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RESEARCH ARTICLE

Mating behavior of *Abdopus aculeatus* (d'Orbigny 1834) (Cephalopoda: Octopodidae) in the wild

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Abstract The mating system of *Abdopus aculeatus* incorporates sneaker matings, mate guarding, sex-specific body patterns, frequent copulations, and male–male competition for mates, making it more similar to that of aggregating decapod cephalopods than any previously known octopus social system. Large male–female *A. aculeatus* occupy 'Adjacent' (G_A) dens and copulate frequently in mate-guarding situations over successive days. Nearby individuals copulate in 'Temporary guarding' (G_T) and 'Transient' (T; non-guarding) situations, the latter of which can involve 'Sneaker' (S) mating. In a focal animal study of these octopuses in the wild (Sulawesi, Indonesia) we addressed the hypotheses that they demonstrate: (1) precopulatory mate choice, (2) differential copulation rates by individuals employing different mating tactics, and (3) distant sex identification. We quantified daily copulation rates of *A. aculeatus* of reproductive size as well as aspects of copulation duration, display, mate-competition, and mate rejection. Mating tactic correlated with daily copulation rates. ♂G_A spent significantly more time copulating than did ♂T, while ♀G_A spent more than twice as much time per day *in copula* than did other females. Sneaker copulations lasted longer than those by males adopting other tactics. Mate-guarding was an effective and important tactic used by males to temporarily monopolize mating with apparently non-selective females. Males demonstrated clear pre-copulatory mate choice by guarding and mating repeatedly with large females (typically ♀G_A). While foraging alone away from the den, ♂G procured 'Transient' copulations with unguarded females. However, mate-guarding reduced the amount of time ♂G were alone and may impede their ability to seek out new mates. Low-copulation rates by ♀T, the smallest female tactic on average, may reflect this trade-off between mate preference and mate-searching by males, or non-receptivity of some females. A male-typical body pattern (black and white stripes) appeared to facilitate distant sex identification. Although mating and aggression were often initiated before contact between individuals, same-sex copulations and intense male–female aggression were rare. By contrast frequent male–female copulations and intense male–male aggression were consistent behavioral components of mating in *A. aculeatus* at these sites. Because the behavioral and ecological characters conducive to this complex system are not exclusive to *A. aculeatus*, it is possible that other octopuses exhibit some or all of these behaviors.

Introduction

Aided by a well-developed nervous system (Young 1971; Williamson and Chrachri 2004) shallow-water octopodids (hereafter referred to as 'octopuses') can be highly visual animals capable of learning and problem-solving (Hochner et al. 2006). By contrast, one of the most important acts of an octopus's life, mating, has been generalized as

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opportunistic, indiscriminate, and almost completely devoid of complex behavior (Hanlon and Messenger 1996). Despite the visual nature of these animals and the presence of sexually dimorphic traits in many species, conclusive evidence for the use of courtship and distant sex identification has not been presented [Wells and Wells 1972; Voight 1991; Cheng 1996; Cheng and Caldwell 2000; we consider courtship to be "behaviors that coordinate the activities of (sexual) partners in time; orient (sexual) partners in space; and increase sexual motivation" Tinbergen 1953]. Mate guarding and mate competition are forms of resource defense in which "animals keep others away from resources by fighting or aggressive displays" (Krebs and Davies 1993). These have not been documented for octopuses even under circumstances in which they might be expected, such as when populations are very dense (Aronson 1989) or in what are considered rare cases when multiple males simultaneously have tried to copulate with a single female (Ambrose in Hanlon and Messenger 1996). These views regarding a simple mating system in octopuses are supported by laboratory studies and brief field anecdotes on more than a dozen species (Cheng 1996; reviewed in Hanlon and Messenger 1996; Cheng and Caldwell 2000), but remain to be tested by any in-depth study in the wild.

Of the octopuses for which mating behavior has been documented, nearly one-third demonstrate behaviors that suggest a more complex mating system than that accommodated in current views. Male and female *Octopus cyanea* form dens adjacent to each other during the mating season (Yarnall 1969; Norman 1992) and a single example of sneaker mating has been reported for this species in the wild (Tsuchiya and Uzu 1997) suggesting the potential for repeated interactions, alternative reproductive tactics, and male–male mate competition. Male mating displays have been described for *Octopus digueti* (Voight 1991), *O. cyanea* (Wells and Wells 1972; Tsuchiya and Uzu 1997), *Octopus vulgaris* (Wells and Wells 1972), and an unidentified member of *Abdopus* (Young 1962). Although all of these behaviors have the potential to influence competition, sex identification, mate choice, and/or courtship, studies have not been performed in ways that would address these topics specifically. These limited and isolated observations exemplify the need for detailed in situ comparisons of the mating behaviors by multiple individuals.

