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Mating Games Squid Play: Reproductive Behaviour and Sexual Skin Displays in Caribbean Reef Squid Sepioteuthis sepioidea

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Mating games squid play: reproductive behaviour and sexual skin displays in Caribbean reef squid *Sepioteuthis sepioidea*

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ABSTRACT

Observation of the sexual interactions of *Sepioteuthis sepioidea* squid during the short reproductive stage of their lives showed a scramble competition system, with both male and female polygyny. Mature females were faithful to a specific location in the daytime, whereas males moved from group to group and formed short-term consortships with females. Males defended females from other males, particularly with an agonistic Zebra display. Male–female pairs exchanged Saddle-Stripe displays, after which males might display an on–off Flicker. There was considerable female choice. Only if a female responded to this display with a parallel Rocking action would she pair and would the males deposit spermatophores at the base of her arms, and only 50% of the time did females move the spermatophores internally to where sperm might be released and stored in the oviducal gland for later fertilization of eggs. This long-term set of interactions and solitary deposition of hidden egg strings contrasts with the attraction of both sexes to a common 'egg mop' laid by many females which was a site of competition in other loliginid squid. Since *Sepioteuthis* is a primitive genus within the family Loliginidae, it may represent a generalist reproductive strategy that evolved into a specialized localization one.

Introduction

Females' reproductive success is limited by access to resources and males' by access to females (Trivers 1972), but this may result in different mating strategies for the sexes. Males often try to monopolize females, and this female defence strategy of males is well understood, but when females are widely dispersed this tactic may not be effective and a scramble competition

mating system may arise (Marmet et al. 2012). These systems are found in solitary bees (Alcock 1980), and polyandry is widespread across the insects (Arnqvist & Nilsson 2000). In mammals, chipmunks and squirrels (Schwagmeyer & Woontner 1986; Marmet et al. 2012), and lemur primates (Kappeler 1997; Eberle & Kappeler 2002) use such a system. In scramble competition, both males and females have multiple mates, but males have far larger home ranges than females, and a premium would be placed on males' ability at navigation. In the Loliginid squid, however, both males and females have multiple mates in a scramble-type system that involves temporary mate guarding, yet a large number of individual at a lek-like gathering (Sauer et al. 1997). What might cause such a mating system to evolve in these animals?

Most loliginind squid live far out in the ocean and come to coastal areas to reproduce, gathering in limited areas where semelparous females lay eggs before dying (Hanlon 1996, *Loligo vulgaris*, Hanlon et al. 2002; Shaw & Sauer 2004; *Doryteuthis (Loligo) pealeii*, Shashar & Hanlon 2013; *Sepioteuthis australis*, Jantzen & Havenhand 2003a). Behavioural observations revealed typical sexual skin displays in males and females (Jantzen & Havenhand 2003b; see Hanlon & Messenger 1996 for summaries). Males had two different mating strategies, called Consort and Sneaker, often accompanied by different mating postures (Iwata et al. 2005; Shashar & Hanlon 2013). Genetic testing showed multiple paternity of the eggs laid by females (Maxwell & Hanlon 2000; van Camp et al. 2004; Buresch et al. 2009; Naud et al. 2016; Wada et al. 2005), partly dependent on these male strategies and possibly with a last-male precedence. In addition, males increased their agonistic behaviour when in the presence of egg mops, as a result of both visual (King et al. 2003) and olfactory (Buresch et al. 2004) cues. When mature animals were so clustered, why would they have a scramble competition?

Part of the answer may be that mating has already occurred, as females may arrive at a spawning area with sperm already stored in their oviducal gland; paternity analyses (Hanlon et al. 2002; Naud et al. 2016) revealed multiple paternity of eggs in strings even when only one consort male has been guarding a female. Because squid were not followed before they arrived at the spawning site, their earlier behaviour was not monitored. In contrast, the nearshore *Sepioteuthis sepioidea* (Caribbean reef squid) live in small groups and their behaviour can be monitored all through the lifespan. Arnold (1965) kept some adults in captivity and observed sexual displays and mating, Moynihan and Rodaniche (1982) observed the species extensively in the field, especially reporting on the skin displays, but without quantitative data. Hanlon and Messenger (1996) included some observations in their book, and Mather (2004) reported on some of the displays in a book chapter. Caribbean reef squid group structure is quite variable, and the lack of individual identification until the present study (see Byrne et al. 2010) made it difficult to trace the sequence of behaviours and states across individuals. Arnold (1965) also noted that *S. sepioidea* were not attracted to either artificial or real egg strings, and females laid their eggs in hiding, accompanied by a single male or alone (Moynihan & Rodaniche 1982).

