Alternative Male Mating Behaviors Dependent on Relative Body Size in Captive Oval Squid *Sepioteuthis lessoniana* (Cephalopoda, Loliginidae)

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ABSTRACT—We observed the reproductive behavior of the oval squid *Sepioteuthis lessoniana* in captivity. The male used three different mating behaviors: male-parallel (MP), male-upturned (MU) and sneaking. Male competition over females frequently occurred before and during the female egg-laying period, and the outcome of most fights depended on male body size. Larger males guarded their partners from other males and performed MP mating during the egg-laying period of the paired females. In contrast, there was no pairing and mate guarding in MU mating and sneaking, which were adopted by smaller subordinate males as alternative tactics outside female egg-laying period and during the period, respectively. MP matings were 95% successful, but more than half of MU matings were unsuccessful. Higher mating success in MP mating was achieved through pairing, whereas males in MU mating were less successful because mating attempts without pair formation were often foiled by escape of the female. Sneaking was successful in all cases but occurred less frequently. Spermatophores were attached at the opening of the oviduct in MP mating, whereas they were attached around the female buccal membrane in MU mating and sneaking. Considering the route of egg transportation, higher fertilization success can be expected in MP mating because of the advantageous location of the attached spermatophores. Our results suggest that MP mating is used by larger, paired males during the female egg-laying period, and that MU mating and sneaking are alternative tactics adopted by smaller, subordinate males. These alternative mating behaviors would be conditional strategy dependent on relative body size, because some individual males displayed both MP and MU mating behaviors.

Key words: alternative mating tactics, mating success, pairing, *Sepioteuthis lessoniana*, sneaking, sperm competition

INTRODUCTION

Alternative male mating behaviors can arise during competition for mates if individual males differ in their competitive abilities, which depend mainly on body size (Gross, 1996). Larger males gain access to more partners due to large size advantage in male-male competition with size-difference, whereas smaller subordinate males often adopt strikingly different and non-competitive behavioral tactics (Alcock, 1979; Dominey, 1984). In several animal taxa such as birds, mammals, reptiles, and insects (e.g., Andersson, 1994; Hanks *et al.*, 1996; Shine *et al.*, 2000), larger body size in males has been reported to increase their mating opportunities and enhance mating success. However, it is difficult to quantify the relationship between male body size and mating success, particularly in many kinds of aquatic organisms. Here we report our empirical and experimental results on how body size in male squid affects their mating success through alternative mating tactics.

In cephalopods both sexes appear to mate promiscuously (Baur, 1998), and, especially in some loliginid squids, complex reproductive behavior have been reported (Hanlon and Messenger, 1996). Larger males form pairs with females and mate with the partners (Sauer *et al.*, 1997; Hanlon *et al.*, 1997; Hanlon *et al.*, 2002), whereas sneaking copulations by smaller males are also known to occur in several *Loligo* species (Hanlon and Messenger, 1996; Sauer *et al.*, 1997). Moreover, such multiple mating behav-

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iors involve different places of attachment of spermatophores on the female's body (Drew, 1911; Hanlon and Messenger, 1996). In particular, four mating types have recently been reported in *Sepioteuthis australis*: "male-upturned mating", "sneaker mating", "male-parallel mating", and "head-to-head mating" (Jantzen and Havenhand, 2002, 2003). However, it is unclear how each mating type is chosen and what the advantages of each are. Moreover, the underlying factors leading to multiple male mating behaviors are still unknown.

We investigated the reproductive behavior of *Sepioteuthis lessoniana* in a large tank. The aim of this study is firstly to describe the female egg-laying behavior and the multiple mating sequence, and then to clarify male mating tactics by comparing their body size, mating success, and places of attachment of spermatophores on the female's body. These comparisons will allow us to discuss how *S. lessoniana* males adopt alternative mating tactics in regard to intra-sexual selection.