Abdopus aculeatus (d'Orbigny 1834) is a diurnal intertidal species that may demonstrate the most complex mating behaviors observed thus far for any octopus species. Despite their small size [to 7 cm mantle length (ML)] and excellent camouflage, individuals are easy to locate and follow in the wild for extended periods. During preliminary observations in Sulawesi, Indonesia, males appeared to exhibit mate guarding, sneaker matings, and aggressive contests during which they fought over mates (Huffard 2007). Large males and females occupied adjacent dens [defined as such if the male could extend his hectocotylus (mating arm) to the female's den while resting at his own] for up to a week and copulated repeatedly both at the dens and on the foraging bouts (Fig. 1a, Supplementary Videos 1, 2). These observations suggest the possibility that mating by *A. aculeatus* involves (1) precopulatory mate choice, (2) differential copulation rates by individuals employing different mating tactics, and (3) distant sex identification, features that are common in other behaviorally complex animals (Andersson 1994). To quantify behaviors and address these hypotheses, two substantial local populations were identified where individuals could be recognized by arm injuries and scars (as with *Octopus cyanea* and *Octopus briareus* in Yarnall 1969 and Aronson 1989, respectively), and den fidelity allowed individuals to be relocated. These attributes allowed for the first long-term (hours to days) observations of interactions among known octopuses in the wild.

Methods

Behavioral categories

Based on preliminary observations of mating behavior, male (♂) and female (♀) octopuses were categorized as 'Adjacent Guarding' (G_A), 'Temporarily Guarding' (G_T),

Fig. 1 **a** Adjacent Guarding (G_A) male and female mating at their dens. Note raised supraocular papilla and 'BWS' body pattern in male. Drawn from frame of video. **b** Male Sitting Tall at den while exhibiting BWS and exposing oral portion of lateral and ventral arms. Drawn from field notes

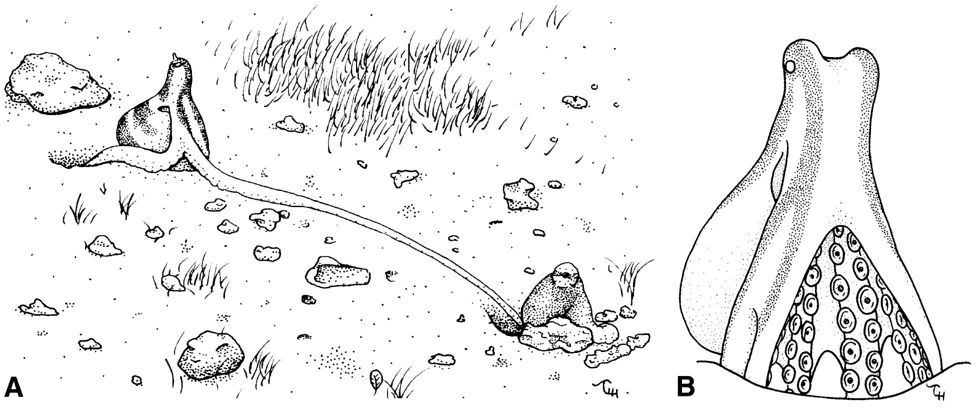

Table 1 Behavioral categories of mating *Abdopus aculeatus* in Sulawesi, Indonesia

Mating tactic	Definition
'Adjacent Guarding' (G_A)	A male–female pair that occupied a den within arm's reach of each other. This pair copulated in mate-guarding situations both at their dens and while out foraging.
'Temporarily Guarding' (G_T)	A male–female pair occupying dens not adjacent to each other, that temporarily entered into a guarding situation.
'Transient' (T)	Any octopus that was not observed in a guarding situation. When observed to mate Transient individuals parted after final withdrawal of the hectocotylus. These included both Sneaker and Non-Sneaker males.
'Sneaker' (S)	Males that visually segregated themselves from guarding males to avoid aggression while mating with the guarded female. Sneaker males were a type of Transient male.

Table 2 Acronyms for behavioral categories used throughout the text

Reproductive tactic	Male	Female
'Adjacent Guarding/Guarded'	♂G_A	♀G_A
'Temporarily Guarding/Guarded'	♂G_T	♀G_T
Guarding/Guarded	♂G	♀G
'Transient'	♂T	♀T
'Sneaker'	♂S	–

'Transient' (T) or 'Sneaker' (S) (Table 1). Acronyms of sex and tactic are used throughout the text (Table 2). Guarding males (1) maintained close proximity (0–3 m, but typically 0–1 m) to a female with which he attempted to mate at the den and/or while she foraged, (2) displayed a pale (often white) background with dark longitudinal stripes ('BWS', Fig. 1a, b), on the mantle, arm crown and arms at some point during guarding, sometimes only half of the body facing the female (Supplementary Videos 1, 2) expressed digitate supraocular papillae during 'BWS', and (4) interacted aggressively with other males that approached the female. G_A and G_T males were pooled together as 'Guarding' (♂G) for calculation of guarding rates. Because Sneaker males (♂S) were a rare and unpredictable type of Transient male (♂T), these categories were pooled for all analyses except that of copulation bout duration.