Although individual squid were difficult to follow, some aspects of mating of *S. sepioidea* have been reported. Males segregated females in consortship and addressed ritualized Zebra agonistic visual displays in stereotyped positions to other males, called a Zebra Spread (Moynihan & Rodaniche 1982; Hanlon & Messenger 1996). Moynihan and Rodaniche (1982) incorrectly specified that the squid in the upper position was the contest 'winner' in obtaining or retaining access to the female. This was countered by Hanlon and Messenger (1996) and

especially with quantitative data by Mather (2004); it is the male underneath. Mather (2004) also noted the Zebra display could be produced in other situations than this formal contest, and that it could be quantified by combining three aspects of intensity as described by Packard (1995). The first two authors noted the female Pied display (renamed Saddle in this study because it is a more accurate description) as a repellent of males, whereas Mather (2004) noted it was produced in several sexual situations. In fact, the apparently stereotyped visual displays have a great deal of variation, as is common for sexual displays (Enquist & Arak 1998), and these variations will be discussed in this paper. Moynihan and Rodaniche (1982) and Hanlon and Messenger (1996) noted that the male's mating attempt was preceded by a Rocking parallel swim, and Moynihan and Rodaniche (1982) that there was another male display of stripes, which they called Streak. This display is renamed Stripe in the present paper because it consists of four stripes, with the pale stripe between two dorsolateral ones being what Moynihan and Rodaniche (1982) noted. Not all of the stripes need be included in the display, and the variation in number represents another quantification of display intensity.

Despite the difficulty in tracing actions and responses, as *S. sepioidea* can be observed across the lifespan it may be a model for the sexual behaviour and displays of other members of the family Loliginidae. The present paper uses individual identification to trace the sequence of actions and displays produced by squid as they mature and to uncover the sexual strategies of males and females more broadly across time and space.

Materials and methods

Subjects

Subjects of the study were small (2–25 member) adult and subadult groups of Caribbean reef squid (*S. sepioidea*), found in near-shore waters throughout the Caribbean (Jereb & Roper 2010) and observed at Bonaire, Netherlands Antilles, near the Venezuela coast, from 1998 to 2001. The groups lived off the leeward and west side of the small island, approximately 2–10 m from shore and in water depths of 1.5 to 5 m, inshore of a sharp drop-off and at approximately the same location. Squid were almost always in groups in the daytime (Moynihan & Rodaniche 1982), but dispersed to hunt at night. Group location was similar over weeks but exact group membership varied somewhat from day to day, which could be a fission–fusion organization heavily influenced by predation (Mather 2010), as is found in many group-living fish (Kelley et al. 2011). The subjects were found in a group of approximately 12 in 1998, identified by location as Oceanfront I. In 1999 subjects were the group Oceanfront II, in the same location but different individuals as the squid's lifespan is 12–16 months (LaRoe 1971). A subadult group of nine, approximately 500 m south of the first one, was also observed in 2001. In 2000, a mixed-age group of 11 at Harbour Village, 1000 m south of the second location, was observed for a month, allowing two females to be followed through their mating period. In 2000, another group of between 8 and 16 at Sand Dollar (between the two locations) was followed for 6 weeks and 2 females observed over most of their reproductive stage. Subjects were designated as subadult rather than fully adult by two criteria: size – mantle length approximately 10–13 cm– and only occasional or out-of-sequence reproductive behaviour. With no hardened endo-or-exoskeleton, cephalopods have few indicators of maturity except size, which is partially dependent on feeding success, and reproductive behaviour only occurs at the end of the lifespan (Mather 2006). Individual squid were identified (see Byrne et al. 2010) using three sets of visual cues, the

most prominent of which was the presence of skin damage left by failed predation attempts by fish. The second was the individualized pattern of large opaque fin dots of mature males and the third was distinctive patterns of green iridocyte dots visible on the dorsal mantle of both sexes. In earlier years, these patterns were traced onto outlines of squid on paper, but later we used digitized photographs, which were assembled in a computer-based identification bank.

