



**HAL**  
open science

# SOCIAL RECOGNITION: A TOP DOWN VIEW OF CEPHALOPOD BEHAVIOUR

J G Boal

► **To cite this version:**

J G Boal. SOCIAL RECOGNITION: A TOP DOWN VIEW OF CEPHALOPOD BEHAVIOUR. Vie et Milieu / Life & Environment, 2006, pp.69-79. hal-03228420

**HAL Id: hal-03228420**

**<https://hal.sorbonne-universite.fr/hal-03228420v1>**

Submitted on 18 May 2021

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

## SOCIAL RECOGNITION: A TOP DOWN VIEW OF CEPHALOPOD BEHAVIOUR

J.G. BOAL

Department of Biology, Millersville University of Pennsylvania, Millersville, PA 17551-0302 USA  
jean.boal@millersville.edu

SOCIALITY  
OCTOPUS  
CUTTLEFISH  
SQUID

**ABSTRACT.** – Social recognition is important to the evolution of cooperative social behavior. Available evidence indicates that at least some cephalopods show some level of social recognition: species, sex and sexual receptivity, and dominance are most likely signaled and recognized in at least some species. Cooperation, including communication, that is based on mutualism is possible. No definitive evidence as yet supports kin recognition, necessary for indirectly selected behavior, or individual recognition, necessary for reciprocity. We have only scratched the surface of cephalopod behavior; field studies coupled with carefully designed laboratory experiments are likely to provide new insights into cephalopod social recognition, cognition, and behavior.

### INTRODUCTION

Have the coleoid cephalopods (hereafter, “cephalopods”) evolved the cognitive, cooperative, and communicative capabilities often found in vertebrates? Clearly, they are capable of learning (reviewed in Sanders 1975, Mather 1995, Hanlon & Messenger 1996; also imprinting, e.g. Darmaillacq *et al.* 2004). But are they communicating with a visual language (Moynihan & Rodaniche 1982), and cooperating to alert each other to danger (“sentinel behavior”, *ibid.*, Moynihan 1985; Hanlon & Forsythe unpublished data, as cited in Hanlon & Messenger 1996)? In this paper, evidence for social recognition in cephalopods is reviewed and is used to distinguish more plausible from less plausible hypotheses about the social behavior of cephalopods.

While this volume is devoted specifically to cuttlefish, our understanding of social recognition in cuttlefish is limited. The scope of this review was expanded so that cuttlefish could be compared with their more solitary relatives, the octopuses, and their more gregarious relatives, the squids, to create a more complete picture of the level of social recognition we can expect from cuttlefish.

#### *Social Recognition*

Social recognition ability ranges widely between species and includes both direct recognition, recognition of the individual or class of individuals, and indirect recognition, recognizing a reliable proxy (e.g. location) for the individual or class of individuals (Colgan 1983, Archawaranon *et al.* 1991, Zayan 1992, 1994, Zayan & Vauclair 1998,

Mateo 2004). Among the categories of individuals that can be recognized are *species* (same/other), *sex* (male/female) and sexual receptivity, *offspring* (own/other), *kin* (kin/non-kin), *familiarity* (familiar/stranger), *mate* (mate/non-mate), *dominance* (dominant/subordinate) or rivals, and *individuals* (unique individual) (Colgan 1983). Species typically show the type of social recognition needed for their life history strategy. For example, some solitary nesting birds do not recognize their offspring from other nestlings, while congener species that nest colonially do (Beecher & Beecher 1979, Medvin *et al.* 1993). More specific types of recognition can be used for less specific categorization, but need not be. For example, stable dominance hierarchies can be maintained with individual recognition; however, they can also be maintained without individual recognition if individuals recognize dominance badges (Colgan 1983), such as feather coloration in great tits (Järvi & Bakken 1984), or other features correlated with dominance, such as size in damselfish (Myrberg 1972).

#### *Cooperation*

Social behavior (e.g. Wilson 1975) can include everything from simple aggregating behavior, such as copepods swarming in sunlit patches of water (Ambler *et al.* 1991), to complex cooperation, such as male dolphins forming coalitions to gain access to mates (Tyack 2003). Interest in sociobiology has focused particularly on cooperative behavior, in which two or more individuals act together to achieve some desired outcome. For such cooperative behavior to evolve, all cooperating participants must benefit, on average, from cooperating (Wilson

1975, Axelrod & Hamilton 1981). Three categories of cooperative behavior are typically recognized (but see discussions in Hammerstein 2003). (i) In mutualism, both individuals benefit directly and immediately from the interaction. For example, pods of dolphins have been observed to work together to herd fish into the shallows where they can be more easily caught and consumed (Gazda *et al.* 2005). All participants benefit because all eat more fish at less energetic cost than if they each fished independently. (ii) In indirect selection, the actor may not benefit directly from the behavior; however, if the benefits to its kin, weighted by their relatedness, outweigh the costs to the actor, the behavior can still be advantageous. For example, in cooperatively breeding cichlids, some individuals do not breed, but instead stay on their natal territory and help with brood care and territory defense. The helpers gain indirect fitness benefits by helping parents produce more brothers and sisters (Brouwer *et al.* 2005). (iii) In reciprocity, the actor could incur some initial cost, but if the recipient returns the favor at a later time, the behavior can still be advantageous. For example, many primates engage in at least some reciprocal grooming (e.g. Manson *et al.* 2004). Reciprocity has proved difficult to document in non-human animals (Stevens & Hauser 2004).

For any species, we can always expect behavior that is directly and immediately selfish, which could include (i) mutualistic cooperation, we can expect (ii) indirectly selected behavior only if individuals can bias their actions to favor kin (i.e. kin recognition), and we can expect (iii) reciprocity only if individuals recognize each other as individuals, to protect against those who do not reciprocate. Clearly, cooperative behavior is closely tied to social recognition ability.

### Social Recognition in Cephalopods

The kind of social recognition we can expect from cephalopods differs by both taxonomic order and species. Octopuses are clearly the most solitary and squids the most gregarious, with cuttlefishes in between. What are reasonable initial hypotheses for social recognition? Species recognition is nearly ubiquitous across animal taxa, and may not require any social experience (Brown & Colgan 1986); it is reasonable to expect that all cephalopods recognize their own species. Recognition of sex (or sexual receptivity) also should be straightforward, as is typical in other mobile, gonochoristic species that mate or spawn in pairs. Offspring recognition appears unlikely because no cephalopod provides parental care beyond the selection of a site for spawning, and guarding and protecting eggs (female octopuses (Boyle 1987) and some deep water squids (Seibel *et al.* 2005)).