Study species

The oval squid *Sepioteuthis lessoniana* is widely distributed throughout the Indo-Pacific area (Okutani, 1995) and is one of the important neritic fisheries resources, especially in southern Japan. In Japanese coastal waters, this species has been divided into three types on the basis of their morphological and genetic differences: AKAIKA, SHIROIKA and KUAIKA type (Izuka *et al.*, 1994, 1996a, 1996b). Moreover, some different characteristics in reproduction between each group have been reported, such as spawning substrate use and number of eggs contained a single egg capsule (Segawa *et al.*, 1993a, b). Although three mating positions have also been known in this species: "male-parallel" (Segawa, 1987), "head-to-head" (Lee *et al.*, 1994), and "male-upturned" (Boal and Gonzalez, 1998), it has not been demonstrated whether such a difference in mating position corresponds to the difference in species type.

MATERIALS AND METHODS

Study animals

Adult *Sepioteuthis lessoniana* (n=201) which is belonging to SHIROIKA type widely distributed around southern Japan (Izuka *et al.*, 1996b) were captured alive by small set nets off the coast near Tsuyazaki (33°47'N, 130°26'E) and Nata (33°41'N, 130°24'E) in Fukuoka Prefecture, Kyushu, Japan, between 22 April and 1 August 1999. The nets were placed about 20–300 m offshore at 10–30 m deep. The living animals were transported by truck to a columnar reserve tank (3.5 m diameter, 1.8 m deep) in the Marine World Uminonakamichi Aquarium at Fukuoka City. All animals were temporarily kept in the reserve tank to habituate to housing conditions.

Animals used for observations were transferred to an observation tank (3.2×6.6×1.8 m depth, about 38000 L) with an acrylic viewing window (1.5×5.2 m). Nine to 32 individuals (17 average) were kept in the observation tank at any one time, and a total of 94 individuals (male, mean mantle length±SD=31.4±4.3 cm, range=22.7–43.2 cm, n=46; female, 25.5±3.0 cm, 19.5–30.5 cm, n=48) were observed over the period from 29 April to 12 August. Males were significantly larger than females (two-sample *t*-test, *t*=6.68, *P*<

0.001). To avoid handling stress, mantle length was measured after death. When the number of squid reduced due to the mortality, new squid were added to the observation tank from the reserve tank (mean 10 individuals at a time). Animals in both the reserve and observation tanks were fed either living or thawed fish and shrimp daily (17:00–18:00 h) in sufficient quantities.

Animal husbandry conditions

The observation tank was supplied with natural seawater (1680 L/h), and an artificial rock (about 1 m high) was set on the sandy bottom. Sea algae, *Sargassum ringgoldianum* and *Sargassum fulvellum*, were fixed on the sandy bottom as a spawning substrate, because egg masses of *S. lessoniana* are attached to substrates under natural conditions (T. Wada, unpublished data). Water temperature was kept between 17°C and 20°C. Water quality (i.e., pH, ammonia, nitrite, and nitrate) was measured once every 2 weeks from May to August. Their values (pH: mean±SD=7.79±0.09; NH_4-N: 0.01±0.01 ppm; NO_2-N: 0.005±0.002 ppm; NO_3-N: 1.0±0.1 ppm) were within the ranges reported previously for culture conditions through multiple generations in this species (Lee *et al.*, 1994; Walsh *et al.*, 2002). Artificial light (3200lux at the surface of the observation tank) was normally provided from 08:30–21:00 h, but the lighting period was sometimes extended when needed for observation: e.g., until the end of continuous egg-laying behavior. Squid's reproductive behavior continued during the extended lighting condition as well as the low lighting condition (only aisle lights in the aquarium).

Observation and recording

Behavioral observation and recording were made primarily between 17:30 and 21:00 h through the window of the observation tank, but sometimes the period was extended to obtain the sequence data of squid's reproductive behavior. In addition, to examine the frequency and diurnal periodicity of female egg-laying, we also recorded the start time of the egg-laying behavior during the other period (21:00–17:30 h). Reproductive behavior was recorded with two digital video cameras, models DCR-VX1000 and CCD-TR1000-NTSC (Sony, Tokyo, Japan). The former was hand-held to record each phase of the mating sequence in detail using the zoom function. This recording was conducted using "*ad libitum* sampling" (cf., Martin and Bateson, 1993) for the duration of observation almost every day. The latter was mounted on a tripod to record continuous series of reproductive behaviors. In the latter recording, we used a wide-angle setting to focus on the spawning substrate and conducted "focal animal sampling" on spawning pairs to acquire the sequence of egg-laying behaviors and mating intervals. Overall, we obtained 9.5 h of videotape recordings by the former method and 45.6 h with the latter. All recordings and postvideo analyses were carried out by the same observer.