Methods

All data were extracted from observations; squid were never captured or interfered with. As the near shore of Bonaire is a Marine Reserve, all marine animals are protected. Squid had a crepuscular daytime activity pattern, so observational effort peaked from 0700–1000 to 1500–1800, normally 4 h/day watching per group. Volunteers assisted the author, and a pair of observers snorkled, remaining as immobile as possible, on the water surface near a squid group. Each followed one, a pair or a few squid and took notes on an underwater slate, transcribed later into computer instances on spreadsheets in data bases. Initial observations isolated general patterns of behaviour, using Moynihan and Rodaniche's (1982) report as a general guide, although in 1998 no individuals were identified. Squid were found both within a larger group and isolated from it by several meters as a 'courting pair', though observations in later years showed us that such isolation was temporary. During 1998, there were sufficient separated pairs to make a comparison of the sexual behaviour of pairs within a group (47.4 h) and those at least three meters separate from it (18.2 h). Mature males and females designated as isolated courting pairs were (1) separated by approximately one body length of 0.3 m, (2) oriented nearly parallel and (3) the male defended the female from other males by interposition and agonistic displays. In 1999 and 2000, individuals were identified, groups followed and particular steps in the sequence of reproductive behaviour (initial courtship, mating attempts and egg laying) and displays (Flicker, Zebra, Saddle, and Stripe, see Table 11–1 in Mather 2004 for their perceptual characteristics) were singled out for intense observation. In 2001, females were followed across time to chart the development of their skin displays. Although these behaviours were likely over-represented (see Altmann 1974) in data collection, there was no indication of bias due to this selection. To compare the instances of Saddle-Stripe associated with male–male challenges, the frequency of Zebra displays to pairs and takeovers of consortships was calculated separately from 10 morning observations (May 1–11, 385 min) in 1999. There were 80 male Zebras and 3 takeovers. In 2000, because the Harbour Village group was tracked for eight weeks, two female squid were observed for most of their reproductive history.

Results

Summary of the interactions

Squid were nearly obligate members of their schools, with a membership of around 5–15 at maturity and between 2 and 50 as young individuals. Subadult squid often formed an approximate linear arrangement with no specific position for any individual. If nearly equal size animals moved into maturity at the same time, they began to produce displays that were incomplete, produced in inappropriate context or to the wrong sex. Sometimes, all the group swam swiftly in parallel for a few metres in a Rush, each showing a sex-appropriate display but not located in any specific relative position. Several days later, a female rose above the group and produced Saddle as the first full sexual signal, but it was not responded to by a display of

males. After a few more days, the Saddle was followed by a male Stripe, and pairs began to form (see the criteria above). At this time, a female would be located at the end of the linear array, separated from the other group members by a male, or several pairs formed along the line. Within a few days more, mature males arrived from outside the group, and one again would gradually separate a female from other group members as much as possible. A male within the group might already pair with a mature female and, after the Saddle-Stripe pairing displays, give a pre-mating Flicker display. This was followed by a female Saddle display, or her departure followed by a male chase. If a female joined the male in mutual Rocking, he might then deposit a spermatophore on her arm bases. Flicker was often followed by an approach of another male with a Zebra display. While two consorts were exchanging Zebra displays, a subordinate Sneaker male might give a Flicker to an unguarded female, and mating could follow. Males who held consortship attempted several matings per day, with the female becoming more and more resistant. Females were more site-faithful as they matured, but males stayed with a group for only a day or two. Subordinate males stayed and acted as a sneaker until they matured, or left the group. After several matings and presumably with sperm stored in her oviducal gland, a female left the group to a distance far greater than the normal spacing of 1–2 body lengths apart and likely to a substrate suitable for egg deposition. She was accompanied by one or several males, who exchanged high-intensity Zebra Spread displays. The successful male mated with the egg-laying female and then she laid several egg strings over approximately 20 min; he ceased guarding her after approximately 10 min. After egg-laying (one or a few times), she produced Zebra displays at male approaches and no longer maintained the 1–2 body length distance between herself and other squid. Males entering senescence stayed within the group or moved from group to group, and produced Zebra Spread displays that might even have indicated dominance, but they did not attempt mating with females.

Table 1. Quantitative score for intensity of Zebra displays of male *Sepioteuthis sepioidea* squid, based on a combination of area of expression and stripe-background contrast.