Kin recognition also appears unlikely; the young of most cephalopod species are planktonic (Boyle 1987, Hanlon & Messenger 1996), so kin are unlikely to remain in close contact with each other after hatching. Recognition of familiar school members could benefit squids that school in small groups. In fish, familiarity was associated with improved shoal cohesion (Chivers *et al.* 1995), more effective anti-predator behavior, reduced aggression in competitive interactions (Ward *et al.* 2003), and improved social learning (Swaney *et al.* 2001). Evidence for social learning is mixed in cephalopods (positive in *Octopus vulgaris*, Fiorito & Scotto 1992, but see Biederman *et al.* 1993; negative in *Sepia officinalis*, Boal *et al.* 2000a), and orientation toward familiar places rather than toward familiar conspecifics can also result in consistent group membership (Kolm *et al.* 2005). Recognition of familiarity in cephalopods is possible, but not certain. Mate recognition is plausible because many cuttlefishes and squids show pre- and post-copulatory mate guarding (reviewed in Hanlon & Messenger 1996). Cuttlefishes and squids show distinct male-male agonistic behavior (ibid); recognition of relative dominance, or some feature correlated with relative dominance, could be beneficial. Recognition of mates and adversaries could be facilitated by individual recognition; thus, individual recognition is plausible, although not necessary.

Most research on cephalopods has focused on a very small number of species of octopuses, cuttlefishes, and squids. The evidence for recognition in these groups will be reviewed here, with a particular focus on cuttlefishes. Current evidence for recognition will be compared with predictions of recognition based on general life history characteristics (Table I). For further information about cephalopod life histories, and for further citations to original research, readers are directed to the excellent reviews previously published (Boyle 1983a,

Table I. – Social Recognition among Coleioid Cephalopods.

	Hypothesis	Octopuses	Cuttlefishes	Squids
Species	Yes	Inferred	Inferred	Inferred
Sex	Yes	Yes	Yes	Yes
Offspring	No	Yes or Proxy: Location	Untested	Untested
Other Kin	No	Untested	Untested	Yes or Proxy: Location
Familiarity	Maybe	Untested	No; Proxy Possible	Yes or Proxy: Location
Mate	Yes	Yes or Proxy: Location	No; Proxy: Proximity	Yes or Proxy
Dominance	Yes	Yes or Proxy	No; Proxy: Size, Agonistic Intent	No; Proxy Possible
Individuals	Maybe	Untested	No; Proxy Possible	Untested

1987, Hanlon & Messenger 1996) as well as the reviews in this volume. Further discussions of social behavior in invertebrates can be found in Webster & Fiorito (2001).

## OCTOPUSES

### *Field Evidence*

Octopuses are generally solitary, although high densities of some species have been reported (*O. joubini*, Mather 1980, 1982; *O. briareus*, Aronson 1986, 1989; *O. bimaculoides*, Forsythe & Hanlon 1988). No evidence for cooperative behavior among octopuses has been reported. Octopuses forage from temporary home dens that they defend from other octopuses (*O. briareus*, Aronson 1986; *O. bimaculoides*, Cigliano 1993; Forsythe & Hanlon 1997), demonstrating spatial learning and territoriality, respectively. Larger areas around dens are not defended (*O. vulgaris*, Altman 1967; Kayes 1974; *O. dofleini*, Mather *et al.* 1985; *O. briareus*, Aronson 1986, 1989).

Cannibalism, including sexual cannibalism, has been documented in the field (*O. cyanea* near Palau, in the Western Caroline Islands, R Hanlon, pers comm); it could be advantageous for octopuses to recognize the sex and reproductive status of other individuals before approaching closely (Hanlon & Wolterding 1989, Walderon *et al.* submitted). Overall body type is remarkably consistent between octopus species (Voight 1994), with little consistent sexual dimorphism (*ibid.*, Stoskopf & Oppenheim 1996, but see Packard 1961, Voight 1991). In some species, some males show enlarged proximal suckers or a distinct hectocotylus, while other individuals do not show such distinct characteristics (e.g. *O. bimaculoides*, *O. digueti*, Stoskopf & Oppenheim 1996; *O. abdopus*, Huffard 2003). Any recognition of sex could be based on non-visual characteristics (chemical cues, for example).

One octopus species, *O. abdopus*, is reported to show mate guarding and alternate male mating strategies (Huffard 2003). Large male and female pairs occupied adjacent dens for up to five days. Guarding males possessed enlarged proximal suckers and defended females from the approaches of other males. Smaller, "satellite" males, typically lacking enlarged suckers, denned nearby. They were sometimes tolerated by guarding males and occasionally obtained "sneaker" matings with guarded females. These observations, if confirmed, suggest that male octopuses could rely on the (unreliable) visual cue of enlarged suckers to identify male rivals. These data cannot distinguish mate recognition from recognition of place (den).

Adult octopuses sometimes consume smaller conspecifics (Hanlon & Messenger 1996); however, females gradually stop feeding after they lay eggs (*ibid.*), eliminating the need for offspring recognition to insure that they do not consume their own offspring once they hatch (offspring at time of hatching are also much smaller than typical prey). No information is available about the genetic relatedness of neighboring octopuses; thus, nothing is known about possible kin recognition.

### *Laboratory Evidence*

Little experimental data exist on social recognition among octopuses. Recognition of sex appears to vary between species. *O. bimaculoides* distinguished same- from opposite-sex conspecifics using odors alone, as measured by changes in ventilation rate (Walderon *et al.* submitted); however, *Hapalochlaena lunulata* males approached and attempted to mate female and male conspecifics equally often (Cheng & Caldwell 2000).

Female octopuses typically guard their eggs until hatching. In captivity, brooding females sometimes leave their eggs for short periods, particularly early in incubation (*pers obs.*). Recognition of own versus another's eggs has not been explicitly tested. Eggs are typically attached to a substrate, and octopuses show good evidence for spatial learning (*O. vulgaris*, Wells 1964, 1965; *O. cyanea*, Papini & Bitterman 1991; *O. bimaculoides*, Boal *et al.* 2000b), which could explain this return behavior. Thus, indirect recognition of eggs via location is plausible.

Distinct dominant and subordinate behaviors and size-based dominance hierarchies have been reported for numerous species (*O. cyanea*, Yarnall 1969; *O. rubescens*, Dorsey 1976; *O. maya*, Van Heukelem 1977; *O. vulgaris*, Boyle 1980; *O. joubini*, Mather 1980; *E. moschata*, Mather 1985; *O. bimaculoides*, Cigliano 1993). Evidence for dominance recognition among groups of three subjects was found in a study of den use in *O. bimaculoides* (Cigliano 1993). Over the three days of study, attacks by subordinates against dominants decreased, and avoidance of dominants by subordinates increased; for dominants, the behavioral trends were the reverse (*ibid.*). By the end of the study, dominant individuals were able to displace subordinate individuals without any direct interaction. In each group, if the individual intermediate in dominance rank distinguished between the other two octopuses, these results would suggest that relative dominance is recognized among at least one octopus species.

No experimental evidence exists (that this author could find) that explicitly addresses recognition of species, offspring, kin, familiarity, or individuals (Table I). Given the solitary nature of



octopuses, sophisticated social recognition abilities are not expected. Experiments addressing each of these types of recognition could yield valuable data that could inform more difficult field studies. Given how commonly laboratory workers attest to captive octopuses recognizing individual caretakers (including in my laboratory), carefully designed experiments that explicitly address individual recognition among octopuses could prove particularly interesting.