Focal animal observations

Focal animal observations of *Abdopus aculeatus* took place on intertidal reef flats of Bunaken (1°35.94′N, 124°46.89′E), Siladen (1°37.6N′ 124°48.27′E), and Hoga (5°27.72′S, 123.68′E) Islands, off the coast of Sulawesi, Indonesia during 2001 and 2002. The operational sex ratio at these sites averaged 1.8 M:1 F. Juveniles also inhabited the study area. During a total of 789 animal observation hours throughout this study, *A. aculeatus* were active (defined as having any portion of the body above the den entrance) at or away from their dens approximately 50% of the time (388 h). A total of 167 individual octopuses were located, identified by size, sex, and arm injury. When necessary to identify injuries and measure the mantle length of animals, octopuses were caught with a dip net and handled briefly in situ with cloth gloves. Males as small as 19 mm ML were easily identified by the presence of an unpigmented groove along the ventral edge of the third right arm (the 'hectocotylus' or 'mating arm' of males). Females of this size or larger were identified by the lack of a groove on the equivalent arm. This study involved individuals 30 mm ML or larger, which represents the approximate lower size limit for mating *A. aculeatus* (Huffard 2007). Observations of each individual were concluded in a time span of less than 3 weeks, a time period shorter than that required for arm-regeneration in a smaller congener (Ward 1998). Because octopuses also returned to the same den at the end of observations, we are confident in our identifications of individuals. Although long-term den occupancy was not measured in this study it is believed to be on the order of days for juveniles to weeks or months for adults (Huffard 2007).

Observations of adult octopuses were performed while on snorkel by following them from a distance of 3–5 m, depending on visibility. Observations continued by reef-walk from the same distance when water level fell below snorkelable depth (approximately 30 cm). Octopuses did not appear to react to observers who remained at this distance. Because we aimed to minimize observer disturbance, we did not approach individual *Abdopus aculeatus* sufficiently close to allow us to quantify sperm input of males by counting spermatophores (opaque sperm mass shorter than 2 cm long, and slightly thicker than a human hair) or the 'arch-pump' motion observed during spermatophore passage in other octopuses (Wells and Wells 1972; Mather 1978). The 'arch-pump' is not always obvious in *A. aculeatus*. Most observations were made by a single observer (CLH), although a second, trained observer (H. Spalding) also participated.

Interactions with conspecifics were timed to the second, and written codes were recorded on underwater paper (Xerox™ Nevertear paper). These behaviors included: approach, retreat, touch with non-hectocotylized arm, extension/insertion/withdrawal of the hectocotylus, mating rejection (male withdraws the extended hectocotylus before insertion into the female's mantle, or the female interrupts the mating attempt of a male by moving away quickly, moving quickly toward the male, or extending one or two dorsal arms quickly toward the male until the hectocotylus is withdrawn), 'grapple' (entanglement or alignment of the arms, sometimes involving enveloping of one individual under the web of another). In some instances, displays were videotaped for subsequent characterization.

A hectocotylus injury during adulthood might preclude any future mating in a male octopus's lifetime. Male *Abdopus aculeatus* are known to pull and cannibalize the arms of conspecifics during mate competition (Huffard 2007), and male *A. aculeatus* hold the hectocotylus close to the body when foraging, presumably to protect it. Thus we assumed that males would extend the hectocotylus toward another individual only for the purpose of mating.

We calculated daily copulation and guarding rates for 15 Guarding pairs [9 Adjacent Guarding (G_A) pairs, 6 Temporarily Guarding (G_T) pairs], 10 Transient females (♀T), and 8 Transient males (♂T). Each of these focal individuals or pairs was followed between approximately 0530 and 1830 hours for either one full day, or two days in the case of individuals in guarding situations. Because guarding individuals sometimes separated, males ($n = 14$) and females ($n = 10$) of pairs were considered focal animals on separate days. In the event of separation, the focal animal was followed at the expense of sometimes abandoning observations of the other individual. Initially we observed octopuses continually for 13 h. Once we established that adults were inactive during very low tides at these sites (Huffard 2007), observations were restricted to daylight hours when at least 2 cm of water covered their dens. The total time spent copulating and in guarding situations was divided by the total active time (time spent with any portion of the body emerged from the den) for that animal on that day.

Additional intermittent observations ranging from a few minutes to several hours were performed opportunistically. These observations were combined with those from daily focal animal studies to quantify (1) duration of mating bouts, (2) percent time spent displaying 'BWS', (3) size distribution of mating individuals, (4) mate rejections, and (5) male–male competition for mates.

Behaviors were scored as encounters (the first known meeting between two individuals for that day) and bouts or acts [individual behavioral actions (such as a single copulation bout, or chase/retreat agonistic act)]. Each encounter may involve multiple bouts or acts.