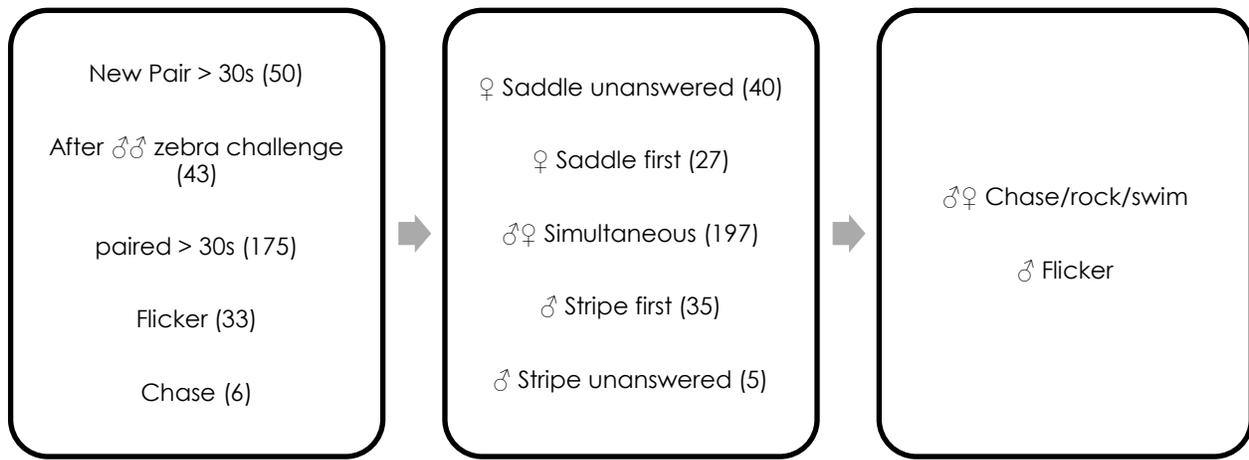| Area	Background	Other	Zebra Score
½ arms	Brown	--	0.5
½ mantle	Brown	--	1
Arms	Brown	--	1
Mantle	Brown	--	2
½ arms	White	--	1
½ mantle	White	--	2
Arms	White	--	2
Mantle	White	--	4
Mantle + Arms	White	--	6
Mantle + Arms	Brown	--	3
Mantle + Arms	Brown	Arms spread >60°	4
Mantle + Arms	White	Arms spread >120°	8
Mantle + Arms	White	Arms spread 360°	10

Displays

Saddle

Females initiated sexual interactions with Saddle displays. In 2000, 299 of these displays were observed, most at the same time as male Stripe and in a female-over position (Table 1). Forty of these were not accompanied by Stripe, but Stripe was seldom (5) displayed alone. When the displays were produced together, 197 appeared simultaneously, 27 resulted from Saddle first and 35 from Stripe first. These exchanges did not appear to be primarily for pair-maintenance, as 50 were observed <30 s after one male 'took over' consortship from another, 43 after a male–male Zebra exchanged challenge and 175 during stable pairing. The expected 50% probabilities of Saddle-Stripe after each of these events were significantly different from those observed, at χ^2 (3) = 78.48, p < 0.001. Thus, the exchange was more pair-initiating than pair-maintaining (Figure 1). In 2000, 159 of male Flicker displays were followed by a female Saddle and 95 of these were followed with a male Stripe (see the suggestion that Saddle signalled de-escalation by Moynihan & Rodaniche 1982 and Hanlon & Messenger 1996). Saddle was seldom observed – three times in 1999 and once in 2000 – by animals known to be male. In each case, a smaller male was responding to a sexual display by a larger one. This display may have functioned in that situation as a device to de-escalate a contest. As well, when a consort pair had been established, females often made a Saddle towards the male on a much reduced display area, a spot of white 2–3 cm in diameter on the posterior mantle, maintained for long periods. Only the occasional spread of the display to the anterior and laterally to produce a much larger area of white suggested a link to the full Saddle. This reduced display, which may have functioned to maintain the consorthip, is probably identical to Moynihan and Rodaniche's (1982) Rear Light.

Stripe

At maximum, this male display consisted of two wide dorsolateral (DLS) and two narrow fin base (FBS) stripes. Moynihan and Rodaniche (1982) probably observed the two dorsolateral stripes only when they described this display as Streak, a paler dorsal stripe between the two darker dorsolateral ones (though see their Figure 25 with three stripes visible). The display was modulated, as a male might produce from one to four of the stripes in a sexual situation. Of 714 Stripe displays, 164 consisted of the dorsolateral pair, 59 of the dorsal stripes and one fin based one and 415 of all four stripes. Of 638 Stripes in which the outcome of the interchange was noted, 76 of displays with only the dorsolateral stripes led to a Flicker, in comparison to 64 after two dorsolateral and one fin base stripe, and 170 following inclusion of all four stripes. These numbers were significantly different from chance occurrence, χ^2 (3) = 18.38, p < 0.001, so perhaps the display was modulated by motivation level. But a Fin Base Stripe (FBS) alone was also observed in an agonistic situation (n = 333), often accompanying a male Zebra display. When FBS to another male was displayed alone, 64 of the displays elicited no response, 6 a Stripe and 24 were followed by a Zebra from the other male. When FBS was accompanied by Zebra, 155 resulted in no response, 79 in a Zebra response and 15 in a return Stripe. These proportions were not different on a chi-square test (p > 0.05), suggesting that the FBS alone was not an agonistic signal but perhaps a token of male identity. In another set of 24 observations, FBS alone was more often displayed to a female (78%) than to a male (12%).