## CUTTLEFISHES

### *Field Evidence*

Cuttlefishes are thought to be solitary most of their lives, forming aggregations of a few to hundreds of individuals for spawning (Hanlon & Messenger 1996). Such aggregations suggest species recognition.

Recognition of sex is likely; sexual dimorphism in body patterning of sexually mature adults is typically obvious and well documented (ibid). In *S. apama*, large males are deceived by smaller males that show body patterning typical of females ("sneaker males" or "female mimics"; Norman *et al.* 1999, Naud *et al.* 2004, Hanlon *et al.* 2005), suggesting that recognition of sex by males is accomplished with visual cues. Observations of pre- and post-copulatory mate guarding by males (*S. latimanus*, Corner & Moore 1980; *S. esculenta*, Natsukari & Tashiro 1991; *S. apama*, Hall & Hanlon 2002) suggest mate recognition (but see laboratory evidence, below).

Evidence supporting the formation of stable groups is lacking. Parental care is limited to the placement of eggs, juveniles disperse from the spawning grounds, and cuttlefish typically move offshore to deeper waters in the winter (Mangold-Wirz 1963, Boyle 1987). These observations provide no evidence suggestive of stable groups that could support recognition of offspring, kin, or familiarity; however, recent work suggests that spawning populations could be genetically distinct (*S. officinalis*, Perez-Losada *et al.* 1999, 2002). Whether any such segregation is accomplished through recognition of kin is not known. Clearly more information is needed to address questions of social recognition under natural conditions.

### *Laboratory Evidence*

Although cuttlefish in typical laboratory tanks rest on the bottom such that they touch one another, those housed in a 6 m diameter round pool spaced themselves as widely as space permitted (*S.*

*officinalis*, Boal *et al.* 1999), supporting the hypothesis that cuttlefish are predominantly solitary.

No experiments exist that explicitly address species recognition in cuttlefish. Visual and chemical cues could both be used. The body patterning of different species is certainly distinctive to humans (reviewed in Hanlon & Messenger 1996). Ventilation rates increased when individuals were exposed to the odors of conspecifics (*S. officinalis*, Boal & Golden 1999); the effect of odors of heterospecific cuttlefish was not tested. Polarized patterns (patterns of light polarization typically found on the arms, around the eyes, and on the foreheads of animals) appear to be important in female recognition of conspecifics (Boal *et al.* 2004). Both male and female *S. officinalis* were more active when they viewed another cuttlefish through transparent glass than when they viewed an empty tank. Females did not increase activity if the viewed conspecific was behind a polarization-distorting filter. Males' activity was unaffected by polarization distortion (ibid).

Recognition of sex has been documented in *S. officinalis*. Interestingly, males appear to distinguish sex using visual cues alone, while females appear to use both visual and chemical cues. In the clearest example of the importance of visual cues to males, unilaterally blinded males did not respond with agonistic, Intense Zebra Displays to males approaching them on the blinded side and challenging them with Intense Zebra Displays (Messenger 1970). This display apparently signals "maleness", or perhaps non-receptivity (females can also show Intense Zebra Displays (Boal *et al.* 2004)), and in the absence of a return signal, the challengers grabbed the blinded individuals in an attempt to copulate (Messenger 1970). In further experiments, males modified their body patterning depending on whether they viewed male or female conspecifics, showing more Intense Zebra Displays to the sight of other males (Boal *et al.* 2004). Males did not show any preference in a y-maze for approaching odors of males or females (Boal & Marsh 1998), suggesting that they did not distinguish between male and female odors. It appears, then, that males rely on visual cues and not chemical cues to recognize sex. Female cuttlefish displayed a newly described body pattern termed Splotch toward their mirror image and toward female conspecifics, but not toward male conspecifics (Palmer *et al.* in press). Females also preferentially approached odors from females rather than odors from males in a y-maze (Boal & Marsh 1998), indicating that female cuttlefish distinguished between the two odor sources. Females probably use both chemical and visual cues to distinguish sex.

Among adult *S. officinalis*, males often mature before females and attempt to mate females that are not yet receptive (pers obs), suggesting that the

males do not recognize sexual receptivity. In a female choice experiment, females preferred males that had recently mated, basing their choices on odor cues alone (Boal 1997), indicating that females do recognize some odor characteristic associated with sexual receptivity.

Although both pre- and post-copulatory mate guarding have been observed in the laboratory and in the field (reviewed in Hanlon & Messenger 1996, see also Hanlon *et al.* 1999, Hall & Hanlon 2002), and humans can distinguish individuals on the basis of unique body patterns (Boal 1996), explicit tests for social recognition in *S. officinalis* revealed no evidence for recognition of either familiarity or mates (*ibid.*). Familiar and unfamiliar same-sex pairs of cuttlefish showed no differences in digitized measures of mantle darkness, congruence of mantle darkness between individuals, movement, distance between individuals, or relative body orientation (*ibid.*). Ventilation rate, a sensitive indicator of arousal in both octopuses (Boyle 1983b) and cuttlefish (Boal & Golden 1999), did not differ when cuttlefish viewed familiar and unfamiliar conspecifics (Boal & Ni 1996). Associations of individuals within a large group of freely moving cuttlefish were not different from random (Boal 1996). In addition, despite clear evidence of mate guarding, no recognition of individual mates was found (*ibid.*). Male-female pairs in adjacent tanks were allowed to mate and establish mate guarding; females were then switched between tanks. Males guarded the new female rather than attempting to copulate, thereby missing an opportunity to fertilize the new females' eggs (*ibid.*). Experimental evidence does not support recognition of familiarity or mates.

Evidence for recognition of dominance is weak. Male *S. officinalis* housed in small groups for several months displayed almost continuously, although with a gradual loss of intensity (Boal 1996). If one male from the group was removed, even for just a few minutes, all males returned to full Intense Zebra Displays once he was returned (*pers obs.*). Laboratory populations of *S. officinalis* established stable dominance hierarchies that influenced feeding (Mather 1986, Warnke 1994, Boal 1996); however, dominance was size-based and statistical, rather than absolute. Relative size could serve as dominance badge in cuttlefish.

Cuttlefish do recognize agonistic intent. In staged encounters between pairs of males, the darkness of the "face" accurately predicted which male-male encounters would escalate to physical contact (Adamo & Hanlon 1996). The authors suggest that the Intense Zebra Display not only serves as a signal of maleness (note that females sometimes show Intense Zebra Displays (Boal *et al.* 2004)), but also as an honest signal of agonistic intent. Females also recognize Intense Zebra Displays as agonistic; in a mate choice experiment,

females avoided males with strong banding patterns (Boal 1997). It is possible that cuttlefish recognize important signals indicating the signaler's motivation rather than the signaler's dominance status.

Cuttlefishes are particularly well-studied, yet definitive evidence for social recognition is quite limited (Table I). Given their relatively solitary life history, with aggregations typically found only at the time of spawning, it is not surprising that recognition appears limited to sex, and perhaps dominance.