Statistical analyses

All statistical analyses were based on observations of adult *Abdopus aculeatus* of reproductive size (30 mm ML or larger) observed in situ. Statistical analyses were performed using StatXact 4.0.1. Even after transformation, data were not normally distributed and variances were heterogeneous. Thus non-parametric statistics were performed. Spearman's Rank Correlation Coefficients were calculated to test for correlations. The Kruskal–Wallis test for independent samples was used to determine whether mean values of multiple test groups differed. Wilcoxon Signed Rank tests (related samples) and Mann–Whitney *U* tests (independent samples) were used to test for post hoc pairwise differences, with a Bonferroni adjustment for multiple comparisons when more than two groups were compared (Bland and Altman 1995). The Mann–Whitney *U* test is particularly useful for unbalanced comparisons (Siegel and Castellan 1988). A binomial test was used according to the methods in Siegel and Castellan (1988). Reported sample sizes reflect the fact that mantle lengths were not known for all individuals, one G_A pair could not be observed for a full day each, and not all Transient individuals were observed to mate.

Results

Behavioral tactics

Mating occurred in four different contexts: (1) G_A, (2) G_T, (3) T, and (4) Sneakers (observed for males only). Six guarding males (three ♂G_A, three ♂G_T) were observed to mate in Transient situations with additional females that they encountered while foraging alone. All of these ♀T were the same size as ($n = 3$) or smaller than ($n = 3$) the females these males guarded and consequently spent more time copulating with. More than half [60% ± 14 (SE), $n = 9$] of the time that guarding males (♂G) spent away from the den each day was spent guarding or mating a particular female. Thus ♂G were alone for approximately 40% of their foraging time.

Three of the 36 males observed to attempt copulations were ♂S. All three ♂S (35, 38, 40 mm ML) were of the same size as or smaller than two other nearby males known to mate with the same female. In order to mate, each ♂S crawled very slowly from a nearby den to the female's den, while dorso-ventrally compressed to the substrate and exhibiting acute crypsis (in *Abdopus aculeatus* acute crypsis involves mottled ochre, brown, and/or gray color patterns and extensive expression of the primary and secondary papillae; Huffard 2007). Two of these cases occurred in clear view of an active ♂G_A. In one case the ♂G_A sat tall (Fig. 1b) presumably to view the ♂S and subsequently attempted to mate with it. The two fought intensely and the ♂S retreated. At some point while mating, all ♂S positioned themselves behind a feature on the substrate and out of view of ♂G_A. After withdrawal of the hectocotylus, ♂S returned (again compressed to the substrate and acutely camouflaged) into their dens and covered the entrances with pebbles. During each of these examples the female was inside her den, and not in view. We did not observe any ♂S to switch tactics and guard a female at other times, although one did approach a female overtly in a manner similar to approaches made by ♂G.

Size

The ♂G$_\mathrm{A}$ were significantly larger than ♂G$_\mathrm{T,}$ which were significantly larger than ♂T (♂G$_\mathrm{A}$: 49 ± 3 mm ML, $n = 9$; ♂G$_\mathrm{T}$: 41 ± 1 mm ML, $n = 13$; ♂T: 37 ± 2 mm ML, $n = 14$; Kruskal–Wallis $H = 9.48$, $df = 2$, $P = 0.013$, followed by pairwise Mann–Whitney tests with Bonferroni adjustment; $\alpha_e = 0.017$). Guarded females (both ♀G$_\mathrm{A}$ and ♀G$_\mathrm{T}$) were significantly larger than ♀T (♀G$_\mathrm{A}$: 56 ± 3 mm ML, $n = 9$; ♀G$_\mathrm{T}$: 50 ± 4 mm ML, $n = 12$; ♀T: 39 ± 2 mm ML, $n = 24$; $H = 13.91$, $P = 0.0001$, $df = 2$, followed by pairwise Mann–Whitney tests with Bonferroni adjustment; $\alpha_e = 0.017$).

Among all individuals of reproductive size found at our sites, females and males were equivalent sizes (females: 46 ± 1 mm ML, $n = 48$; males: 42 ± 1 mm ML, $n = 69$; $U = 1928$, $P = 0.06$). Males were significantly smaller than their mates [Relative sizes of mating pair (male size/female size × 100) = 91 ± 3%; Wilcoxon Signed Rank $P < 0.01$, $n = 46$ mating pairs for which sizes of both individuals were known).

Insertion rates

Preceding all but three copulations, males approached females to initiate mating rather than vice versa. Copulation bouts averaged 4.8 ± 0.8 min in duration, with a maximum of 32.0 min (48 combinations of males and females, 223 bouts). The average duration of copulation bouts was not related to male, female, or relative body size, or den location. However, copulations involving ♂S lasted significantly longer than those involving guarding males (♂S: 8.5 ± 3.9 min; $n = 3$; ♂G: 4.5 ± 0.9 min, $n = 22$; $U = 110.0$, $P = 0.035$).