Figure 1. Circumstances and sequence of actions in the exchange of female Saddle and male Stripe displays by courting adult *Sepioteuthis sepioidea* squid (*n* = 307).

New Pair > 30s (50)

After ♂♂ zebra challenge (43)

paired > 30s (175)

Flicker (33)

Chase (6)

→

♀ Saddle unanswered (40)

♀ Saddle first (27)

♂♀ Simultaneous (197)

♂ Stripe first (35)

♂ Stripe unanswered (5)

→

♂♀ Chase/rock/swim

♂ Flicker

Zebra

This display of rows of diagonal slashes (not really the cohesive stripes seen in mammalian zebras) is similar in appearance to those displays known as agonistic in other cephalopod species (Hanlon & Messenger 1996). It was produced by subadults and adults only, and differentially by the two sexes and to different targets. Males and females observed in 1999 produced Zebra displays a similar number of times (67 and 55) to approaching threats such as fish (Mather 2010), females sometimes to males (197) but seldom (1) to other females. Males seldom (29) directed this display to females but very often (864) to other males. The difference in number of Zebra displays by the two sexes and to different targets was highly significant, $\chi2$ (6) = 1051, p < 0.001. Packard (1995) pointed out that cephalopod display intensity could be modulated by area (for Zebra, of the arms and mantle on which it was displayed, see Mather 2004), intensity of the display units themselves (not commonly useful) and intensity of the background (pale brown vs white). Low-intensity displays were commonly unilateral, and always on the side towards the male, or fish if appropriate . Mather (2004) calculated a minimum intensity score of 0.5 for Zebra on brown background on half the arms, maximum 10 for the male positioned underneath in a Zebra Spread challenge, on white background with all arms splayed back 270 degrees to parallel with the mantle, noted as Zebra Spread by all three authors (see Table 1 for scores of different area/intensities of Zebra).

Males often swam in consortship, interposed between a female and another male. During consortship, males usually displayed some area of Zebra to other males. They could produce Zebra displays on either half of the body (always towards the male) or all of the mantle and/or arms, either on brown or white background. Not only could the display intensity vary by area and contrast, but it also changed area/amount during the time a male was guarding. Of 317 low intensity Zebra displays sequences produced by 10 males, the most common area was on arms only (86), less on mantle and arms (70) equal numbers (54) on mantle only or half the arms

only, 53 on half the mantle and half the arms. The average number of different area combinations on which Zebra displays were extended during one sequence of mate-guarding was 5.4, range 2–8. This variation was likely due to motivational changes in the circumstances. In 2001, 11 male–male-female trios were followed as the male–male distances changed. As a peripheral male moved closer to the male–female pair, the consort male increased the intensity of his skin display and it remained quantitatively more intense than that of the peripheral male.

As noted in Mather (2004), escalation to the Zebra Spread resulted in a ritualized visual exchange, maintained for up to minutes and in over–under positions, though with little to no physical contact (see Moynihan & Rodaniche 1982, Figure 27). These high-intensity displays were more likely after entry of a novel male into the group, when two consort pairs were close together, and especially if a pair within a group displayed Saddle-Stripe or one male displayed Flicker.
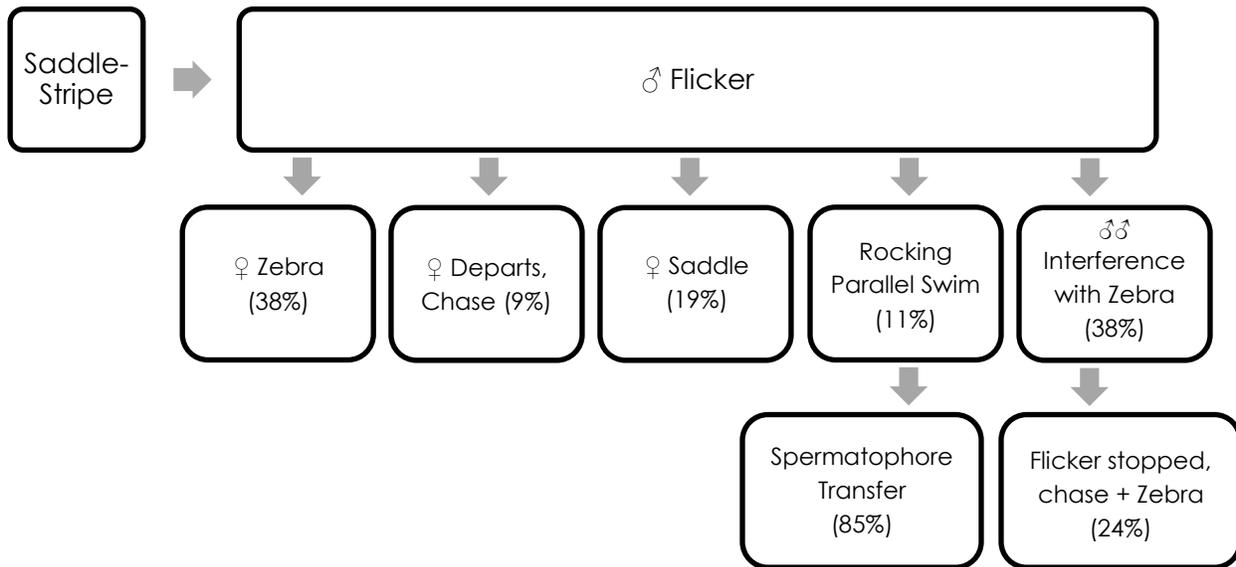
Flicker