## SQUIDS

### *Field Evidence*

Loliginid and some neritic oegopsid squids live in schools (groups with polarized swimming orientation) that range from a few to hundreds of individuals; other squids form more loosely organized shoals (Hanlon & Messenger 1996). Within schools, individuals sometimes sort by size (*Sepioteuthis sepioidea*, Moynihan & Rodaniche 1982, Boom *et al.* 2001; *S. lessoniana*, Adamo & Weichelt 1999) and show distinct spatial organization (*op cit.*; *Illex illecebrosus*, Mather & O'Dor 1984). Species recognition is assumed based on observations of schooling squids; most, but not all, form single-species schools (e.g. *S. sepioidea* sometimes school with *Loligo plei* (Moynihan & Rodaniche 1982, Hanlon & Messenger 1996)).

Recognition of kin has been thought unlikely, at least in part because those squids that school do not begin to do so until they are several weeks old (Boletzky 2001), when they could have already dispersed. New data suggests otherwise. *L. pealeii* migrates between near-shore spawning grounds and off-shore feeding areas; genetic stocks are mixed offshore but segregate inshore (Buresch *et al.* in press). Whether this segregation is accomplished through recognition of kin or place is not yet known.

Field observations indicate that males and females typically show very different displays in mating encounters (reviewed in Hanlon & Messenger 1996), supporting recognition of sex. Males appear to rely on visual cues to distinguish sex. As in *S. officinalis*, male *L. plei* typically approach any conspecific and display an agonistic pattern. If the reply is an agonistic display, the squid is treated as a male; otherwise, the squid is treated as a female (Hanlon & Messenger 1996). In further evidence, large males are deceived by smaller males that show body patterning typical of females ("sneaker males", "female mimics"; *L. vulgaris reynaudii*, Sauer *et al.* 1997; *L. pealei*, Hanlon 1998;

*Sepioteuthis australis*, Jantzen & Havenhand 2003a; *L. bleekeri*, Iwata *et al.* 2005; *S. lessoniana* (laboratory observation), Wada *et al.* 2005).

Membership in smaller groups of *S. sepioidea* appears stable for at least a few days (Moynihan & Rodaniche 1982; Hanlon & Forsythe, unpubl data, as cited in Hanlon & Messenger 1996), and possibly for as long as five weeks (R Byrne, pers comm). Whether group stability is accomplished directly through social recognition (familiarity) or indirectly through spatial learning is currently unclear. Several particular male-female pairs were seen together, from pre- through post-spawning, within a larger stable group over several days (R Byrne, pers comm). Assuming that groups disperse at dusk and reform at dawn (Hanlon & Messenger 1996), this observation suggests that mate recognition is possible.

### Laboratory Evidence

Few laboratory experiments have been conducted on social recognition in squids. Thus far, data are mixed on the question of sex recognition. In one laboratory study, male *S. lessoniana* mated with both females and other males (Boal & Gonzalez 1998). These results could represent an artifact of captivity; however, similar results have been found in the laboratory for octopuses (*Hapalochlaena lunulata*, Cheng & Caldwell 2000) and in the field for some littorinid snails (Erlandsson 2002).

For at least one species of squid, conspecific eggs contain important information that serves to coordinate reproductive behavior (*L. pealeii*, King & Adamo 1999, King *et al.* 2003, Buresch *et al.* 2003, 2004). Recognition of conspecific eggs involves both vision and chemoreception. Squids approach eggs, even when enclosed in a glass container (King & Adamo 1999, King *et al.* 2003); the eggs must be touched and a pheromone, probably a peptide, detected before male-male agonistic behavior associated with competition for females begins (op cit, Buresch *et al.* 2003, 2004). Recognition of conspecific eggs is perhaps a form of species recognition, but is not evidence for offspring recognition because the eggs are not necessarily the offspring of the individual responding to them.

Squids, like cuttlefishes, give distinct displays to communicate agonistic intent (e.g. Lateral Display of *L. plei*; Zebra Spread Display of *S. sepioidea*; Hanlon & Messenger 1996). In *L. plei*, male wild-caught squid established dominance relationships in 1-4 days, with larger males dominant to smaller males (DiMarco & Hanlon 1997). In staged encounters between pairs of males, although winners were larger than losers, contest duration was not correlated to size difference (ibid), sug-

gesting the squid recognized neither dominance nor size as a dominance badge.

Squids are the most gregarious of cephalopods; studies of social recognition in squids could prove highly informative. Field studies are providing tantalizing suggestions for recognition (see Table I), but such hypotheses must be confirmed with carefully controlled experiments. Squids survive captivity poorly, making laboratory experiments with squids exceptionally challenging. Clear, concise questions addressed with simple, elegant experimental designs will be required to answer many of these questions. Clearly the study of social recognition among squids is in its infancy.

## CONCLUSIONS

### Social Recognition

Our understanding of the social behavior of cephalopods is limited by (a) the few species that have been studied, (b) the difficulties inherent in field studies of active, mobile marine animals, and (c) the relative paucity of experimental work explicitly addressing social behavior in cephalopods. To date, we have no evidence to suggest that social recognition in cuttlefishes is different from that in octopuses or squids. With the data available (summarized in Table I), it appears that at least some species of octopuses, cuttlefishes, and squids recognize species and sex. Evidence for or against the recognition of dominance, offspring, other kin, familiarity, mates, and individuals is largely lacking. Clearly, there is much that we do not yet know about social recognition in cephalopods.

Social recognition is expected to evolve only when it is needed. Among cephalopods, other behavioral mechanisms could be adequate. Recognition of a reliable proxy, such as den or substrate for a female octopus and her eggs, physical proximity for a male cuttlefish and his mate, relative size for contesting males, and geographic location for squids that shoal together in the day but forage alone at night, could permit socially discriminative behavior even if direct recognition is lacking. Direct social recognition abilities could be unnecessary for cephalopod life history strategies.

### Cooperation

Based on the fragmentary data available, it appears reasonable to expect cooperation in cephalopods that is directly selfish (i, mutualism), while cooperation that requires recognition of kin (ii, indirect selection) or individual recognition (iii, reciprocity) is probably unlikely. Squids are clearly the most gregarious of the cephalopods; experiments



addressing social recognition in squids would be particularly illuminating.

Moynihan (Moynihan & Rodaniche 1982, Moynihan 1985) and others (Hanlon & Forsythe unpubl data, as cited in Hanlon & Messenger 1996) have suggested that *S. sepioidea* shows sentinel behavior. Sentinel behavior occurs when vigilance is divided among group members such that an individual (a) takes turns in a conspicuous location watching for danger instead of foraging or resting, and (b) alerts other individuals in less conspicuous locations to the arrival of potential danger (Bednekoff 1997). Is this plausible for cephalopods? It was long thought that sentinels incurred greater risk of mortality than foragers; consequently, sentinel behavior required either (ii) indirect selection or (iii) reciprocity to evolve. Recent data suggest that sentinels could be in less danger than foragers, and models (ibid) and empirical evidence (e.g. Clutton-Brock *et al.* 1999, Wright *et al.* 2001, Bednekoff & Woolfenden 2003) indicate that sentinel behavior can be supported by behavior that is directly selfish. For the sentinel-like behavior of squids to constitute true sentinel behavior, evidence must be provided to show that individual squid take turns functioning as sentinels (condition a, above), and that sentinels do not produce the same "alarm signals" when they are alone as they do when they are in a group (condition b, above). The details of possible sentinel behavior in cephalopods remain to be explored, but sentinel behavior could prove to be an example of complex social behavior in cephalopods that does not rely on social recognition.

