

## Reproductive Behavior of the Japanese Spineless Cuttlefish *Sepiella japonica*

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**Abstract:** The reproductive behavior of the Japanese spineless cuttlefish *Sepiella japonica* was observed in a tank. The males competed for females before egg-laying and then formed pairs with females. The male then initiated mating by pouncing on the female head, and maintained the male superior head-to-head position during the mating. Before ejaculation, the male moved his right (non-hectocotylized) arm IV under the ventral portion of the female buccal membrane, resulting in the dropping of parts of spermatangia placed there during previous matings. After the sperm removal behavior, the male held spermatophores ejected through his funnel with the base of hectocotylized left arm IV and transferred them to the female buccal area. The spermatophore transfer occurred only once during each mating. The female laid an egg capsule at average intervals of 1.5 min and produced from 36 to more than 408 egg capsules in succession during a single egg-laying bout. Our results also suggested one female produced nearly 200 fertilized eggs without additional mating, implying that the female have potential capacity to store and use active sperm properly. The male continued to guard the spawning female after mating (range=41.8–430.1 min), and repeated matings occurred at an average interval of 70.8 min during the mate guarding. Although the time spent on the sperm removal in *S. japonica* was shorter than in other sperm-removing cuttlefishes, the shorter sperm removal duration may be compensated by the post-copulatory mate guarding and repeated matings in this species.

**Keywords:** Spineless cuttlefish, *Sepiella japonica*, mating, sperm removal, egg-laying

### Introduction

Sperm competition, the competition between sperm of different males to fertilize a female's eggs (Parker, 1970), is a major selective force shaping many aspects of sexual behavior including frequency and duration of copulation, sperm displacement, mate guarding and cryptic female choice (for review, Birkhead & Møller, 1998; Eberhard, 1996). Most near-shore decapod cephalopods are well known for their promiscuous mating system and complex reproductive behavior (Hanlon & Messenger, 1996). In the giant Australian cuttlefish *Sepia apama*, the males adopt sophisticated tactics for access to females such as female mimicry (Norman *et al.*, 1999) and sneaking (Hall & Hanlon, 2002), resulting in high fertilization success (Naud *et al.*, 2004; Hanlon *et al.*, 2005). Moreover, to avoid subsequent sperm competition, the males of *Sepia officinalis* and *Sepia esculenta* remove sperm masses attached during previous matings before spermatophore transfer (Boal, 1997; Hanlon *et al.*, 1999; Wada *et al.*, 2005). Although many experimental studies of sperm-removing insects have demonstrated that the last male to mate with the female fathers the most offspring (*e.g.* Waage, 1979; Siva-Jothy & Tsubaki, 1989; Simmons & Siva-Jothy, 1998), the effectiveness of sperm displacement (*i.e.* the removal of previous sperm and replacement with own sperm; Parker, 1970) is still unknown in cuttlefish.

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Post-copulatory mate guarding is another possible mechanism that can increase a male's paternity assurance (Sherman, 1989; Simmons, 2001). Although guarding males must delay searching for other mates, they may insure their paternity by reducing the probability that the female will remate with other males (Yamamura, 1986). Temporary mate guarding by males after mating has been reported in some cuttlefishes (Hanlon & Messenger, 1996; Hall & Hanlon, 2002). The mechanisms of sperm precedence in cuttlefishes are not known, but post-copulatory mate guarding would be an effective strategy for increasing male reproductive success if the last male to mate fertilizes the most eggs. In some insect species, post-copulatory guarding behavior often coexists with repeated copulations or sperm displacement to achieve last-male sperm precedence (Simmons & Siva-Jothy, 1998).

The Japanese spineless cuttlefish *Sepiella japonica* (family Sepiidae) is distributed in the East China Sea including southern Japan (Okutani, 2005) and is an important fisheries resource in Japanese coastal areas. The species grows to about 18 cm in mantle length during its lifespan of one year (Natsukari & Tashiro, 1991). Mature individuals make a wide-scale spawning migration (Hayashi & Tako, 1983; Ueda, 1985), but little is known about their reproductive behavior (Yamamoto, 1982; Teramura, 1989). Teramura (1989) reported that the mating of *S. japonica* lasted 3 to 10 seconds and repeatedly occurred during the female egg-laying period. There have been some observations on the mating and egg-laying behavior under culture conditions in the related species *Sepiella inermis* (Boonprakob *et al.*, 1983; Nabhitabhata, 1997), but a male mating strategy associated with sperm competition has not been mentioned for any species of the genus *Sepiella* in the previous reports. In the present study, we investigated the reproductive behavior of *S. japonica* in a tank, focusing especially on the male mating strategy involving sperm competition.