After a Saddle-Stripe paired display, a male might display an on–off modulation of a pale background called Flicker and take up a position posterior–lateral to and under the female. This very obvious display was probably noted by Moynihan and Rodaniche (1982) as they mentioned a Pastel colouring, but not the intensity modulation and relative position. Saddle-Stripe nearly always preceded Flicker. Of 159 Flicker displays observed during the study, 38 were interrupted by another male approaching with a Zebra display, to which the displaying male responded with a Zebra and sometimes a chase. One subordinate male used this approach 18 times in a row, and the displaying male never did proceed to a mating attempt. Sixty-one of Flicker displays were answered by a female Zebra, 14 by a female escape swim with male pursuit and 29 by a female Saddle (called de-escalating by previous authors). After only 17 of the Flicker and Rocking displays, a female responded with a similar movement and the pair performed a parallel Rocking swim of about 1.5 metres, followed ($n = 15$, $p = 0.85$) by a quick male placement of spermatophores at her dorsal arms bases (Figure 4). A chi-square test of likelihood of mating attempts following these four female actions was significantly different from equal, $\chi2$ (4) = 108.17, $P < .001$. In 2000, the team noted whether females subsequently grasped spermatophores and moved them inside the mantle cavity near the oviducal sac for sperm storage. After 18 cases of spermatophore deposition there were 9 transfers, but we were not able to distinguish if characteristics of the male (such as size) or situation (such as length of pairing) influenced this action. During the consortship of a pair, females also became less receptive to mating attempts. Clearly, males attempted control of the interaction but females exerted considerable choice.

Lateral silver

If males succeeded in separating a female from the group by more than 2 metres, they often maintained a Lateral Silver display, with normal brown background towards the female and bright silver-white to the other group members (see Figure 5). The observations in 1998 allowed comparison of sexual behaviour between in-group and separated-out pairs, to ascertain if the Lateral Silver and separation were adaptive for male mating success. There were similar frequencies of Saddle paired with Stripe displays (2.9/h in and 1.7 out), Flicker displays (0.8 and 0.7/h) and mating attempts (0.2 and 0.3/h). There were similar frequencies of Formal Zebra

display exchanges (1.0 and 0.6/h), but there were 0.6 consort replacements per hour in the group and 0 out of it, suggesting a pair stability advantage.

Figure 5. Sequence of actions after male squid *Sepioteuthis sepioidea* squid made a Flicker sexual skin display to a nearby female (*n* = 159).(Image used with permission of the author).

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┌──────────┐      ┌─────────────────────────────────────────────────┐
│ Saddle-  │ ──▶  │                   ♂ Flicker                      │
│ Stripe   │      └─────────────────────────────────────────────────┘
└──────────┘
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♀ Zebra (38%)	♀ Departs, Chase (9%)	♀ Saddle (19%)	Rocking Parallel Swim (11%)	♂♂ Interference with Zebra (38%)
			Spermatophore Transfer (85%)	Flicker stopped, chase + Zebra (24%)