Communication is fundamental to many forms of cooperation. It is often speculated that the three most famous attributes of cephalopods, complex nervous systems, sophisticated visual systems, and complex body patterning, could all serve to support complex, visual intraspecific communication. Moynihan articulated this hypothesis most clearly with his suggestion that cephalopods have a sophisticated social behavior that includes visual language, accomplished through rapid changes in body patterning (Moynihan & Rodaniche 1982). Shashar and colleagues followed up on an earlier discovery that octopuses perceive the orientation of polarized light (Moody & Parriss 1960, Moody 1962), and demonstrated that squid and cuttlefish can control the polarization of their own body patterns (Shashar & Cronin 1996, Shashar & Hanlon 1997, Shashar *et al.* 2002). They suggested that the polarization of body patterns could serve as an additional, "hidden communication channel" (Shashar *et al.* 1996), free from the kind of "eaves dropping" by vertebrate predators that visual communication using achromatic signals would enable.

Signals that contain information associated with reproduction, such as species, sex and receptivity, and fitness advertisements, benefit the signaler to

the extent that they are perceived and responded to by potential mates, and benefit the recipient to the extent that the recipient is also looking for mating opportunities. As such, they are an example of (i) mutualism. As expected, such mating signals are widespread throughout the animal kingdom, and have been documented for cuttlefishes, squids, and possibly also octopuses (op cit; reviewed in Hanlon & Messenger 1996). Communication of agonistic intent benefits both senders and receivers if it results in fewer risky confrontations (Adamo & Hanlon 1996); such signals have been documented in both cuttlefishes and squids (reviewed in Hanlon & Messenger 1996). Detailed descriptions of body patterning (ibid; see also *S. officinalis*, Hanlon & Messenger 1988; *L. pealei*, Hanlon *et al.* 1999; *S. sepioidea*, Byrne *et al.* 2003; *S. australis*, Jantzen & Havenhand 2003b), the mechanisms underlying the control of patterning (reviewed in Messenger 2001; see also Chiao & Hanlon 2001a, 2001b, Gaston & Tublitz 2004, Chiao *et al.* 2005), and the functional significance of body patterning (op cit; cf *S. officinalis*, Hanlon *et al.* 1999; *L. opalescens*, Hunt *et al.* 2000; *O. cyanea*, Mather & Mather 2004; *S. sepioidea*, Mather *et al.* a, b submitted) are active areas of current research. In addition, chemical communication in cephalopods is a new area of research that is expanding rapidly. Thus far, it is clear that octopuses (Walderon *et al.* submitted), cuttlefishes (Boal 1997, Boal & Golden 1999, Boal & Marsh 1999, Boal & Nagle unpublished data; see also Henry *et al.* 1999, Zatylny *et al.* 2000a,b, Marvin *et al.* 2001, Zatylny *et al.* 2002), and squids (King & Adamo 1999, King *et al.* 2003, Buresch *et al.* 2003, 2004) all use chemical signals to coordinate reproductive behavior. To date, cephalopod communication appears to support directly selfish behavior, including (i) mutualism. We can expect further progress in our understanding of cephalopod communication in the future.

ACKNOWLEDGMENTS. – I thank RT Hanlon & RA Byrne for their helpful comments on previous drafts of this manuscript, L Dickel for his help with translations, and two anonymous referees for their exceptionally helpful assistance with references. This work was supported by National Science Foundation grant #IOB 0414546.

## REFERENCES

- Adamo SA, Hanlon RT 1996. Do cuttlefish (Cephalopoda) signal their intentions to conspecifics during agonistic encounters? *Anim Behav* 52: 73-81.
- Adamo SA, Weichelt KJ 1999. Field observations of schooling in the oval squid, *Sepioteuthis lessoniana* (Lesson, 1830). *J Moll Stud* 65: 377-380.
- Altman JS 1967. The behaviour of *Octopus vulgaris* Lam. in its natural habitat: a pilot study. *Underw Assoc Rep* 1966-67: 77-83.