## Materials and Methods

### *Animals and maintenance conditions*

This study was conducted at Marine World Uminonakamichi Aquarium in Fukuoka Prefecture, Kyushu, Japan, 30 May–26 June 2000 and 28 May–3 July 2002. Adult cuttlefish *Sepiella japonica* were captured in small set nets off the coast of Tsuyazaki, 33°47'N, 130°26'E, near the aquarium. All animals were transported by truck and temporarily kept in a rectangular reserve tank (200×300×75 cm depth) for acclimation to the housing condition. A total of 18 individuals (length; male, mantle mean±SD=14.0±0.8 cm, n=6; female, 13.0±1.0 cm, n=12) used for observations were transferred to an observation tank (85×135×100 cm depth) with an acrylic viewing window (90×110 cm). Between three and nine individuals (mean=6.4) were kept at any one time in the observation tank. The sex ratio was maintained 2:1 female bias in accordance with that of collected samples.

The observation tank was supplied constantly with natural seawater (132 l/h), and some rocks were set on the sandy bottom. Tree branches were provided as a spawning substrate. Water temperature was kept between 20°C and 23°C. Water quality was measured four times during the study period, and the values (in mean±SD: pH=8.02±0.16; NH<sub>4</sub>-N=0.04±0.03 ppm; NO<sub>2</sub>-N=0.006±0.004 ppm; NO<sub>3</sub>-N=1.45±0.06 ppm) were maintained within the ranges reported previously for multiple culture systems in other cuttlefishes (Forsythe *et al.*, 1994; Milton *et al.*, 2001). Artificial light was normally provided from 08:30–21:00 hours, but the lighting period was sometimes extended to obtain the complete sequence data of reproductive behavior. The cuttlefishes were fed thawed fish and shrimp daily in sufficient quantities for the number of animals in the tank.

### *Observation, recording, and analysis of reproductive behavior*

Behavioral observation and recording were made primarily between 17:30 and 21:00 hours through the acrylic window of the tank, but sometimes this period was extended as mentioned above. The reproductive behavior was recorded by using two digital video cameras, models

DCR-VX1000 and TRV9-NTSC (Sony, Tokyo). The former was hand-held to record each phase of mating and egg-laying behavior by zooming, and the latter was mounted on a tripod to record continuous series of reproductive behaviors. We conducted "ad libitum sampling" in the hand-held recording, "focal animal sampling" on spawning pairs in the continuous recording (cf. Martin & Bateson, 1993). Overall, we obtained 1.2 and 42.1 h of videotape recordings, respectively. The video recordings were analyzed on a high-resolution monitor (PVM-14M4J, Sony). The time data were referenced to the internal clocks on the video cameras. To obtain accurate time data of egg capsule deposition interval, we omitted the intervals interfered by the occurrence of mating or male-male competition. Sexes were discriminated by examining the patterns of the dorsal mantle (Yasumoto, 1938) and by the animal's sexual behavior. Individual identification was carried out using some unique scars on the posterior end of the mantle or partial defects of an arm or fin. We used a Mann-Whitney *U* test to compare the times spent for the sperm removal behavior in cases where the previous male to mate with the partner was the same and in cases where it was not. The statistical test procedures were performed with StatView 5.0.

