

Chapter 4

Social Recognition in Hermit Crabs

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Abstract The types of social recognition shown by hermit crabs are reviewed. Three aspects of hermit crab behavioral ecology that are important in social recognition are discussed. First, movement patterns can increase the probability of repeated interactions between individuals, thus increasing the possibility of social recognition based on past experience. Second, the phenomenon of individuality and consistency in the execution of behaviors is a necessary feature for individual social recognition. And finally, the evidence for dominance hierarchies in hermit crabs and the linkage to social recognition are considered. The experimental evidence for social recognition in hermit crabs is reviewed. While most studies have demonstrated just binary or class recognition (e.g., familiar versus non-familiar), the work of Gherardi and coworkers provide good evidence for possible true individual recognition in the hermit crab *Pagurus longicarpus*. The special considerations arising from the use of gastropod shells for protection by hermit crabs are discussed as they relate to aspects of social recognition.

Introduction

The crustaceans called hermit crabs would not have a place in a volume about social recognition, if one considered what is implied by their common name. But hermit crabs do have a rich repertoire of social behaviors (Hazlett 1966) and the hermit crab *Pagurus bernhardus* was one of the first invertebrates to be examined for evidence of social recognition (Hazlett 1969). However, the methodology used in that 1969 paper was not sufficient to establish true individual recognition. Hermit crab behavior is strongly influenced by the use of a mobile shelter and the quality of the inhabited shell affects almost all aspects of hermit crab behavior

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including social interactions (Tricarico and Gherardi 2007; Tricarico et al. 2011). One type of social interaction, territoriality, in the strictness sense is not shown by any hermit crab but if one looks at the gastropod shell occupied as a mobile territory, than all species of hermit crabs are territorial and the search by crabs for a better “territory” is an ongoing aspect of hermit crab behavior that can certainly influence other aspects of their behavior including social recognition.

If we included the processes of sex recognition and kin recognition in the general idea of social recognition, hermit crabs would have a mixed score. Recognition by males of females, and discrimination of individual females that are ready to mate, has been widely reported and olfactory cues are often implicated (e.g., Hazlett 1996a; Goshima et al. 1998). On the other hand kin recognition appears to be unlikely in hermit crabs given the dispersal of planktonic larvae such that close kin are unlikely to be found very near each other. Of the various types of recognition, social recognition and in particular, individual recognition (Steiger and Müller 2008; Tibbetts et al. 2008), have been studied in hermit crabs the most.

This review will, in large part, be a review of recent work of Dr. Gherardi and her coworkers on social recognition because they have done the majority of the research directly addressing social recognition. By incorporating the work of others, I hope to increase the generality of the ideas put forth by Dr. Gherardi. In the first sections of this review I will address some general concepts in ethology and behavioral ecology that are either necessary conditions or at least increase the possibility of social recognition in hermit crabs (repeated interactions, individuality, and dominance hierarchies). I will then focus on recent work examining social recognition in hermit crabs.

Repeated Interactions

For natural selection to favor the ability of individual crabs to recognize signals from particular conspecific individuals, individuals must encounter other individuals repeatedly. This constraint was addressed by Gherardi et al. (2012a) in their seminal review and they mentioned one situation where individual hermit crabs would interact repeatedly, namely interactions at a gastropod predation site. This occurs when a gastropod snail is being eaten by a predatory gastropod and an empty shell will result from the predation. One of the hermit crabs at the site will have access to the new shell and a series of shell switches can take place among the other individual crabs gathered at the site. The hermit crabs gathered at the predation site interact repeatedly for a number of hours or even several days (McLean 1973; Hazlett 1979), establishing an apparent dominance hierarchy with the “alpha” crab in the location where the new empty shell is most likely to appear. Interactions and multiple shell changes at a predation site can be either intraspecific or interspecific (Hazlett et al. 1996). It is conceivable that crabs could have repeated interactions with individuals of other species as they fight via visual displays for the best positions near the predation activity, thus recognition of individuals of other species is a possibility.