- Ambler JW, Ferrari FD, Fornshell JAI 1991. Population structure and swarm formation of the cyclopoid copepod *Dioithona oculata* near mangrove cays. *J Plankton Res* 13(6): 1257-1272.
- Archawaranon M, Dove L, Wiley RH 1991. Social inertia and hormonal control of aggression and dominance in white-throated sparrows. *Behaviour* 118: 42-64.
- Aronson, RB 1986. Life history and den ecology of *Octopus briareus* Robson in a marine lake. *J Exp Mar Biol Ecol* 95: 37-56.
- Aronson, RB 1989. The ecology of *Octopus briareus* Robson in a Bahamian saltwater lake. *Am Malac Bull* 7: 47-56.
- Axelrod R, Hamilton WD 1981. The evolution of cooperation. *Science* 211: 1390-1396.
- Bednekoff PA 1997. Mutualism among safe, selfish sentinels: a dynamic game. *Am Nat* 150(3): 373-392.
- Bednekoff PA, Woolfenden GE 2003. Florida scrub-jays (*Aphelocoma coerulescens*) are sentinels more when well-fed (even with no kin nearby). *Ethology* 109: 895-903.
- Beecher MD, Beecher IM 1979. Sociobiology of bank swallows: reproductive strategy of the male. *Science* 205: 1282-1285.
- Biederman GB, Davey VA, Suboski MD, Muir D, Hall D, Fiorito G 1993. Social Learning in Invertebrates. *Science* 259: 1627-1629.
- Boal JG 1996. Absence of social recognition in laboratory-reared cuttlefish, *Sepia officinalis*, L. (Mollusca: Cephalopoda). *Anim Behav* 52(3): 529-537.
- Boal JG 1997. Female choice of males in cuttlefish (Mollusca: Cephalopoda). *Behaviour* 134: 975-988.
- Boal JG, Dunham AW, Williams KT, Hanlon RT 2000b. Experimental Evidence for Spatial Learning in Octopuses (*Octopus bimaculoides*). *J Compar Psychol* 114(3): 246-252.
- Boal JG, Golden DK 1999. Distance chemoreception in the common cuttlefish, *Sepia officinalis* (Mollusca: Cephalopoda). *J Exp Mar Biol Ecol* 235: 307-317.
- Boal JG, Gonzalez SA 1998. The social behavior of individual oval squids (*Sepioteuthis lessoniana*) within a captive school. *Ethology* 104: 161-178.
- Boal JG, Hylton R, Gonzalez SA, Hanlon RT 1999. Effects of crowding on the social behavior of cuttlefish (*Sepia officinalis*). *Contemp Top Lab Anim Sci* 38: 49-55.
- Boal JG, Marsh S 1998. Social recognition using chemical cues in *Sepia officinalis* (Mollusca: Cephalopoda). *J Exp Mar Biol Ecol* 230: 783-792.
- Boal JG, Ni JN 1996. Ventilation rate of cuttlefish in response to visual stimuli. *Veliger* 39(4): 342-347.
- Boal JG, Shashar N, Grable M, Vaughan K, Loew E, Hanlon RT. 2004. Behavioral evidence for intraspecific signals with achromatic and polarized light by cuttlefish (Mollusca: Cephalopoda). *Behaviour* 141: 837-861.
- Boal JG, Wittenberg KM, Hanlon RT 2000a. Observational learning does not explain improvement in predation tactics by cuttlefish (Mollusca: Cephalopoda). *Behav Proc* 52: 141-153.
- Boletzky Sv 2001. The visual world of hatchling and juvenile cephalopods. *Adv Ethol* 36: 86.
- Boom S, Byrne RA, Mather JA 2001. Schooling behavior of the Caribbean reef squid *Sepioteuthis sepioidea* in Bonaire. *Adv Ethol* 36: 88.
- Boyle PR 1980. Home occupancy by male *Octopus vulgaris* in a large seawater tank. *Anim Behav* 28: 1123-1126.
- Boyle PR ed. 1983a. Cephalopod Life Cycles. Vol. 1: Species Accounts. Academic Press, London.
- Boyle PR ed. 1983b. Ventilation rate and arousal in the octopus *Octopus vulgaris*. *J Exp Mar Biol Ecol* 69(2): 129-136.
- Boyle PR 1987. Cephalopod Life Cycles. Vol. 2: Comparative Reviews. Academic Press, London.
- Brouwer L, Heg D, Taborsky M 2005. Experimental evidence for helper effects in a cooperatively breeding cichlid. *Behav Ecol* 16(3): 667-673.
- Brown JA, Colgan PW 1986. Individual and species recognition in centrarchid fishes: evidence and hypotheses. *Behav Ecol Sociobiol* 19: 373-379.
- Buresch KC, Boal JG, Knowles J, DeBose J, Nichols A, Erwin A, Painter SD, Nagle GT, Hanlon RT 2003. Contact chemosensory cues in egg bundles elicit male-male agonistic conflicts in the squid *Loligo pealeii* (Mollusca: Cephalopoda). *J Chem Ecol* 29(3): 547-560.
- Buresch KC, Boal JG, Nagle GT, Knowles J, Nobuhara R, Sweeney K, Hanlon RT 2004. Experimental evidence that ovary and oviducal gland extracts influence male agonistic behavior in squids. *Biol Bull* 206: 1-3.
- Buresch KC, Gerlach G, Hanlon RT. In press. Multiple genetic stocks of the longfin inshore squid *Loligo pealeii* in the NW Atlantic: stocks segregate inshore in summer, but aggregate offshore in winter. *Mar Ecol Prog Ser*.
- Byrne R, Griebel U, Wood JB, Mather JA 2003. Squids say it with their skin: a graphic model for skin displays in Caribbean reef squid *Sepioteuthis sepioidea*. In Warnke K, Keupp H, Boletzky S v eds, Coleoid Cephalopods Through Time. *Berliner Palaobiol Abh* 3: 29-35.
- Cheng MW, Caldwell RL 2000. Sex identification and mating in the blue-ringed octopus, *Hapalochlaena lunulata*. *Anim Behav* 60 (1): 27-33.
- Chiao CC, Hanlon RT 2001a. Cuttlefish camouflage: visual perception of size, contrast and number of white squares on artificial checkerboard substrata initiates disruptive coloration. *J Exp Biol* 204: 2119-2125.
- Chiao CC, Hanlon RT 2001b. Cuttlefish Cue Visually on Area – Not Shape or Aspect Ratio – of Light Objects in the Substrate to Produce Disruptive Body Patterns for Camouflage. *Biol Bull* 201: 269-270.
- Chiao CC, Kelman EJ, Hanlon RT 2005. Disruptive body patterning of cuttlefish (*Sepia officinalis*) requires visual information regarding edges and contrast of objects in natural substrate backgrounds. *Biol Bull* 208: 7-11.
- Chivers DP, Brown GE, Smith R, Jan F 1995. Familiarity and shoal cohesion in fathead minnows (*Pimephales promelas*): Implications for antipredator behaviour. *Can J Zool* 73(5): 955-960.
- Cigliano JA 1993. Dominance and den use in *Octopus bimaculoides*. *Anim Behav* 46: 677-684.