## Results

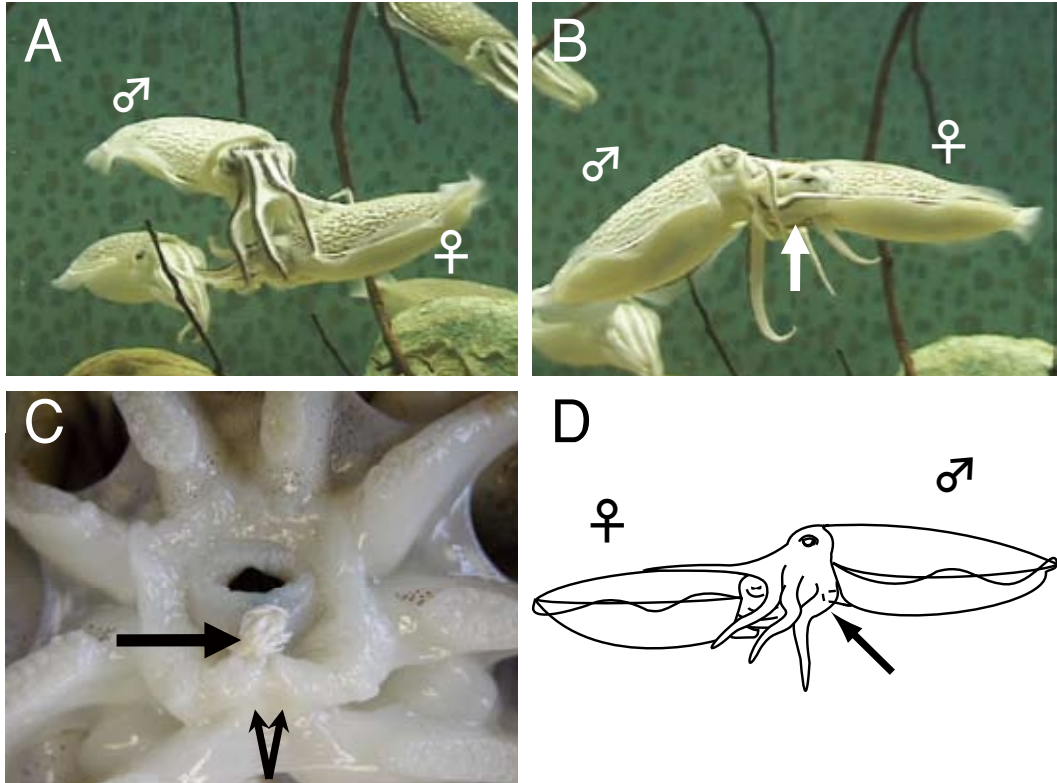
### *Mating behavior*

We observed 34 mating sequences of 17 *Sepiella japonica* pairs drawn from among six males and ten females (mean duration $\pm$ SD=49.2 $\pm$ 12.9 s, range=31–96 s). The males competed for females as mating partners immediately before the female egg-laying period, and the winners formed pairs. During the female egg-laying bout, the paired male guarded her against other males and succeeded in attaching spermatophores to the female's buccal area (41.5% of 82 mating trials). The remaining 48 cases were rejected by the female immediately after the mating initiation. Both males and females mated with multiple partners in the tank during the study period, suggesting a promiscuous mating system in this species. The behavioral process of mating is described below.

The paired male initiated a mating by pouncing down on the female's head (Fig. 1A) and copulated with her in a head-to-head position. Immediately after achieving the mating position, the male moved his right (non-hectocotylized) arm IV under the ventral portion of the female buccal membrane (28.6 $\pm$ 9.0 s, 18–63 s; Fig. 1B), resulting in dispersal of white debris into the water column. The debris would comprise sperm mass particles, because many spermatangia were attached under the female buccal area where the paired seminal receptacle is located (Fig. 1C). After the sperm removal behavior, the male held spermatophores ejected through his funnel with the base of his hectocotylized left arm IV (Fig. 1D) and then transferred them to the female buccal membrane. The spermatophore transfer was finished in less than a second and was performed once during each mating. Finally, using the same arm, the male continued to deposit and attach the spermatophores on the ventral portion of the female buccal membrane (20.4 $\pm$ 6.1 s, 11–38 s).

### *Egg-laying behavior*

The female egg-laying behavior was divided into three phases according to the location of the egg transported from the mantle cavity to arms (Fig. 2A). In the first phase before an egg capsule passed through the female funnel, she was usually hovering close to the spawning substrate (mean duration $\pm$ SD=34.6 $\pm$ 11.7 s, n=115 by 3 females; Fig. 2A-1). Secondly, the egg capsule was transferred into the female's arms by inserting the funnel between the bases of arms IV (34.9 $\pm$ 1.4 s, n=101; Fig. 2A-2). Each egg capsule produced through the female funnel was already stained black. Thirdly, the female deposited the egg capsule on the spawning substrate after holding it in her arms (13.6 $\pm$ 4.7 s, n=98; Figs. 2A-3, 2B). This egg-laying process was continuously repeated at average intervals of 1.5 min (SD=0.6 min, n=1553 by 9 females). The females produced from 36 to more than 408 egg capsules (n=11; including one incomplete sequence data) during a single



**Fig. 1.** Mating behavior of *Sepiella japonica*. **A.** Mating initiation by male. **B.** Sperm removal by using his right arm IV (white arrow). **C.** Sperm masses (spermatangia) attached on the ventral portion of the female's buccal membrane. The twin arrows indicate location of paired seminal receptacles. **D.** Spermatophore transfer using the base of the hectocotylized left arm IV (black arrow). The spermatophores seem likely to be held with his modified basal portion of the hectocotylus.