Individuals using different mating tactics spent different proportions of the day mating (calculated as time spent mating/total active time for that day; Fig. 2; Males: $H = 12.34$, $P = 0.002$, $df = 2$. Females: $H = 11.19$, $P = 0.004$, $df = 2$). ♂T spent (0.1 ± 0.1%, $n = 6$) a smaller percentage of their daily active period mating than did both ♂G$_\mathrm{A}$ (3.7 ± 1.2%, $n = 8$; $U = 63.00$, $P = 0.0003$) and ♂G$_\mathrm{T}$ (1.4 ± 0.8 %, $n = 6$; $U = 38.00$, $P = 0.003$). Although daily copulation rates between ♂G$_\mathrm{A}$ and ♂G$_\mathrm{T}$ did not differ significantly ($U = 36.00$, $P = 0.06$), all ♂G$_\mathrm{A}$ copulated during our observations, which was not the case for ♂G$_\mathrm{T}$. On average, ♀G$_\mathrm{A}$ (4.8 ± 1.4%, $n = 8$) spent more than twice as much time per day *in copula* than did other females. Still, when applying the Bonferroni adjustment for multiple comparisons ($\alpha_e = 0.017$), their daily copulation rates were significantly higher than those of ♀G$_\mathrm{T}$ (0.9 ± 0.3%, $n = 6$; $U = 6.00$, $P = 0.01$) and ♀T (0.9 ± 0.8, $n = 10$; $U = 8$, $P = 0.003$). ♀G$_\mathrm{T}$ and ♀T did not spend significantly different proportions of their day copulating ($U = 17.00$, $P = 0.05$), although this was heavily skewed by the high copulation rate of one ♀T (Fig. 2a).

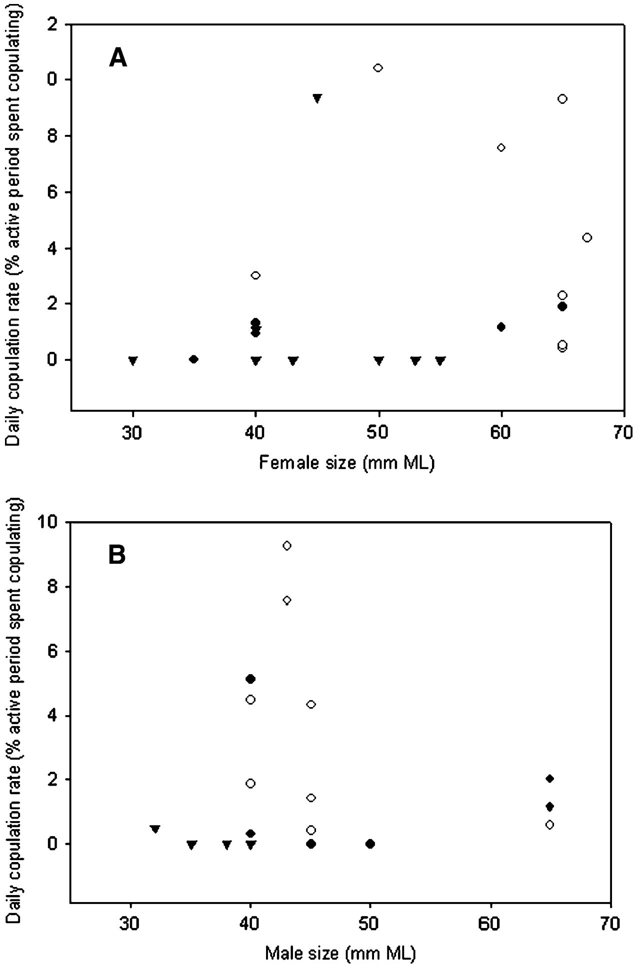

Fig. 2 Daily copulation rates of female (**a**) and male (**b**) *Abdopus aculeatus* by size, with reference to mating tactic (Transient = *triangles*; Temporarily Guarding = *closed circles*; Adjacent Guarding = *open circles*). Values were calculated as the percent of daily active time spent copulating. Note that these charts reflect data only for animals that were followed for their entire active period (full day)

Larger females spent a greater percentage of their day copulating than did smaller females ($\rho = 0.44$, $P = 0.02$, $n = 24$). Eight out of ten ♀T did not copulate during these observations (Fig. 2a). Two of these eight ♀T did encounter males but refused their mating attempts. We found no relationship between male size and the amount of time spent mating per day ($\rho = 0.20$, $P = 0.2$; $n = 19$ males for which size was known). Rather, males of intermediate size had the highest copulation rates (Fig. 2b).

Mate rejections

Males attempted copulations with 29 females. Of these females, 28 accepted at least one copulation by each male that attempted to mate them.

We observed a total of 17 female mate-rejections (approximately 7% of total mating attempts by all males). Approximately one-third of mating females (9 of 28 females) rejected at least one insertion attempt. The rejection rate between these male–female combinations was 30.3 ± 7.2% (SE) of total observed mating attempts between them. These females rejected ♂G_A ($n = 4$), ♂G_T ($n = 4$), and ♂T ($n = 2$) males approximately equally [average 1.6 ± 0.3 (SE) rejections/copulations per male]. Because ♂S mated only while females were inside their dens, we do not know if females might have rejected their mating attempts if they were within view. Female mate rejection rates did not correlate with male size ($\rho = -0.27$, $P = 0.2$, $n = 10$), female size ($\rho = 0.03$, $P = 0.5$, $n = 10$), or relative sizes of males and females ($\rho = 0.37$, $P = 0.1$, $n = 10$).