Another type of event that can facilitate repeated interactions among individual hermit crabs is their shell exchange behavior. In some species it has been reported that a shell exchange attempt (one crab attempting to obtain the shell inhabited by another crab) attracts other crabs to the site (Rittschof 1980). Numbers of crabs gather around the interacting pair and numerous agonistic interactions occur. While these “scrum” (Hazlett and Rittschof 1997) do not appear as organized as the interactions of crabs at a predation site and they do not appear to last as long as predation sites, repeated interactions between individuals can occur.

In addition to interactions at a predation site or shell exchange attempt, individual hermit crabs have the opportunity to interact repeatedly under other circumstances because their patterns of daily movements keep them near each other. The Caribbean species *Clibanarius tricolor* and *Pagurus miamensis* both aggregate in large clusters of conspecific individuals every day (following dispersal at night) and they orient, by odors from groups of conspecific individuals, to the same group day after day (Hazlett 1966). These groups can be large but repeated individual interactions are possible. Clustering also occurs in the Mediterranean species *Clibanarius erythropus* (Gherardi and Benvenuto 2001). A similar pattern of repeated interactions can occur in the Hawaiian species *Calcinus elegans*, where individuals stay in the same small tide pool for at least 4–7 days, when the crabs occupy certain species of shells (Hazlett and Bach 2009). Similarly, individuals of *Calcinus hazletti* can be found on coral reefs within a few cm of the same location and other marked individuals for at least 3–4 days in a row (Hazlett and Bach, unpublished results of mark-recapture studies). In general, crabs occupying the high intertidal often cluster together at low tide (Gherardi and Vannini 1993) and have the opportunity for repeated interactions among individuals.

It would appear that for a number of species of hermit crabs, movements result in crabs returning to the same location on a daily basis and thus repeated interactions between individuals could occur. In other species, this does not appear to be the case. For example, the daily movements of *Clibanarius vitattus* in North Carolina are quite extensive (individual crabs move many meters daily) and marked individuals do not end up near the same marked individuals very often (Hazlett 1981). If repeated interactions between individuals are a prerequisite for natural selection favoring the capabilities (both sending and receiving signals identifying individuals) necessary to show individual recognition, we can predict which species are more likely to show social recognition (including individual recognition) by knowing something about their patterns of daily movement.

Individuality

It would seem obvious that for hermit crabs to show social recognition, and especially individual recognition, there should be both differences among individuals in some features detectable by receivers and consistency in those differences. Crabs must show differences in some features if other individual crabs are to

detect and react to those differences. And unless crabs are to some degree consistent in their behavioral tendencies, social interactions that include responses to differences in behavioral tendencies should not occur. It may not be critical for social recognition that animals show behavioral syndromes (behaving with similar ranks in the execution of different behaviors), but consistency in at least some behaviors is critical. While some workers have used the term “animal personalities” (see Bergmuller and Traborsky 2010) to indicate that there are consistent differences among individuals, I prefer the non-anthropomorphic term individuality.

While there have been a number of recent studies demonstrating individuality (and behavioral syndromes) in a number of species, there are relatively few such studies involving hermit crabs (Gherardi et al. 2012b). Briffa and coworkers (Briffa et al. 2008; Briffa and Twyman 2011) have shown that individuals of *P. bernhardus* differ from one another in the tendency to execute certain behavior patterns and are consistent in these differences across environmental conditions. However, some aspects of individual consistency in *P. bernhardus* were affected by temperature (Briffa et al. 2013), that is, the degree of consistency can be affected by general environmental conditions. Hazlett and Bach (2012) examined the defensive responses of three species of Hawaiian hermit crabs and found that there were significant individual differences within species in the strength of those responses and that the ranks of crabs in one type of test correlated well with the ranks in a second type of test (i.e., crabs showed behavioral syndromes). However, there was evidence of individuality (and behavioral syndromes) in only two of the species, *Calcinus laevimanus* and *C. elegans*. In the third species, *Calcinus haigae*, there were no significant differences among individuals in the strength of their responses to cues indicating increased predation risk. We can speculate that *C. haigae* is different because it appears to be in very well-fitting shells in nature. It seems clear that we can predict that social recognition and individual recognition would be more likely in individuals of *P. bernhardus*, *C. laevimanus* and *C. elegans* than in individuals of *C. haigae*.