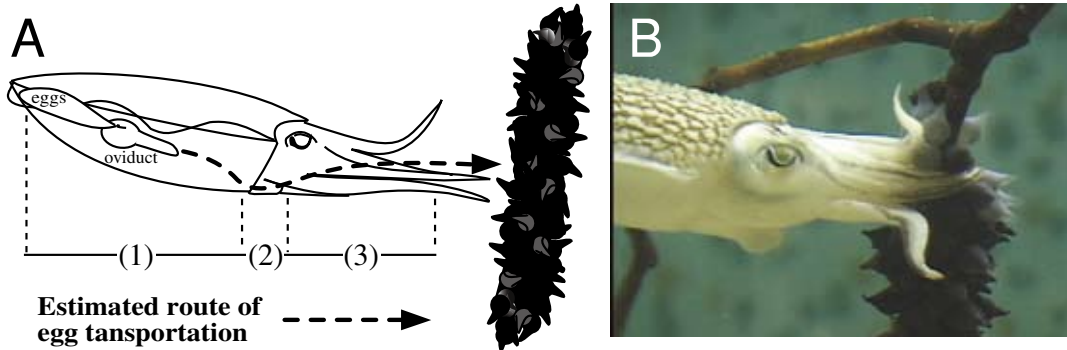
egg-laying bout (mean duration $\pm$ SD=211.3 $\pm$ 102.1 min). The egg-laying bout was repeated multiple times during the study period.

#### ***Post-copulatory mate guarding and repeated matings***

The paired male swam beside his partner and guarded her from other males even after mating (Fig. 3). The post-copulatory mate guarding lasted 41.8–430.1 min (mean duration $\pm$ SD=129.3 $\pm$ 124.9 min,  $n=9$ ; from only complete sequence data), during which time the male repeated matings at average interval of 70.8 min (SD=37.4 min, range=31.0–153.2 min,  $n=11$ ). The sperm removal behavior was performed in all observed matings regardless of whether the last male to mate with the partner was himself (*i.e.* repeated matings) or not. The time spent on the sperm removal behavior did not differ significantly whether the last male to mate with the partner was the removing male (duration; mean $\pm$ SD=29.8 $\pm$ 5.3 s,  $n=10$ ) or a different male (26.4 $\pm$ 5.7 s,  $n=14$ ;  $z=-1.37$ ,  $p>0.05$ ).

### **Discussion**

The mating behavior of *Sepiella japonica* observed in the present study was basically similar to those of other *Sepia* spp. (Hanlon & Messenger, 1996), but we found some differences in the behavioral pattern during the mating initiation and in the mating positions of paired male and female.



**Fig. 2.** Female egg-laying behavior of *Sepiella japonica*. **A.** Estimated route of egg transportation. **B.** Egg deposition to the spawning substrate.



**Fig. 3.** Post-copulatory mate guarding by male (upper).

The male *S. japonica* pounced on the female's head without courtship at the initiation of mating and then maintained the male superior head-to-head position during the mating (Fig. 1A, B, D). In *Sepia esculenta* and *Sepia latimanus*, the males slowly initiated mating and achieved the head-to-head position so that the arms of the pair were intertwined after showing the courtship displays with their body color changes (Arakawa, 1960; Corner & Moore, 1980). Although the relationship between the courtship display and mating success has not been examined in the cuttlefishes, the female *S. esculenta* frequently rejected mating by a particular male (T. Wada, unpublished data). Because also in *S. japonica* the female often escaped from the mating attempts of the male before achieving the mating position, the forced mating initiation and male superior head-to-head position may have the effect of preventing the female physically from refusing the male mating attempt.

The time spent on sperm removal behavior and mating duration by *S. japonica* was relatively shorter than those observed in other cuttlefishes (Table 1). Because for *S. esculenta* the time allocated to sperm removal was positively correlated with the volume of removed sperm mass debris (Wada *et al.*, 2005), the shorter sperm removal duration for *S. japonica* was assumed to be related to a low rate of sperm displacement. In addition, males of *S. japonica* removed previous sperm masses regardless of whether the last male to mate with the partner was themselves or not; in other words males remove not only rival sperm but also their own. Although the actual effect of sperm removal is still unclear in the cuttlefishes, many experimental studies with insects have demonstrated that the sperm displacement leads to high last-male sperm precedence of the displacing male (Simmons & Siva-Jothy, 1998; Simmons, 2001). In damselflies and dragonflies, well-known