Positioning over space and time

As mentioned in the overview above, squid were near-obligate daytime group members, but group membership shifted from day to day and even within a single day when a group fled at the approach of a potential predator (Mather 2010). Group members varied in their maturity stage, and subadult males chose one of two localization strategies. They could remain in an apparently stable group, as did the subadults in 1999 in which out-of- context visual sexual displays and truncated courtship were first observed. Or they could leave and join an adult group as subordinate sneakers, interfering in mating attempts (see Flicker) and mating with females (who often did not reject them) when consort males were conducting agonistic contests. Peripheral males matured and became adults, able to form consortships. They could especially gain such opportunities when the adult males left or ceased to respond to sexual displays, as did peripheral males at Oceanfront II and Sand Dollar. Subadult males did not normally respond to subadult females, even when they made Saddle displays, so some chemical cue may indicate full maturity. Males and females were attracted to the largest member of the opposite sex and larger males normally won display contests, so several pairs in a group might be sorted on the basis of size.

Males and females had different spatial strategies. This was apparent in the somewhat isolated Harbour Village group over 29 days; its mean group number was 11. Adult females maintained stable group membership, with 4 present for 26, 27, 28 and 29 days duration. These 4 female members began as subadults, and 2 small males, present for 14 and 13 days, mated with

them a few times. Six adult females and seventeen adult males were identified in the group at any time, but females averaged 21 days present and males four, a significantly different membership duration, $t(21) = 3.29$, $p < 0.01$. Nine males were in the group only once, one left and returned after several days and another was reported at two other groups hundreds of meters away on subsequent days. One was present for nine days but gained no mating opportunities. He moved 1000 m away to a pair of mature females, who did not respond to his courtship displays. During the observation time, two adult females produced unanswered Saddle displays before they began to exchange displays with visiting males, mated and then gradually passed to responding to male courtship with Zebra displays and remaining unpaired. One was seen in consort with 4 males over 16 days, observed mating with 2 and laying eggs once. A second was paired with 9 males over 26 days and seen mating with four.

In 2001, two females in the larger and more fluid Sand Dollar group were observed until males no longer approached them (behavioural data suggested egg laying but we did not observe it). One was in consort with 11 males over 22 days and the other with 10 males over 26 days. Perhaps because the group was larger, several adult males were present. One left the group for six days and returned, and eight males were observed escorting and defending both females on different days. The same pattern of male presence in the group for a few days was observed, and the mean and mode of duration of mate-guarding was a single day (only once did a pair continue for two consecutive days and twice for three, out of a total of 27 pairings).

Apart from the group-centred data, casual observations suggested that adult males ranged much more widely than adult females and monitored the maturity of females within their home ranges. In 2001, a group of subadults at Sand Dollar was monitored long-term. They showed no sign of sexual maturity from 10 May to 22 May. During this time an adult male BA, who was being observed as part of a group about 300 m away, arrived at the group, swam around it and then returned directly to his group. A large male appeared in the group on 1 June 1 and began a consort relationship with one of the females. The male BA returned to the group on 9 June 9, this time stayed and maintained a consort pairing with one of the females over three days. Along with the departure-return information from the Harbour Village group, this confirms that adult males not only occupied larger home ranges than adult females, but also monitored the maturity status of females within this area. Females rejected males more as the consortship duration increased, but it was not obvious whether males left groups spontaneously or as a result of increasing female rejection.

Discussion

The mating system of *S. sepioidea* squid, when seen across the several weeks of maturity in their semelparous reproductive system (Mather 2006) is a complex one. The male–male aggression and male consortship maintenance of females that seemed so obvious in other loliginid squid only observed at mating aggregations was a major component of male behaviour (though see Jantzen & Havenhand 2003a for *S. australis*). As with other loliginids, temporary consortships were set up during the mating period, but both males and females mated with multiple partners. Jantzen and Havenhand (2003a) catalogued behaviour of *S. australis,* and there is genetic evidence of multiple paternity in the same species (van Camp et al. 2004). Female choice was more obvious than in the gatherings of other loliginid species, although there was considerable female rejection in *S. australis,* especially of smaller males (Jantzen & Havenhand 2003a). Males

were not able to proceed to spermatophore transfer without female consent (see also Hanlon & Messenger 1996 for *S. sepioidea*), and the spermatophores themselves were transferred from the arm bases to the mantle cavity by the female. After several matings, females became more reluctant to mate and after one or a few days males abandoned the consortship. This sequence would result in multiple paternity, although this has not been proven for *S. sepioidea*. As well, spermatophore deposition immediately before egg laying right into the female's mantle cavity might have assured her fertility yet allowed for the sperm precedence which is debated about in this group (Buresch et al. 2009; Naud et al. 2016).