Analysis of the recordings and anatomy

Video recordings were analyzed on a high-resolution monitor (PVM-14M4J, Sony). Time data were referenced to the internal clocks on the video cameras; the clocks were set before every recording. Mating behavior was analyzed at 30 frames per second. To compare the relative body sizes of mated male and female (significance tested by a chi-squared test) we examined suitable stationary frames. In these comparisons, we used only data from easily discernable cases. Stationary frames were also used to compare the body sizes of fighting males. Sexes were discriminated by examining the stripe patterns of the dorsal mantle (Ikeda, 1933) and by the squid's behavior. To analyze the mating position performed by each male and the number of egg capsules produced by each female, some males and females were individually identified by their external characteristics (e.g., unique scars on the posterior end of the mantle or defects of the arm or fin). We defined mating success as successful spermatophore transfer to the female during

Table 1. Differences between the three mating behaviors

	MP mating (n=174)	MU mating (n=85)	Sneaking (n=7)
Body size	Male > Female	Male = or < Female	Male = or < Female
Timing	During the egg-laying period	Outside during the period	During the egg-laying period
Attachment place of spermatophores	Opening of the oviduct	Around buccal membrane	Around buccal membrane
Pairing and mate guarding	Present	Absent	Absent
Mean duration (sec)	15.0±4.4	8.4±2.1	7.8±1.9
Success rate (%)	95.4	47.8	100

the mating. To confirm the places of attachment of spermatophores, we dissected 62 females that had died in the reserve and observation tanks. The sperm masses found on the dead females were regard as those transferred by the males in this captivity, because the attached sperm masses fall out of female buccal membrane after several weeks (Wada and Kobayashi, 1995).

RESULTS

Reproductive behavior of *Sepioteuthis lessoniana*

Female egg-laying behavior occurred from 16 May to 4 August, whereas mating behavior was observed on every day of the study period. The female laid an egg capsule on the spawning substrate at average intervals of 4.2 min (SD=1.3 min, n=1427 by 14 females) and produced 24–159 egg capsules (mean±SD=75.1±42.7) in succession during a single egg-laying bout (mean observation time / individual±SD =5.1±3.1 h, n=19 egg-laying bouts by 14 females; the overall duration was defined as a female egg-laying period). The egg-laying bout was repeated several times during the study period (maximum of four times per female). The female usually started laying eggs in the morning (07:00–09:00 h, 21% of 19 egg-laying bouts) or evening (18:00–22:00 h, 52%).

Both males and females exhibited promiscuous mating behavior by mating with more than one partner. Three different matings were observed (Table 1): male-parallel mating (MP mating; Fig. 1a), male-upturned mating (MU mating; Fig. 1b) and sneaking. At least three individual males showed both MP and MU mating positions. The behavioral process of each mating is described below.

Male-parallel mating (MP): MP mating was observed 174 times and was performed by distinct pairs. The pair swam side by side and the male guarded its partner against other males (which was defined as a pairing behavior). This mating occurred only during egg-laying period by the paired female. Paired males repeated the MP mating at 29.5 min intervals on average (SD=39.8 min, range=0.8–324.5 min, n=155). Males succeeded in attaching spermatophores to females in 166 MP matings (95%). The successful MP mating sequence was as follows.