Of the 36 males that extended the hectocotylus toward the mantle of a female, 20 males withdrew this arm before insertion at least once with each given female. Although we did not quantify why males retracted their long, flexible hectocotylus from females, predator presence, male–male aggression, and strong tidal surges were common factors. These 20 males withdrew 40.2 ± 6.0% (SE) of insertion attempts that were not otherwise rejected by females. However, in all but two of these cases, males eventually mated with those particular females. One of these females was a small (35 mm ML) ♀T refused by a ♂G_A. The other was a moderately sized (40 mm ML) ♀T that had rejected all mating attempts but one by this and another male. Male mate rejection rate did not correlate with male size ($\rho = 0.01$, $P = 0.48$, $n = 19$), female size ($\rho = -0.24$, $P = 0.2$, $n = 19$), or relative sizes of males and females ($\rho = -0.21$, $P = 0.2$, $n = 19$).

Male–male mate competition

Aggression was common between males and occurred almost exclusively in defense of a female (26 of 29 male–male combinations) both at and away from the den. In all but three direct interactions, larger ♂G chased smaller intruder males from the female. Aggressive behaviors included chase, touch, 'whip' with one straight arm, and grapple. Guarding males chased an average of one (0–4) male per day away from the female. On four occasions guarding males ended mating bouts to fight another male. In one case a male successfully chased away a rival even though his hectocotylus remained inserted in the female. ♂S were not attacked while mating but did fight twice with other males at other times during the observation period when they overtly attempted to approach the female. Male–male aggression did not physically involve females in any way.

Chromatic display

Males spent far more time displaying 'BWS' than did females (males: 21.3 ± 3.4%, $n = 53$, females: 4.2 ± 2.5%, $n = 35$; $U = 568.0$; $P > 0.0001$). Only 4 out of 35 females of reproductive size displayed 'BWS' for more than 1% of the time they were observed. Two of these were ♀G_A and two were ♀T. Males observed both with a female and then temporarily alone at some other point spent far more time displaying 'BWS' in the presence of a female than alone (with female: 43.5 ± 7.5%, alone: 0.5 ± 0.1%, $n = 21$; $z = 3.84$, $P < 0.0001$). ♂G_A and ♂G_T spent equivalent amounts of time displaying 'BWS' (♂G_A: 25.1 ± 5.9%, $n = 9$; ♂G_T: 36.7 ± 10.8 %, $n = 13$; $U = 52.0$, $P = 0.50$).

Sex identification

Although agonistic acts were generally initiated before individuals touched, males behaved differently toward other males than toward females. 'Grappling' comprised 12% (30 out of 231) of total male–male agonistic acts. Aggression between males and females involved fewer total acts than male–male interactions ($U = 271.5$, $P = 0.03$), and were less likely to incorporate grappling ($U = 145.0$, $P = 0.05$). Despite this disparity in which sex combinations grappled, male–male grappling was not consistently preceded by touch (Binomial test $p = 0.41$; $n = 18$ separate male–male encounters involving grappling).

Males targeted insertion attempts almost exclusively toward females rather than males, and did not require physical contact beforehand to ensure copulating with the opposite sex. Touching with a non-hectocotylized arm preceded hectocotylus insertion during less than 12% (6 out of 51) of separate male–female encounters during which mating eventually took place. Most individual mating bouts (206 out of 223 insertions) began with males touching the female with the hectocotylized arm rather than touching first with one of their seven non-hectocotylized arms (17 out of 223 insertions). This difference was significant (binomial $z = -12.6$, $P << 0.0003$). Only six same-sex insertion attempts were recorded during more than 170 male–male encounters. These same-sex insertion attempts always lead to grappling.

Discussion

We found no evidence for pre-copulatory mate choice by female *Abdopus aculeatus*, a result that supports previous speculation regarding the indiscriminate nature of female octopus mating behavior (Wells and Wells 1972; Hanlon and Messenger 1996). Although nearly one-third of females occasionally rejected a mating attempt, on the whole they accepted nearly every opportunity to copulate with a male in this study and did not appear to reject males based on size or mating tactic. Yet ♂G still secured more copulations than ♂T because they gained immediate access to mates and were also capable of interrupting the approaches of other males. Thus mate-guarding was an effective and important tactic used by males to temporarily monopolize mating with apparently non-selective females.

As with many other invertebrates (reviewed in Bonduriansky 2001), male *Abdopus aculeatus* demonstrated clear pre-copulatory mate choice by guarding and mating most often with large females. Larger female octopuses produce more eggs than do smaller females (Joll 1976) and by mating with them males may increase their number of offsprings. Additionally, although size at spawning is highly variable in octopuses (Semmens et al. 2004), a very large female *A. aculeatus* is more likely to be gravid and close to spawning than a small female. Similar mate preference may also occur in male *Octopus digueti* which, when in captivity, appear to mate with gravid females more readily than non-gravid females (Voight 1991). We do not know if this mate choice occurs in the relatives of *A. aculeatus* or if size preference has been a major selective force throughout the evolution of *Abdopus* spp. and their relatives. However, it is interesting to note that this clade is perhaps the most size-variable among all octopuses, represented by pygmies such as *Abdopus abaculus* (Norman and Finn 2001; ML to 33 mm) as well as the very large sister taxon *Octopus cyanea* (Guzik et al. 2005; ML to 160 mm).