Observation of squid through their mating period showed a contrast in male and female use of space. Mature females stayed in limited locations, perhaps for access to resources such as a suitable substrate for egg laying. Mature males ranged over a much larger area, monitoring females for maturity. This produced a scramble competition mating system similar to that of solitary bees (Alcock 1980), squirrels (Schwagmeyer & Woontner 1986) and lemurs (Kappeler 1997), although it is not obvious why male squid could not defend females for a longer duration. Other loliginind squid had similar short-duration consortships at mating arenas, even though there were up to hundreds of animals present (Hanlon et al. 2002; Jantzen & Havenhand 2003a; Shashar & Hanlon 2013). Perhaps short-term consortship and male mobility are normal coleoid cephalopod strategies. Jozet-Alves et al. (2008) found that mature male cuttlefish were more active in an open-arena test than females or juveniles, and used a visual guidance of turns rather than a motor one in a learning task.

Although quantitative data were few, male octopuses also moved more widely and pursued mating with more stationary females (Mather, personal observation for *Octopus joubini*). Pattern displays from the complex skin display system (Messenger 2001), perhaps adapted from the camouflage that is general in the cephalopods (Mather 2004), are well known in the squid courtship system. Moynihan and Rodaniche (1982) carried out extensive observation on *S. sepioidea*, hoping to prove that the squid made a visual language on their skin, and Hanlon and Messenger (1996) gathered appearance repertoires from several species. The present observations are the first quantitative data on display exchange and, as Moynihan and Rodaniche (1982) observed, they showed much variation, including both modulation of intensity and inclusion of peripheral sub-displays. Relative positions of over-under in Zebra contests and Saddle-Stripe, as well as diagonal and parallel in Flicker–Rocking, may play a part in communication, perhaps using the squid's extensive mechanoreceptive capacity in the lateral line analogue organ (Budelmann 1995).

The detailed analyses of the different displays in this paper revealed an unexpected modulation and complexity that demonstrates the sophistication of the coleoid group. The Zebra was normally a male–male agonistic display, yet both directional and intensity modulated, depending on the intensity of the interaction. Its highest intensity was the ritualized Zebra Spread exchange (Mather 2004), which seemed to replace any physical contest. Still, one might ascribe a 'meaning' of annoyance to it, as Zebra was displayed by females to males as well as by both sexes to approaching fish (Mather 2010). Evidence for emotions in animals is difficult to obtain (Bekoff 2007), but the widespread use of this display makes it difficult to ascribe a simple motivation.

The Saddle-Stripe exchange seemed stereotyped at first glance, but had many variations, and a female Saddle appeared to indicate different expectations and resulted in different replies in different circumstances. There were also many combinations of major displays with sub-displays, as pointed out by Moynihan and Rodaniche (1982), the inclusion of which we do not yet understand. For instance, during intense Zebra competition, adult males often had brown fins, which demonstrated the pattern of individually identifiable fin dots very clearly. This allowed human observers to identify individual squid more easily and might have done the same for conspecific squid. Perhaps, the most interesting variation in a display reported here is the Fin Base Stripe of males, which was displayed both to males and females yet seemed not to modify the result of male–male contests. Added to the Dorsolateral Stripes, it increased the salience of a male's Stripe displays, and it was also seen without any other display, mostly unilaterally to females. Perhaps it was a signal of maleness, shown in several different circumstances. Studies using visual models would begin to tease apart these differences.

Does the pattern of sexual behaviour across the mating period of *S. sepioidea* represent changes across the whole duration of maturity, of which the exchanges of other loliginids at egg clusters are only a part? In *S. sepioidea*, sneakers were early adult males whose mating strategy changed to consortships as they matured. Observers have not followed other loliginids across time to know whether sneaker is also a temporary strategy in these species. Species-typical strategies cannot have been completely parallel across the group, as eggs of *Loligo* and *Doryteuthis* were a powerful attractant to males (King et al. 2003; Buresch et al. 2004) while *S. sepioidea* females laid eggs solitarily and males were not attracted to eggs (Arnold 1965). The contrasts in gatherings for egg-laying may be influenced by the differences in ecology. When suitable substrate is scarce, *S. australis* gather in large groups, but when it is abundant there are many more yet smaller mating areas (Steer et al. 2005), more like those of *S. sepioidea*. Since the genus *Sepioteuthis* occupies a basal position within the Loliginidae (Anderson 2000) perhaps the generalist strategy of egg laying at widespread locations evolved to a specialist one of attraction to eggs. Yet the scramble competition with male and female polygyny is similar across the group, so comparisons contain a mixture of similarity and variation, Clearly, much remains to be understood about loliginind squid reproductive strategies, especially as display messages could be tested with visual models.

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