First, the paired male usually raised up either his right arm I or both arms I vertically (91% of 174 matings), and swung the arm(s) back and forth beside the female (Fig. 1a-1). Second, the male moved toward the ventral side of the
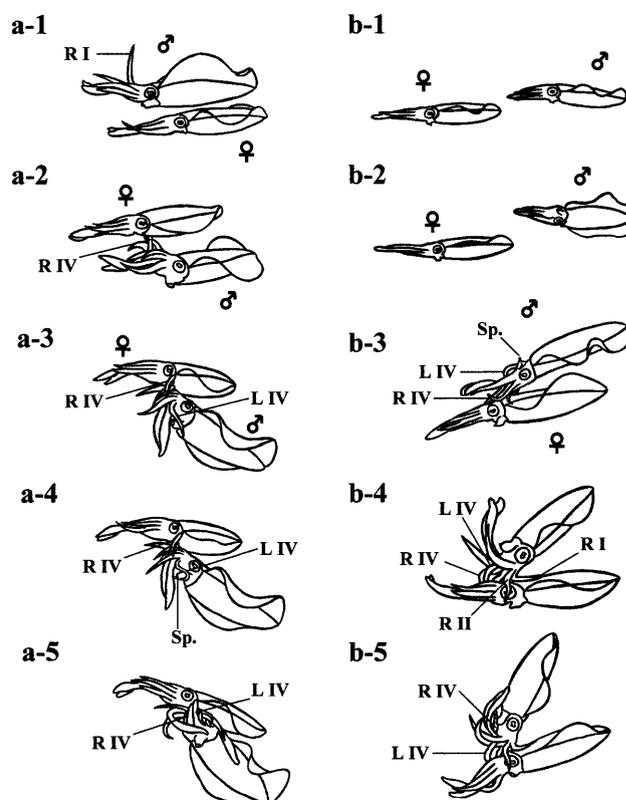
Fig. 1. Behavioral sequences of two matings in *Sepioteuthis lessoniana*: a; male-parallel mating, b; male-upturned mating. For details see text. *R=Right, L=Left, Sp.=Spermatophores, I–IV=Arm number

female and touched her neck or the anterior part of the mantle with his right arm IV (Fig. 1a-2). Third, his right arm IV (non-hectocotylized) was inserted into the female's mantle cavity through the left part of the opening (Fig. 1a-3). Then, several spermatophores ejected through the funnel were held with the modified part of the hectocotylized left arm IV (Fig. 1a-4). The left arm IV was also inserted into the female's mantle cavity alongside the right arm IV (Fig. 1a-5). After a short time (mean insertion time±SD=4.8±1.2 s; uninterrupted sequence data were available at 116 MP matings; Fig. 2), the male released the spermatophores and withdrew both arms IV. The time spent for a MP mating, which starts from male's approach to a female and ends at the release of the female, was 15.0 s on average (SD=4.4 s, range=6.5–29.1 s, n=102; from only uninterrupted sequence
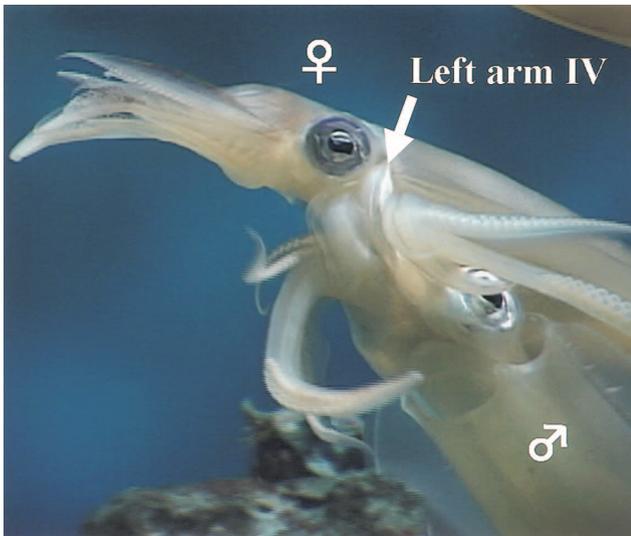
Fig. 2. Larger male inserting left arm IV (hectocotylus) into female's mantle cavity through the left part of the opening (MP mating).

data). Immediately after mating, the female often ejected only the outer sheaths of the spermatophores through her funnel. Males transferred spermatophores only once during each MP mating, except in one case in which they were transferred twice (0.6% of 166 successful matings). Sperm masses were confirmed on only the opening of the oviduct within the mantle cavity of female, and those that still had the outer sheaths of the spermatophores were found in two individuals among all dissected females (Fig. 3).

