat following contact with conspecifics, regardless of conspecific sex or size. Larger females are also more receptive to mating attempts (Morse et al. 2015). Both of these findings suggest larger female *H. maculosa* are more likely than smaller females to tolerate the presence of conspecifics. However, cannibalism is an extreme form of social intolerance

Fig. 4 The effect of shared mating history on the relative frequency of retreat behaviour by male *H. maculosa* after initiating contact with female conspecifics



(Chiara et al. 2019), and sexual cannibalism occurs in the *Hapalochlaena* genus (Cheng and Caldwell 2000). Where this behaviour has been observed in other octopuses in the wild, it has been expressed by large females (Huffard and Bartick 2015). In order to reproduce successfully, large female octopuses must tolerate males in their presence, and suppress any aggressive motivation to cannibalise before spermatophores have been transferred to the oviduct. It might be that females would be more likely to cannibalise males with which they have already mated, because they have already stored their sperm. If so then this tendency could induce strong selection for males to avoid females that are former mates. Serotonergic neurotransmission may play a role in suppressing aggressive asocial or antisocial tendencies in *O. vulgaris*, thereby releasing conserved prosocial behaviours (Edsinger and Dölen 2018). If this mechanism is present in *H. maculosa* as well, then results here suggest it may develop as females grow in size.

The evolution of chemotactile social recognition by male *H. maculosa* may have been influenced by the risk of sexual cannibalism, and mate preference for novel females in the context of significant biological and ecological constraints. In stomatopods, the species with the best social recognition capabilities are also the most aggressive (Vetter and Caldwell 2015). Given the prevalence of cannibalism among octopuses (Ibáñez and Keyl 2010), males have likely evolved

the means to recognise those individuals most likely to initiate sexual cannibalism (e.g. large females). This recognition may be especially acute for males that also prefer to mate with large females (e.g. *A. aculeatus*, Huffard et al. 2008). Male *H. maculosa* do not share this preference (Morse et al. 2015), but nonetheless appeared more likely to retreat after contacting larger females. It is curious that sex recognition requires male *H. maculosa* to physically contact potentially cannibalistic females, especially when distance chemosensory sex identification can be achieved by females (Morse et al. 2017). Furthermore, males do not appear to use sex identification information to reduce male-male mating attempts. Do males instead require uniquely chemotactile cues to evaluate mate quality? Male *H. maculosa* appear to prefer novel females (Morse et al. 2015), and efforts to maximise mating opportunities with those females yield paternity benefits (Morse et al. 2018a). This choosiness has evolved in the context of limited mating capacity of both males and females (i.e. ~ 50 spermatophores and ~ 50 eggs: Morse et al. 2015), likely significant energy expenditures associated with mating (Franklin et al. 2012), and demersal young with limited dispersal capabilities and gene flow (Morse et al. 2018b). Matings between siblings and half-siblings are less successful than those between more distantly related individual (Morse et al. 2018a). Therefore, it may

pay for males to maximise the total number of mates and therefore the genetic combinations of their young.

The preference of male *H. maculosa* for novel females, supported by chemotactile social recognition, likely benefits both sexes. Females will be freed to mate with more males if repeat pairings are avoided. Polyandry is associated with faster egg production and larger hatchlings in another cephalopod (*Euprymna tasmanica*, Squires et al. 2012). Any risk of male fitness lost to cannibalism while obtaining information about female novelty must be lower than the fitness risk of falsely identifying novel mates (i.e. accidentally mating with the same female twice rather than leaving to seek new females). The fitness risks of a “false positive” in sex identification by males (i.e. seeking a novel female but encountering and attempting copulation with a male) also appear to be low. Male-male chemotactile interactions and mating attempts in *H. maculosa* are common, and rarely lead to aggression or injury (Morse et al. 2015). Contrastingly, females may experience entirely different risks associated with the act of mating. During copulation, male *Hapalochlaena* spp. mounts and wraps his arms tightly around the female’s mantle (Cheng and Caldwell 2000), possibly interfering with ventilation and oxygenation of the gills. Females sometimes expend significant effort to terminate mating attempts by males (Cheng and Caldwell 2000; Morse et al. 2015). Therefore, individual females that can identify males via chemosensory cues from a distance (Morse et al. 2017), and can preclude mating attempts by unpreferred males by avoiding them altogether, may gain a selective advantage.