We do not know the mechanisms by which male *Abdopus aculeatus* chose larger females. They may directly assess the large body size of the female, as may occur in some crustaceans (Jormalainen 1998 and references therein) or they may assess the state of female maturity. In cephalopods, reproductive organ development is a much better indicator of maturity and proximity to spawning than body size (Semmens et al. 2004). To humans the distended ovary of a gravid female *A. aculeatus* can be visible as a pale globose mass in the posterior mantle. If male *A. aculeatus* are also able to see this cue, they may be able to assess potential mates according to ovary development. A role for chemical stimuli in octopus mating systems has been proposed based on physiological evidence in *Octopus vulgaris* (Di Cristo et al. 2005) and it is possible that mature females may chemically signal their reproductive state.

Mate choice may impact mate-searching behavior in male *Abdopus aculeatus*. Mate preference often leads to a trade-off between guarding high-quality females and searching for other mates (reviewed in Bonduriansky 2001). Only one adult male was found occupying a den within 3 m of more than one female (Huffard 2005). Thus males were unlikely to find additional females by viewing neighbors from their dens. Rather, males generally encountered mates when out and about. Indeed, all males that mated with more than one female encountered additional females while away from their den in non-guarding situations. For guarding males, more than half of the time away from the den was spent guarding and mating a particular (typically large) female, a tendency that may have impeded their ability to seek out additional mates.

Three-fourths of the ♀T we observed for at least a full day did not copulate. This may reflect a trade-off between mate-searching and mate preference by males, or non-receptivity of some females. On average, ♀T were significantly smaller and presumably less preferred as (repetitive) mates than their guarded congeners. Males that encountered and mated ♀T did not choose to remain with them for future copulations. Thus, mating activity of ♀T appeared to be limited at least partly by a lack of opportunity. As occurs in other animal groups (Wiley and Poston 1996), male preference in *Abdopus aculeatus* has the potential to influence female copulatory activity. While it is possible that some ♀T were not sexually receptive, this is not the case for all ♀T. Half of the ♀T that had an opportunity to copulate did so. Regardless of receptivity, half of the unmated ♀T did not encounter a male and thus did not copulate.

To our knowledge this study provides the first evidence for distant sex identification in wild octopuses. This is not a surprising result, as sex-identification is likely widespread among cephalopods because they are gonochoristic (Boal 2006). Unlike *Hapalochlaena lunulata* and *Octopus bocki* (Cheng 1996; Cheng and Caldwell 2000), sex identification by *Abdopus aculeatus* typically occurred before direct contact. As during mate assessment, male *A. aculeatus* may use visual and/or distant chemical cues for sex identification during copulation and aggression, regulating both the intense act of grappling, and extension of a male's only mating arm. Males frequently exhibited the 'BWS' body pattern in the presence of a female and during aggression, while females typically remained camouflaged. Although we do not know whether 'BWS' served to communicate the sender's male sex to receivers or if it reflected arousal by the presence of another individual, *A. aculeatus* may have used this male-typical body pattern (or lack thereof) to help identify the sex of conspecifics. The rare cases of same-sex mating were with small males that exhibited camouflage rather than displaying 'BWS.' The use of pheromones in sex identification by *A. aculeatus* has not been explored. Regardless of mechanism, distant sex identification may be useful to some octopuses in which sexual cannibalism occurs (Boal 2006). We do not know if the single case in which we observed a female *A. aculeatus* cannibalize another individual of unknown sex (Huffard 2007) took place during mating.

Sperm removal and sperm loading are behaviors males can incorporate to reduce sperm competition. To our knowledge neither of these behaviors has been demonstrated conclusively for octopuses, although our observations add to support for their occurrence. Sneaker males in other animal groups sometimes perform sperm loading to displace or outnumber rival sperm (Parker 1998). Direct removal of rival sperm is also widespread among invertebrates with internal fertilization and in many cases involves the use of a specialized sperm removal structure (Parker 1998). In octopuses, both sperm removal and sperm loading could take place as the hectocotylus is inserted. This could partially explain why guarding *Abdopus aculeatus* copulated so frequently. Sneaker male *A. aculeatus* demonstrated longer mating bouts than other males presumably in response to sperm competition, although we do not know if this time was spent (1) passing more spermatophores to employ sperm loading, (2) removing rival sperm, or (3) performing some other behavior. Behavioral responses to sperm competition in *Octopus cf. joubini* may involve sperm removal using the spermatophore-transfer organ (ligula) at the end of the modified mating arm (hectocotylus) (Cigliano 1995). In *Octopus bimaculoides* this organ can become erect and may be used for scooping out previously deposited sperm (Thompson and Voight 2003).