Male-upturned mating (MU): MU mating was observed 85 times. Neither pairing nor male mate guarding was observed

Fig. 3. Sperm masses with the outer sheaths of spermatophores attached on opening of the oviduct. *a=Sperm masses, b=Opening of oviduct, c=Outer sheaths of spermatophores

in this pattern. MU mating occurred outside the egg-laying period of the female. Males succeeded in attaching spermatophores to females in 37 MU matings (44%). The successful MU mating sequence was as follows.

First, the male abruptly approached the female from any directions and stayed behind her (Fig. 1b-1). Second,
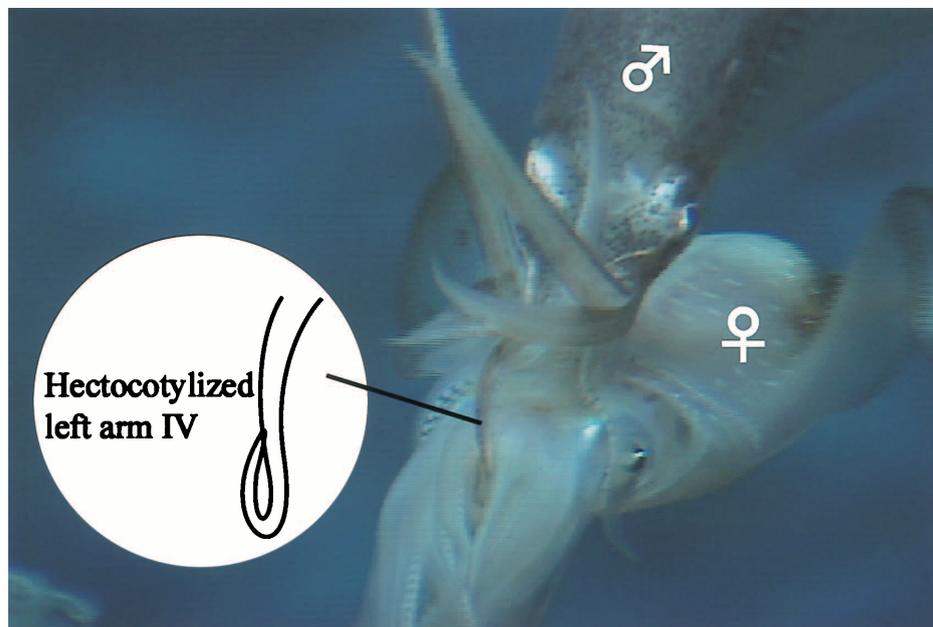
Fig. 4. Smaller male inserting left arm IV (hectocotylus) into female's buccal cavity (MU mating).

Table 2. Relative size-differences between males and females at MP (n=149), MU and sneaker matings (n=66)

	Male > Female	Male ≒ Female	Male < Female
MP mating	110 (74%)	24 (16%)	15 (10%)
MU mating and sneaking	14 (21%)	32 (49%)	20 (30%)

the male flipped upside-down (Fig. 1b-2). Before flipping, the male often shook his body minutely. Third, the male touched the dorsal mantle or head of the female while maintaining an upside-down position (Fig. 1b-3). Simultaneously, the male ejected several spermatophores through his funnel and held them with his left arm IV, while the right arm IV was inserted into the female's buccal cavity. Then, the male inserted the spermatophores with his hectocotylized left arm IV into the female's buccal cavity alongside the right arm IV, while the right and left arms I and II held the female's body (Fig. 1b-4). Finally, the right arm IV was withdrawn from the female's buccal cavity, leaving only the left arm IV inside (mean insertion time±SD=3.1±1.3 s; uninterrupted sequence data were available at 28 MU matings) (Fig. 1b-5). The hectocotylized left arm IV was bent at the end holding the spermatophores (Fig. 4). The mated male and female were released each other or the female swam backwards at the end of mating. No spermatophore was observed in the withdrawn left arm IV. The time spent for a MU mating (from male's approach to the release of the female), was 8.4 s on average (SD=2.1 s, range=5.7–12.3 s, n=13; from only uninterrupted sequence data). Males transferred spermatophores only once during each MU mating. Many sperm masses were confirmed around the buccal membrane in all dead females.