Dominance Hierarchies

When a set of individuals interact repeatedly and there is a predictable winner in agonistic interactions with one animal winning over all others, a “beta” animal winning over all animals except the most dominant, and so on to the omega animal which loses to all others in the group, this is called a dominance hierarchy. In a classical dominance hierarchy the intensity of agonistic interactions decreases over time as individuals presumably recognize each other and retreat from one another without executing the strong displays used in the initial interactions establishing the hierarchy. Social inertia can also contribute to the stability seen in established hierarchies. The hermit crab *Pagurus pollicaris* appears to form dominance hierarchies as they gather around a snail predation site both in the field (McLean 1973) and in the laboratory (Hazlett 1979). However, while the linear order of dominance is quite strong, the intensity of agonistic interactions did not decrease over

time so one could question whether individuals of *P. pollicaris* are recognizing one another based on past interactions or simply reliably reacting to behavioral cues shown by other individuals. That is, an ordered arrangement of dominance could occur without individuals recognizing other individuals based on past interactions. The observations of Gherardi and Atema (2005a) showed that individuals of *Pagurus longicarpus* recognize group members after initial interactions, even before a stable hierarchy is established. However, the recognition reported by Gherardi and Atema (2005b) is binary (familiar versus unfamiliar individuals) rather than individual recognition in the strict sense.

Evidence for Social Recognition in Hermit Crabs

While my 1969 paper on *P. bernhardus* may have been the first to try to examine social recognition in crustaceans, the methodology used was not sufficient to conclude that individual recognition occurs in hermit crabs, and thus the use of quotation marks around the word “individual” in the title of that paper. Crabs that had been repeatedly interacting with one another for a week did interact differently with a “stranger” that was introduced on the last day of observations. Thus individuals of *P. bernhardus* did appear to recognize the class “non-group member” or “unfamiliar” but not necessarily a particular individual.

The recognition of two or more classes of individuals has been termed binary recognition (Boal 1996), and has been reported in the hermit crab *P. longicarpus* Gherardi and Tiedemann (2004a, b). They recorded the frequency of behavior patterns executed by focal individuals when those crabs were exposed either to just chemical cues, just visual cues, or both visual and chemical cues from familiar and unfamiliar conspecifics. The focal crabs clearly differentiated between the classes “familiar” and “unfamiliar” thus showing binary recognition. Moreover, crabs discriminated more clearly using olfactory cues than when using just visual cues. Of course the importance of chemical cues in the behavior of aquatic organisms in general is well known, including the Paguroidea (Gherardi and Tricarico 2011). In addition, Gherardi and Tiedemann (2004a, b) demonstrated that individuals of *P. longicarpus* showed self-recognition, responding differently to self-odor compared to odors from other familiar conspecifics. Multimodal recognition has been reported in other crustaceans (Crook et al. 2004; Aquiloni and Gherardi 2010) thus it is not surprising that hermit crabs may use sensory modalities in addition to olfaction in their social interactions.

The ability of hermit crabs to recognize individuals in the strict sense was tested most critically by Gherardi et al. (2005). Working with *P. longicarpus* they compared the behavior of focal individuals (the “receivers” of potential chemical signals) to two familiar individuals and to two unfamiliar individuals. The two crabs in each of the categories (familiar and unfamiliar) occupied different qualities of shell. In the tests with both classes of “senders”, individual *P. longicarpus* differentiated between self-odor and non-self-odor, as shown by Gherardi and Tiedemann (2004a, b). Receivers did not differentiate between the two unfamiliar