In both group and paring situations, social behavior involves individuals of the same species "keeping together (or apart in the case of competition) on the basis of reacting to each other" (Tinbergen 1953). Some shallow-water decapods have long been recognized as social organisms, engaging in schooling behavior (Adamo 1999) and even structured mating aggregations (Corner and Moore 1980; Sauer et al. 1992). Several species also exhibit complex mating behavior in spawning aggregations (Hall and Hanlon 2002; Jantzen and Havenhand 2003). However, reproductive gatherings do not necessarily constitute social behavior (Tinbergen 1953). By contrast, octopuses are generally considered asocial, with opportunistic copulations during sporadic and infrequent interactions (Hanlon and Messenger 1996). The mating system of *Abdopus aculeatus* incorporates sneaker matings, mate guarding, sex-specific body patterns, frequent copulations, and male–male competition for mates, making it more similar to that of aggregating decapods than any previously known octopus system. Although *A. aculeatus* interacted frequently during daily activities, they did not "keep together on the basis of reacting to each other" (Tinbergen 1953) for any apparent reason other than reproduction. Although their behaviors were fairly complex, individual *A. aculeatus* simply aimed to maximize their reproductive success in a competitive environment.

In theory, sneaker mating has evolved as a reaction to the superior competitive ability of other males (Parker 1990). Sneaker males have prior knowledge of their (in)abilities compared to other individuals in a group and adjust their behavior accordingly to reduce aggression and procure copulations (Parker 1990), a situation that would require frequent interaction. Indeed all three ♂S *Abdopus aculeatus* were competitively inferior to at least two other males in the area. ♂S exhibited acute camouflage and hid behind rocks thereby effectively avoiding aggression from guarding males while mating with guarded females. However one ♂S also overtly approached a female in clear view of her guarding male despite the aggressive consequences, indicating that the competitive environment alone does not regulate male mating tactics in these octopuses.

Although the ♀♂G_A association persisted for multiple days, we found no evidence that this pairing situation represents a social bond. Displaying males followed females for the purpose of mating, defending her whether she was near their dens or out foraging. In rare cases when ♂G_A mated with females other than the ♀G_A, ♂G_A returned to the ♀G_A afterward. However we do not know if this reflects fidelity to his den or to the ♀G_A. For a male *Abdopus aculeatus*, pairing may simply aim to maximize guarding of the largest female he has encountered, rather than enforcing a social bond with her. Although ♀G_A did not aggressively chase ♂G_A we found no evidence that these males were preferred over other potential mates. Thus ♀G_A *A. aculeatus* appear to be under 'pair bondage' (Gowaty 1996). In this situation, it is less costly for a female to tolerate a male's presence than to chase him from her territory (Gowaty 1996).

The ecology of *Abdopus aculeatus* may facilitate frequent interactions without the need to form mating aggregations per se. Moderate population density, clumping according to microhabitat preferences, the propensity to forage during a limited tidal window, and diurnal activity in clear waters (Huffard 2007) enable repeated encounters and visual signaling among *A. aculeatus* in their normal habitat, and throughout their post-settlement life. These densities and the ensuing complex behaviors were observed year-round, and in the same habitat occupied by juveniles. Other members of *Abdopus* (Ward 1998; Norman and Finn 2001; Huffard 2007) as well as *Octopus cyanea* in unfished areas with moderate densities (CLH, personal observations), also demonstrate various combinations of these ecological attributes and may express similar behaviors during frequent interactions.

The mating behavior of *A. aculeatus* was drastically different from that generalized based on laboratory studies and limited field observations of other octopuses. However, because of the lack of in-depth studies of mating by any other octopuses in the wild we hesitate to claim that the behaviors reported here are rare among the group. Rather than assuming octopuses to have a simple mating system because many appear to be asocial (Hanlon and Messenger 1996) we may be more successful making predictions based on the known behavior of relatives (Huffard 2007) or by drawing upon well-established patterns from other animal groups. For example, male–male competition and mate guarding often intensify when sex ratios are male-biased (Jormalainen 1998), as in *A. aculeatus*. We may be then more likely to observe these or similar behaviors in other octopus populations that have male-skewed sex ratios, such as sometimes occurs with *Octopus digueti, Octopus tehuelchus* and *Enteroctopus dofleini* (Hartwick 1983; Iribarne 1991; Voight 1992) than in populations for which sex ratios are approximately even (as in *Octopus bocki*, *Octopus cyanea*, *Octopus mimus*, and *Octopus briareus*; Van Heukelem 1983; Aronson 1989; Cheng 1996; Cortez et al. 1999). Although aquarium studies are extremely useful for addressing the fine details of these activities (as in Cigliano 1995; Cheng 1996; Cheng and Caldwell 2000) the interactions observed here would be difficult to replicate in the laboratory. This study demonstrates that natural history observations remain necessary for testing behavioral paradigms, and that a concerted effort should be performed to document the mating behavior of additional octopus populations in the wild.

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