- Clutton-Brock TH, O'Riain MJ, Brotherton PNM, Gaynor D, Kansky R, Griffin AS, Manser M 1999. Selfish sentinels in cooperative mammals. *Science* 284: 1640-1644.
- Colgan P 1983. Comparative Social Recognition. John Wiley & Sons, New York.
- Corner BD, Moore HT 1980. Field observations on the reproductive behavior of *Sepia latimanus*. *Micronesica* 16: 235-260.
- Darmaillacq A-S, Chichery R, Poirier R, Dickel L 2004. Effect of early feeding experience on subsequent prey preference by cuttlefish, *Sepia officinalis*. *Devel Psychobiol* 45(4): 239-244.
- DiMarco FP, Hanlon RT 1997. Agonistic behavior in the squid *Loligo plei* (Loliginidae, Teuthoidea): fighting tactics and the effects of size and resource value. *Ethology* 103: 89-108.
- Dorsey EM 1976. Natural history and social behavior of *Octopus rubescens* Berry. M Sc thesis, Univ Washington.
- Erlandsson J 2002. Do reproductive strategy and breeding season influence the presence of mate recognition in the intertidal snail *Littorina*? *Invert Reprod Devel* 41(1-3): 53-60
- Fiorito G, Scotto P 1992. Observational learning in *Octopus vulgaris*. *Science* 256: 545-547.
- Forsythe JW, Hanlon RT 1988. Behavior, body patterning and reproductive biology of *Octopus bimaculoides* from California. *Malacologia* 29(1): 41-55.
- Forsythe JW, Hanlon RT 1997. Foraging and associated behavior by *Octopus cyanea* Gray 1849, on a coral atoll, French Polynesia. *J Exp Mar Biol Ecol* 209: 15-31.
- Gaston MR, Tublitz NJ 2004. Peripheral innervation patterns and central distribution of fin chromatophore motoneurons in the cuttlefish *Sepia officinalis*. *J Exp Biol* 207: 3089-3098.
- Gazda SK, Connor RC, Edgar RK, Cox F 2005. A division of labour with role specialization in group-hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. *Proc R Soc Lond B* 272 (1559): 135-140.
- Hall KC, Hanlon RT 2002. Principle features of the mating system of a large spawning aggregation of the giant Australian cuttlefish *Sepia apama* (Mollusca: Cephalopoda). *Mar Biol* 140(3): 533-545.
- Hammerstein P 2003. Genetic and Cultural Evolution of Cooperation. MIT press and Dahlem University Press, 450 p.
- Hanlon RT 1998. Mating systems and sexual selection in the squid *Loligo*: how might commercial fishing on spawning squids affect them? *CalCOFI Rep* 39: 92-100.
- Hanlon RT, Ament SA, Gabr H 1999. Behavioral aspects of sperm competition in cuttlefish, *Sepia officinalis* (Sepioidea: Cephalopoda). *Mar Biol* 134: 719-728.
- Hanlon RT, Maxwell MR, Shashar N, Loew ER, Boyle K-L 1999. An ethogram of body patterning behavior in the biomedically and commercially valuable squid *Loligo pealei* off Cape Cod, Massachusetts. *Biol Bull* 197: 49-62.
- Hanlon RT, Messenger JB 1988. Adaptive coloration of young cuttlefish (*Sepia officinalis* L.): the morphology and development of body patterns and their relation to behaviour. *Phil Trans R Soc Lond B* 320: 437-487.
- Hanlon RT, Messenger JB 1996. Cephalopod Behaviour. Cambridge Univ Press, Cambridge.
- Hanlon RT, Naud MJ, Shaw PW, Havenhand JN 2005. Behavioural ecology: Transient sexual mimicry leads to fertilization. *Nature* 433: 212.
- Hanlon RT, Wolterding MR 1989. Behavior, body patterning, growth and life history of *Octopus briareus* cultured in the laboratory. *Am Malacol Bull* 7(1): 21-45.
- Henry J, Zatylny C, Boucaud-Camou E 1999. Peptidergic control of egg-laying in the cephalopod *Sepia officinalis*: involvement of the FMRFamide and FMRFamid-related peptides. *Peptides* 20: 1061-1070.
- Huffard CL 2003. Mating strategies in a member of the *Octopus abdopus* sub-genus from Sulawesi Indonesia: first report of mate guarding in *Octopus*. In Cephalopod International Advisory Council. Biology, Recruitment & Culture of Cephalopods. 17-21 February, Phuket, Thailand.
- Hunt JC, Zeidberg LD, Hamner WM, Robison BH 2000. The behaviour of *Loligo opalescens* (Mollusca: Cephalopoda) as observed by a remotely operated vehicle (ROV). *J Mar Biol Assoc UK* 80: 873-883.
- Iwata Y, Munehara H, Sakurai, Y 2005. Dependence of paternity rates on alternative reproductive behaviors in the squid *Loligo bleekeri*. *Mar Ecol Prog Ser* 298: 219-228.
- Jantzen TM, Havenhand JN 2003a. Reproductive behavior in the squid *Sepioteuthis australis* from south Australia: Interactions on the spawning ground. *Biol Bull* 204: 305-317.
- Jantzen TM, Havenhand JN 2003b. Reproductive behavior in the squid *Sepioteuthis australis* from south Australia: Ethogram of reproductive body patterns. *Biol Bull* 204: 290-304.
- Järvi T, Bakken M 1984. The function of the variation in the breast stripe of the great tit (*Parus major*). *Anim Behav* 32(2): 590-596.
- Kayes RJ 1974. The daily activity pattern of *Octopus vulgaris* in a natural habitat. *Mar Behav Physiol* 2: 337-343.
- King AJ, Adamo SA 1999. Contact with squid egg capsules increases agonistic behavior in male squid (*Loligo pealei*). *Biol Bull* 197: 256.
- King AJ, Adamo SA, Hanlon RT 2003. Squid egg mops provide sensory cues for increased agonistic behavior between male squid. *Anim Behav* 66: 49-58.
- Kolm N, Hoffman EA, Olsson J, Berglund, A Jones AG 2005. Group stability and homing behavior but no kin group structures in a coral reef fish. *Behav Ecol* 16(3): 521-527.
- Mangold-Wirz K 1963. Biologie des Céphalopodes benthiques et nectoniques de la Mer Catalane. *Vie Milieu Suppl* 13: 1-285.
- Manson JH, Navarrete CD, Silk JB 2004. Time-matched grooming in female primates? New analyses from two species. *Anim Behav* 67(3): 493-500.
- Marvin LF, Zatylny C, Leprince J, Vaudry H, Henry J 2001. Characterization of a novel *Sepia officinalis* neuropeptide using MALDI-TOF MS and post-source decay analysis. *Peptides* 22: 1391-1396.