Sneaking: Sneaking was observed 7 times. Although the mating position and attachment place of spermatophores in sneaking were the same as those observed in MU mating (see above and Fig. 1b), the sneaking males mated with the females pairing with larger males during the female egg-laying period. Sneaking was successful in attaching spermatophores to females in all 7 cases (100%).

Male–male competition and mating success

Male competition over females was observed particularly during and immediately before the female egg-laying period. Fighting males often extended their arms (especially arms III) and changed their body color from white to dark brown. The displays determined the outcome of fights in the most contests: Relatively larger males were more likely to win the competition. Even when sometimes grasping each other, larger males usually chased away and defeated smaller ones (93% of 27 fights). The winner paired with the female and maintained the partner, resulting in that male body size was significantly larger in MP than in MU mating and sneaking (χ^2=51.8, *P*<0.001). Mated males were larger than their partners in 74% of 149 MP matings, but in only

21% of 66 MU mating and sneaking (Table 2).

Mating success rate was higher in MP (95%) than in MU matings (44%) (χ^2=90.6, *P*<0.001). MP matings were 100% successful (157 cases) when the male started just when the female transferred the egg from the mantle cavity to her arms through her funnel, but were less successful in other cases (53% of 17 cases) because the females escaped from the mating attempts of the males. Unsuccessful MU matings (n=40, excluding eight indiscernible cases) could be attributed to the escape of females during these trials (60%) or interruption by the males themselves (40%).

DISCUSSION

Male *Sepioteuthis lessoniana* belonging to SHIROIKA type used three different matings dependent on the relative body size: male-parallel (MP) mating by larger, paired males, and male-upturned (MU) mating and sneaking by smaller, unpaired males. MP mating and sneaking occurred during the female egg-laying period, whereas MU mating outside the period.

MP mating is common in loliginid squids (Table 6.2 in Hanlon and Messenger, 1996), whereas MU mating seems to be quite unusual but is the same pattern described by Boal and Gonzalez (1998) and Ueta *et al.* (2002) in this species and by Jantzen and Havenhand (2002) in the related species *Sepioteuthis australis*. Sneaking of *S. lessoniana* occurred during the female egg-laying period with a male-upturned (MU) position, as has been reported for *S. australis* (Jantzen and Havenhand, 2003). Moreover, the final phase of MU mating (32% of 37) was similar to the head-to-head mating position reported in *Loligo* spp. (Drew, 1911; Hanlon *et al.*, 2002; T. Wada, unpublished data), which occurred when the female swam backwards at the end of mating and pulled the male. The head-to-head mating position should be regard as a variation of MU mating in this species.

The mating success rate in male *S. lessoniana* was significantly higher in MP than in MU mating. Male mating success depended on the timing of occurrence, and so higher success in MP mating seemed to be achieved through pairing. Males in MP mating that paired before mating started the mating mostly during egg transportation of paired female through her funnel, and fully succeeded in attaching spermatophores. That is, mating timing determines mating success because the female cannot supply jet propulsion from her funnel for the escape. In contrast, males in MU mating were less successful, because mating attempts without pair

formation were often avoided owing to escape of the female. Thus, pairing before mating is indispensable for high mating success of males. MP mating was adopted by larger males because they won against smaller males in the competition to pair with females. The outcome of most fights was correlated with relative body size. Although relative size advantage in aggressive contests over females has been reported in other loliginid squids, *L. pealei* and *L. plei* (Arnold, 1962; Moynihan and Rodaniche, 1982; DiMarco and Hanlon, 1997), the effect of body size on male mating success was not mentioned in these papers. Our data are therefore the first to confirm that large body size in male loliginid squid is an important factor leading to high mating success. The sexual size dimorphism in some loliginid species might have evolved partly through intra-sexual selection (i.e., male–male competition). Moreover, small unpaired males of *S. lessoniana* sometimes adopted sneaking tactics and thereby fully succeeded in attaching spermatophores to females. Although it was not clear why sneaking occurred less frequently (n=7), sneaking males were often chased away by larger paired males after the spermatophore transfer. There may be higher costs and risks for sneaking than for MP and MU matings.