**Table 1.** Durations of mating and sperm removal in cuttlefishes

Species	Mating duration (min)	Mean duration and method of sperm removal	Reference
<i>Sepiella japonica</i>	0.8 in average (range 0.5–1.6)	0.5 min by arm	Present study
<i>Sepiella inermis</i>	1–5	no data	Nabhitabhata (1997)
<i>Sepia esculenta</i>	5.4 in average (range 1.5–14.3)	1.6 min by arms	Wada <i>et al.</i> (2005)
<i>Sepia officinalis</i>	7–14	5.9 min by flushing water	Hanlon <i>et al.</i> (1999)
<i>Sepia apama</i>	2.4 in average (SE 0.1)	1.7 min by flushing water	Hall & Hanlon (2002)
<i>Sepia latimanus</i>	0.5–1.5	no data	Corner & Moore (1980)
<i>Sepia pharaonis</i>	1–30	no data	Nabhitabhata & Nilaphat (1999)

for sperm-removing among insects, the last male to mate with the partner continued to guard her from other males to the end of the female's oviposition period, thereby gaining the majority of fertilizations (Cooper *et al.*, 1996; Corbet, 1999). Male mate guarding behavior after mating for *S. japonica* usually lasted to the end of the female egg-laying bout (Fig. 3), presumably implying the possibility of last-male precedence by sperm removal. Moreover, repeated matings during the mate guarding period would increase the relative number of the male's own sperm on the female buccal area (sperm storage site). Therefore, the persistent post-copulatory mate guarding and repeated matings may compensate for the low rate of sperm displacement predicted by short-term sperm removal in this species.

The number of laid egg capsules during a single egg-laying bout varied from 36 to more than 408 for *S. japonica*. Similarly, high variation in batch size has been estimated from the number of mature ovarian eggs reported in this species (*i.e.* 100–300 eggs laid per day; review in Natsukari & Tashiro, 1991), therefore, the variations in batch size may be attributed to the differences in female age or body size (Boletzky, 1987; Gabr *et al.*, 1998). The time required to produce an egg capsule for *S. japonica* was 1.5 min on average, which was shorter than for *S. esculenta* and *Sepia lycidas* (4–6 min; Watanuki *et al.*, 2000; T. Wada, unpublished data). Females of *S. esculenta* and *S. lycidas* spent considerable time camouflaging each egg capsule against predation by attaching sand to the surface. *S. japonica*, however, would not need this extra time to lay an egg capsule because the capsule is covered with black ink and may thus not need further camouflage.

Our results also showed that one female continuously produced nearly 200 fertilized egg capsules without additional mating, implying that females have the potential to store and use sperm properly. The fertilization was thought most likely to occur while the female held each egg capsule in her arms (Fig. 2A–3), because most eggs are fertilized by sperm from spermatangia attached on the female buccal area in *Sepia apama* (Naud *et al.*, 2005). However, it is still unclear when and how the sperm stored within the seminal receptacles were used for fertilization in cuttlefishes. It will be necessary for the future study to address the female aspects of sperm competition including cryptic female choice (Eberhard, 1996).

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## シリヤケイカの繁殖行動

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### 要 約

水槽内でのシリヤケイカ *Sepiella japonica* の繁殖行動を観察した。シリヤケイカの雄は雌が産卵を開始する前に雌をめぐって闘争し、ペアを形成した。ペア雄は雌の頭部に覆い被さる形で交接を始め、雄上位のままで雌雄の頭部が向き合う交接体勢を維持した。雄は自らの精莢を射出する前に、雌の口球周口膜下部で右第IV腕を動かすことによって、過去の交接によってそこに付着させられていた精子塊の一部を落下させた。その精子除去行動後、雄は交接腕である左第IV腕の根元で漏斗から吐き出した精莢をつかみ、雌の口球下部に渡した。この精莢輸送は各交接で1回だけであった。雌は平均1.5分の間隔で産卵基質に卵嚢を1つずつ産みつけ、一連の産卵行動で36から408個以上の卵嚢を産出した。また、本研究では1個体の雌が追加の交接なしで200個近くの受精卵を産出することが示され、シリヤケイカの雌は過去の交接によって貯えられた精子を必要な時に受精に使う能力を持つと考えられた。それに対して雄は交接後も産卵雌を他雄からガードし続け(交接後ガード時間の範囲=41.8~430.1分)、そのガード行動中に平均70.8分の間隔で繰り返し交接を行った。シリヤケイカの雄が精子除去に費やす時間は他のコウイカ類のそれらと比べて短かったが、永続的な交接後ガード行動と繰り返し交接が短時間の精子除去から推測された本種の低い精子置換率を補償しているかもしれない。