- Mateo JM 2004. Recognition systems and biological organization: The perception component of social recognition. *Ann Zool Fennici* 41(6): 729-745.
- Mather JA 1980. Social organization and use of space by *Octopus joubini* in a semi-natural situation. *Bull Mar Sci* 30: 848-857.
- Mather JA 1982. Factors affecting the spatial distribution of natural populations of *Octopus joubini* Robson. *Anim Behav* 30(4): 1166-1170.
- Mather JA 1985. Behavioural interactions and activity of captive *Eledone moschata*: Laboratory investigations of a "social" octopus. *Anim Behav* 33(4): 1138-1144.
- Mather JA 1986. A female-dominated feeding hierarchy in juvenile *Sepia officinalis* in the laboratory. *Mar Freshw Behav Physiol* 12(4): 233-244.
- Mather JA 1995. Cognition in Cephalopods. *Adv Study Behav* 24: 317-353.
- Mather JA, Griebel U, Byrne RA. a. Sending the right message: Characteristics of squid skin displays addressed to different receivers. Submitted.
- Mather JA, Griebel U, Byrne RA. b. Squid dances: movement and postures of *Sepioteuthis sepioidea* with a muscular hydrostat system. Submitted.
- Mather JA, Mather DL 2004. Apparent movement in a visual display: the 'passing cloud' of *Octopus cyanea* (Mollusca: Cephalopoda). *J Zool* 263: 89-94.
- Mather JA, O'Dor RK 1984. Spatial organization of schools of the squid *Illex illecebrosus*. *Mar Freshw Behav Physiol* 10(4): 259-271.
- Mather JA, Resler A, Cosgrove J 1985. Activity and movement of *Octopus dofleini*. *Mar Behav Physiol* 11: 301-314.
- Medvin MMB, Stoddard PK, Beecher MD 1993. Signals for parent-offspring recognition: a comparative analysis of the begging calls of cliff swallows and barn swallows. *Anim Behav* 45: 841-850.
- Messenger JB 1970. Optomotor responses and nystagmus in intact, blinded and statocystless cuttlefish (*Sepia officinalis* L.). *J Exp Biol* 53: 789-796.
- Messenger JB 2001. Cephalopod chromatophores: neurobiology and natural history. *Biol Rev* 76: 473-528.
- Moody MF 1962. Evidence for the intraocular discrimination of vertically and horizontally polarised light by *Octopus*. *J Exp Biol* 134: 119-129.
- Moody MF, Parriss JR 1960. Discrimination of polarized light by *Octopus*. *Nature* 186: 839-840.
- Moynihan M 1985. Communication and Noncommunication by Cephalopods. Indiana University Press, Bloomington.
- Moynihan M, Rodaniche AF 1982. The behavior and natural history of the Caribbean reef squid *Sepioteuthis sepioidea*. With a consideration of social, signal and defensive patterns for difficult and dangerous environments. *Adv Ethol* 25: 1-151.
- Myrberg A 1972. Social dominance and territoriality in the bicolor damselfish *Eupomacentrus partitus* (Poey) (Pisces: Pomacentridae). *Behaviour* 41(3-4): 207-231.
- Natsukari Y, Tashiro M 1991. Neritic squid resources and cuttlefish resources in Japan. *Mar Behav Physiol B* 18: 149-226.
- Naud MJ, Hanlon RT, Hall KC, Shaw PW, Havenhand JN 2004. Behavioural and genetic assessment of reproductive success in a spawning aggregation of the Australian giant cuttlefish, *Sepia apama*. *Anim Behav* 67(6): 1043-1050.
- Norman MD, Finn J, Tregenza T 1999. Female impersonation as an alternate reproductive strategy in giant cuttlefish. *Proc R Soc Lond B*: 266: 1347-1349.
- Packard A 1961. Sucker display of *Octopus*. *Nature* 190: 736-737.
- Palmer ME, Calvé R, Adamo SA. Response of female cuttlefish *Sepia officinalis* (Cephalopoda) to mirrors and conspecifics: evidence for signaling in female cuttlefish. *Anim Cogn*. In press.
- Papini MR, Bitterman ME 1991. Appetitive conditioning in *Octopus cyanea*. *J Compar Psychol* 105: 107-114.
- Perez-Losada M, Guerra A, Sanjuan A 1999. Allozyme differentiation in the cuttlefish *Sepia officinalis* (Mollusca: Cephalopoda) from the NE Atlantic and Mediterranean. *Heredity* 83(3): 280-289.
- Perez-Losada M, Guerra A, Carvalho GR, Sanjuan A, Shaw PW 2002. Extensive population subdivision of the cuttlefish *Sepia officinalis* (Mollusca: Cephalopoda) around the Iberian Peninsula indicated by microsatellite DNA variation. *Heredity* 89(6): 417-424.
- Sanders GD 1975. The Cephalopods. In: Corning WC ed, Invertebrate Learning, Vol. 3. Plenum, New York: 1-101.
- Sauer WHH, Roberts MJ, Lipinski MR, Smale MJ, Hanlon RT, Webber DM, O'Dor RK 1997. Choreography of squid's "nuptial dance." *Biol Bull* 192: 203-207.
- Seibel BA, Robison BH, Haddock SHD 2005. Post-spawning egg care by a squid. *Nature* 438: 929.
- Shashar N, Cronin TW 1996. Polarization contrast vision in *Octopus*. *J Exp Biol* 199(4): 999-1004.
- Shashar N, Rutledge PS, Cronin TW 1996. Polarization vision in cuttlefish – a concealed communication channel? *J Exp Biol* 199(9): 2077-2084.
- Shashar N, Hanlon R 1997. Squids (*Loligo pealeii* and *Euprymna scolopes*) can exhibit polarized light patterns produced by their skin. *Biol Bull* 193: 207-208.
- Shashar N, Milbury CA, Hanlon RT 2002. Polarization vision in cephalopods: neuroanatomical and behavioral features that illustrate aspects of form and function. *Mar Freshw Behav Physiol* 35(1-2): 57-68.
- Stevens JR, Hauser MD 2004. Why be nice? Psychological constraints on the evolution of cooperation. *Trends Cogn Sci* 8(2): 60-65.
- Stoskopf MK, Oppenheim BS 1996. Anatomic features of *Octopus bimaculoides* and *Octopus digueti*. *J zoo wildl* 27(1): 1-18.
- Swaney W, Kendal J, Capon H, Brown C, Laland KN 2001. Familiarity facilitates social learning of foraging behaviour in the guppy. *Anim Behav* 62(3): 591-598.
- Tyack P 2003. Animal social complexity: Intelligence, culture, and individualized societies. In de Waal FBM, Tyack PL eds, Animal Social Complexity: Intelligence, Culture, and Individualized Societies. Harvard University Press, Cambridge, MA: 342-362.
- Van Heukelem WF 1977. Laboratory maintenance, breeding, rearing, and biomedical research potential of the Yucatan octopus (*Octopus maya*). *Lab Anim Sci* 27: 852-859.
- Voight JR 1991. Enlarged suckers as an indicator of male maturity in *Octopus*. *Bull Mar Sci* 49(1-2): 98-106.



- Voight JR 1994. Morphological variation in shallow-water octopuses (Mollusca: Cephalopoda) *J Zool Lond* 232(3): 491-504.
- Wada T, Takegaki T, Mori T, Natsukari Y 2005. Alternative male mating behaviors dependent on relative body size in captive oval squid *Sepioteuthis lessoniana* (Cephalopoda, Loliginidae). *Zool Sci* 22: 645-651.
- Walderon MD, Prosser KN, Nagle GT, Holm JB, Boal JG. Evidence for water-borne pheromonal communication in *Octopus bimaculoides*. Submitted.
- Ward AJW, Axford S, Krause J 2003. Cross-species familiarity in shoaling fishes. *Proc Roy Soc Lond B* 270(1520): 1157-1161.
- Warnke K 1994. Some aspects of social interaction during feeding in *Sepia officinalis* (Mollusca: Cephalopoda) hatched and reared in the laboratory. *Vie Milieu* 44(2): 125-131.
- Webster SJ, Fiorito G 2001. Socially guided behaviour in non-insect invertebrates. *Anim Cogn* 4(2): 69-79.
- Wells MJ 1964. Detour experiments with octopuses. *J Exp Biol* 41: 621-642.
- Wells MJ 1965. Learning and movement in octopuses. *Anim Behav* Suppl 1: 115-128.
- Wilson EO 1975. Sociobiology. Belknap Press of Harvard University Press, Cambridge, MA.
- Wright J, Maklakov AA, Khazin V 2001. State-dependent sentinels: an experimental study in the Arabian babbler. *Proc R Soc Lond B* 268: 821-826.
- Yarnall JL 1969. Aspects of the behaviour of *Octopus cyanea* Gray. *Anim Behav* 17: 747-754.
- Zatylny C, Gagnon J, Boucaud-Camou E, Henry J 2000a. ILME: A waterborne pheromonal peptide released by the eggs of *Sepia officinalis*. *Biochem Biophys Res Comm* 275(1): 217-222.
- Zatylny C, Gagnon J, Boucaud-Camou E, Henry J 2000b. The SepOvotropin: A new ovarian peptide regulating oocyte transport in *Sepia officinalis*. *Biochem Biophys Res Comm* 276(3): 1013-1018.
- Zatylny C, Marvin L, Gagnon J, Henry J 2002. Fertilization in *Sepia officinalis*: The first mollusk sperm-attracting peptide. *Biochem Biophys Res Comm* 296(5): 1186-1193.
- Zayan R 1992. La représentation du congénère individuel chez les Gallinacés. *Psychol Fr* 37: 37-46.
- Zayan R 1994. Special issue: individual and social recognition. *Behav Proc* 33: 246.
- Zayan R, Vauclair J 1998. Categories as paradigms for comparative cognition. *Behav Proc* 42: 87-99.

Received October 10, 2005  
Accepted November 2, 2005