Conclusion

Social recognition in octopuses points to a number of underexplored connections between male mate preference, sensory biology, neural control, and evolutionary ecology. *Hapalochlaena maculosa* uses multi-channel sensory inputs in rapid decision-making, with apparent sex differences in those mechanisms. The neural templates underpinning sex recognition are likely stable across generations, and therefore unlikely to require learning (Tumulty and Sheehan 2020). By contrast, recognition of former mates is contextual and requires a recognition template to be both learned and updated throughout the lifetime (Tumulty and Sheehan 2020). Hormones may play an important role in this recognition system, both as dermal cues used by males, and by suppressing female aggression allowing for successful conspecific interactions. Finally, the constraints of limited gene flow and reproductive potential of both males and females in this relatively asocial lineage may provide strong selective forces behind the evolution of social recognition and the sensory mechanisms that facilitate it.

Appendix

Appendix 1: Raw frequencies of stay and retreat behaviours by individual focal animals, after initiating chemotactile interaction with conspecifics, during laboratory trials.

Trial	Trial length	Focal animal ID	Focal animal sex	Focal animal size (g)	Conspecific sex																
					Female						Male										
					Novel		Familiar		Unmated		Mated		Novel		Familiar		Unmated		Mated		
Stay (N)	Retreat (N)	Stay (N)	Retreat (N)	Stay (N)	Retreat (N)	Stay (N)	Retreat (N)	Stay (N)	Retreat (N)	Stay (N)	Retreat (N)	Stay (N)	Retreat (N)	Stay (N)	Retreat (N)						
1	120 h	F1	Female	8	-	-	3	4	-	-	-	-	1	0	5	0	3	0	3	0	
		F2		3	0	1	2	4	-	-	-	-	0	1	9	4	9	5	-	-	
		F3		5	0	2	1	2	-	-	-	-	-	-	2	1	2	1	-	-	
		F4		12	2	1	4	1	-	-	-	-	-	-	5	0	2	0	3	0	
		M1	Male	7	3	0	12	9	12	8	3	1	-	-	3	0	-	-	-	-	
		M2		4	1	2	12	6	13	6	0	2	1	0	3	0	-	-	-	-	
		F5	Female	5	-	-	0	2	-	-	-	-	-	1	0	6	3	2	0	5	3
		F6		6	1	0	0	1	-	-	-	-	-	0	1	0	1	0	2	-	-
		M3	Male	4	2	0	5	0	5	0	2	0	1	0	28	2	-	-	-	-	
		M4		3	2	0	9	8	2	0	9	8	1	1	24	6	-	-	-	-	
		M5		4	2	0	6	2	6	1	2	1	-	-	22	4	-	-	-	-	
		M6		3	-	-	9	3	5	0	4	3	-	-	22	2	-	-	-	-	
3	78 h and 43 min	F7	Female	5	-	-	0	1	-	-	-	-	1	0	1	1	1	0	1	1	
		F8		9	-	-	1	1	-	-	-	-	2	0	3	2	2	2	3	0	
		F9		1	1	0	2	3	-	-	-	-	0	1	1	1	1	2	-	-	
		M7	Male	2	1	1	9	2	10	3	-	-	1	0	12	1	-	-	-	-	
		M8		3	-	-	7	8	4	0	3	8	-	-	0	3	-	-	-	-	
		M9		5	1	0	8	5	4	2	5	3	2	0	2	3	-	-	-	-	
		F10	Female	8	-	-	0	5	-	-	-	-	0	1	0	7	0	8	-	-	
		F11		9	1	0	5	0	-	-	-	-	1	0	4	8	2	0	3	8	
		F12		12	0	1	0	0	-	-	-	-	-	-	2	0	2	0	-	-	
		M10	Male	9	-	-	9	3	4	2	5	1	1	0	3	0	-	-	-	-	
		M11		7	-	-	3	0	1	0	2	0	-	-	0	0	-	-	-	-	
		M12		5	-	-	3	1	3	1	-	-	1	0	3	0	-	-	-	-	

g = wet weight in grams; N = frequency of behaviours observed per individual focal animal in response to chemotactile contact with the specified demographic of conspecific; Novel = conspecifics that the focal animal has not yet had a chemotactile interaction with; Familiar = conspecifics that the focal animal has previously had a chemotactile interaction with, regardless of which individual initiated the prior interaction; Unmated = conspecifics of the opposite sex that the focal animal has not copulated with; Mated = conspecifics of the opposite sex that the focal animal has copulated with previously; ‘-’ designates that the focal animal never initiated chemotactile interaction with the specified demographic during trials.

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Declarations

Conflict of interest The authors have not disclosed any competing interests

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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