In addition to high mating success, higher fertilization success is expected in MP mating because of the advantageous location of the attached spermatophores and repeated matings during the egg-laying period of the paired female. With MP mating, sperm attached on the opening of the oviduct would come into contact with unfertilized eggs earlier than those attached around the buccal membrane by MU mating and sneaking, because all eggs first pass through the oviduct after ovulation (illustrated in Fig. 5). Analyses of dead females confirmed the presence of sperm masses around the buccal membrane in all of these females, whereas sperm masses remained at the opening of the oviduct in only two dead females. Because males inserted the hectocotylized left arm IV holding the spermatophores into the female's mantle cavity during each MP mating (Fig. 2), spermatophores should have been deposited on the opening of the oviduct in only MP mating. It is unclear at present why sperm masses were not found on the opening of the oviduct in the other dead females. Moreover,
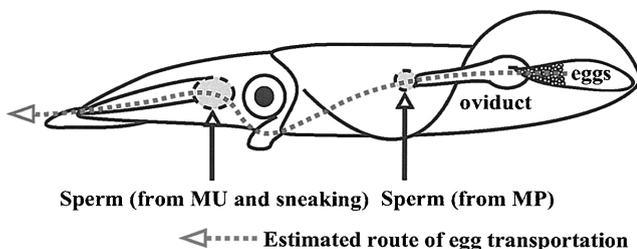
repeated MP matings (mean=29.5 min interval) by the paired male during the female egg-laying period would increase the fertilization opportunities. Thus, the sperm in MP mating may have a higher probability of fertilizing more eggs than those in MU mating and sneaking.

When are sperm that were attached around the female buccal membrane by MU mating and sneaking used for the fertilization? Wada and Kobayashi (1995) have reported for *S. lessoniana* that the females continuously produced fertilized eggs at least during 20 days after isolation from males. In such cases, the eggs were most likely fertilized from sperm stored in the seminal receptacle at the ventral portion of female buccal membrane because there is no sperm storage organ around the opening of oviduct (i.e., for MP mating). Although the mechanism underlying fertilization including cryptic female choice (i.e., sperm selection; Eberhard, 1996) in *S. lessoniana* is still unknown, the female can store up and release active sperm for nearly one month without mating (Wada and Kobayashi, 1995). Therefore, the female may make effective use of sperm stored from MU mating and sneaking for the fertilization when sperm at the opening of oviduct are not present.

The present study found that MP mating is used by larger, paired males during the female egg-laying period, whereas MU mating and sneaking are adopted by smaller, subordinate males as alternative mating tactics. These alternative mating behaviors would be conditional strategy dependent on relative body size, because some individual males showed both MP and MU matings. The larger males have a mating advantage leading to higher mating success (i.e., pairing), and sperm attached in MP mating may have a greater chance of fertilizing more eggs than those in MU mating and sneaking. Therefore, though there is no direct evidence, we believe that males in MP mating gain more paternity than those in MU mating and sneaking. However, a high percentage of fertilization by small sneaker or satellite males has been reported in the Australian giant cuttlefish *Sepia apama* (Naud *et al.*, 2004) and in other animal groups (e.g., Brockmann *et al.*, 2000; Fu *et al.*, 2001). In the future studies it will be necessary to confirm the paternity of each of the offspring from alternative male mating tactics by molecular biological analysis using microsatellite DNA markers (e.g., Shaw and Boyle, 1997; Buresch *et al.*, 2001; Shaw and Sauer, 2004).

Fig. 5. Places of attachment of sperm attached by three different matings, and estimated route of egg transportation. In our hypothesis on the fertilization mechanism, sperm at the opening of the oviduct from MP mating would have a positional advantage for fertilization.

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