individuals occupying shells of different qualities. However, when the two senders were both familiar to the focal crab, that focal crab responded differently to the two individuals. Moreover, when the senders were placed in shells of different qualities than they inhabited when they first interacted with the focal animals, the discrimination of familiar individuals by the focal crab was no longer shown. That is, individuals of *P. longicarpus* were able to use chemical cues to recognize both individual crabs and something about the quality of the shell which each of the two familiar crabs occupied. In the Gherardi et al. (2005) study, it appears that what could be termed possible true individual recognition occurs. It remains unclear whether crabs were responding to any chemical cues from the shells themselves or to some chemical or chemicals given off by a hermit crab when it is occupying a shell of a particular quality.

In their review, Gherardi et al. (2012a) rightfully question if senders will always profit from identifying themselves. The phenomenon of shell exchanges in hermit crabs may provide a reason for identification. Shell exchanges are energetically expensive for the initiator (Mowles et al. 2010) and dangerous for both crabs given that predators may be attracted to the interaction. In the case of hermit crabs involved in a shell exchange attempt, there could be special complications, which derive from the fact that the “quality” of a particular shell varies with the size of the crab. The signals from the non-initiator crab presumably indicate something about that crab and what the quality of the shell is to that crab. There is a separate piece of information about how good the shell will be to the other crab (the initiator/aggressor) involved in the shell exchange. The advantage to the sending crab (the non-initiator in a shell exchange) is that the signal should indicate to the initiating crab how resistant the non-initiating crab will be to leave its current shell and this information may deter some interactions by a potential initiator (Hazlett 1996b). Initiating crabs (Hazlett 1996b) appeared to select shells occupied by other crabs that were not only better for them in size, but that were not particularly good for the non-initiator occupying them. It would also be advantageous to potential initiators to not repeatedly engage in shell exchange behavior with individuals that will not exchange shells with them assuming the initiators could identify such individuals (as long as they are in the same-quality shell, Gherardi et al. 2005). This avoidance of executing behaviors when success of shell exchange is low is similar to the avoidance of shells with the entrance blocked based upon past experience (Jackson and Elwood 1989). It should be noted that there are advantages to social recognition in shell exchange behaviors whether the crabs appear to be following the negotiations model (Hazlett 1996b) or aggression model (Briffa et al. 1998) of shell exchange.

In their summary of the properties of social recognition systems, Gherardi et al. (2012a) listed a number of potential properties of social recognition systems, in particular true individual recognition, and outlined the extent to which those properties have been demonstrated in hermit crabs. Of the 8 properties, 6 have been demonstrated in hermit crabs, primarily for *P. longicarpus*. One property is compatibility of TIR (True Individual Recognition) with the social system of the study organisms. In this review, I have added some aspects of hermit crab social systems that would increase the occurrence of repeated interactions and thus the possibility

of TIR. A second property is adaptive value of the TIR and I have mentioned a possible additional feature of hermit crab interactions (shell exchange) that may increase the adaptive value of individual recognition. The other four properties listed by Gherardi et al. (2012a) that have been demonstrated in hermit crabs were compatibility of the TIR system with receiver's physiology, association of the TIR system with the receiver's experience, plasticity of templates and matching, and sender specificity of the receiver's actions. The two properties that Gherardi et al. (2012a) felt have not been demonstrated for hermit crabs both involve the signature cues utilized (specificity of signature cues and inter-individual variation of signature cues). Signature cues refer to the signals that are used by a receiver to identify individuals. Almost all published reports on social recognition in hermit crabs suggest that the cues will be chemical in nature, but the chemical identity of those cues and the question of specificity in the cues will require additional research. Variation in signature cues also needs to be addressed explicitly once the class of chemicals used as signature cues has been identified.

In conclusion, as the methodologies developed by Gherardi and co-workers are applied to other species of hermit crabs, we can begin to look at questions of the effects of differences in ecology on social recognition and look for phylogenetic patterns. Both of these lines of inquiry will of course require testing taxa in addition to model organisms such as *P. longicarpus* and *P. bernhardus*.

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