

Off-Host Observations of Mating and Postmating Behaviors in the Cat Flea (*Siphonaptera: Pulicidae*)

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ABSTRACT A blood meal was necessary for a male cat flea, *Ctenocephalides felis* (Bouché), to display the mating attempts to an unfed or fed female. More mating pairs resulted when both sexes were fed. Copulation occurred when fed fleas were placed on surfaces with temperatures from 34 to 42°C. This article not only describes the mating and postmating behaviors of cat fleas, but also compares them with those of other fleas. The sequence of mating behavior began when a male approached a female ventrally, and the male's antennae and claspers became erect to attach to the abdomen of the female. Clasper attachment lasted until copulation ended, whereas the male retrieved his antennae immediately after genitalia linkage. The male generally grasped the female's tarsi with his claws during mating. The length of the mating interval terminated by the male ranged from 25 to 110 min and was significantly longer than that terminated by the female (averaging 12.11 min). After the mating pair separated, the male displayed a series of postmating behaviors discussed herein. This article documents grasping and postmating behaviors of the male cat flea.

KEY WORDS *Ctenocephalides felis*, cat flea, blood meal, temperature, mating behavior, postmating behavior

THE CAT FLEA, *Ctenocephalides felis* (Bouché), is a notorious pest found on pet animals worldwide. Nearly 80 and 60% of stray cats and dogs, respectively, in Taipei (Taiwan) were infested (Shyu et al. 1993). Shyu's questionnaire survey (1992) revealed that >11.7% of families in Taipei suffered from fleabites and >5.1% of school children had been bitten by fleas. Shyu et al. (1993) also indicated that the proportions of male cat fleas on cats and dogs peaked 1 mo before the flea season. According to Osbrink and Rust (1984), fecundity was higher in microcells containing a single female and five males than in those containing four females and four males, eight females and eight males, or 11 females and 13 male fleas. We have reported that multiple-mated females laid significantly more fertile eggs than single-mated ones (Hsu and Wu 2000). Therefore, in this study we described the process of mating behavior, and attempted to see if a blood meal and a rising temperature were crucial to the trigger of mating.

Although virgin female cat fleas laid nonviable eggs following a blood meal, parthenogenesis was not found in this species, that is, only mated female fleas laid fertile eggs (Zakson-Aiken et al. 1996). Several

authors have described the mating behavior of fleas. However, the research has focused mainly on various members of Ceratophyllidae (Mitzman 1910; Holland 1955; Humphries 1967a, 1967b; Iqbal and Humphries 1970, 1974, 1976; Iqbal 1973). Mating acts of pulicid fleas, including the chigoe, *Tunga penetrans* (L.), and the sticktight flea, *Echidnophaga gallinacea* (Westwood), were also recorded. The females of both these species stick tightly either in or on the skin of host animals (Suter 1964). Therefore, as widely assumed, the mating behaviors of these two species markedly differ from those of free-living cat fleas. The cat flea is a permanent ectoparasite on an extensive range of host species. Adult fleas spend most of their lives on a host, leaving the animal when either the corporeal population is extremely high or their host is dead. Georgi and Georgi (1990) indicated that the adult cat flea displayed little tendency to leave its dog or cat host unless the population approached ≈ 200 . Therefore, a blood meal and the surface temperature may trigger the mating act of cat fleas. According to Dean and Meola (1997), the epididymis of the unfed male cat flea was blocked with folded columnar epithelial cells. Thus, the blood meal appears to play an important role in stimulating sperm transfer into the epididymis.

The entire process of mating behavior of cat fleas has never been described. While performing a contact pheromone experiment, Akin (1984) used glass probes rubbed against female flea bodies to touch the males to stimulate the mating behavior. However, none of the cat fleas mated off-host. To understand the relationships among the multiple mating, sex ratio, and

This study was conducted according to the "Guide for the Care and Use of Laboratory Animals" promulgated by the Committee on Care and Use of Laboratory Animals of the Institute of the Laboratory Animals Resources, National Research Council, 1996. Protocol for the use of cats in this research is on file and was performed according to Animal Protection Law set forth by Council of Agriculture, Taipei, Taiwan, and approved by the Laboratory Animal Care Committee, Department of Entomology, National Taiwan University.

population dynamics of cat fleas, the difficulty in observation of off-host mating should be overcome beforehand. This study investigated how a blood meal and surface temperatures affected the mating behavior of cat fleas. We have resolved many of the obstacles and present the complete process of mating behavior, including the postmating behavior.

Materials and Methods

Fleas Rearing. Cat fleas were taken from the Taipei colony established in 1990 with fleas collected from five infested stray cats on the streets of Taipei. The colony is maintained on cats as hosts, as described by Hsu and Wu (2000).

Microcells. The microcells as described by Hsu and Wu (2000) were used to confine fleas on cats for blood feeding, and were modified to observe the mating behavior of cat fleas off-host. A microcell was constructed from a plastic cylinder (3 cm diameter by 1 cm tall) with a disc of 35 mesh/cm nylon screen glued to the bottom to effectively avoid egg loss. Our microcell contained no cat hair, because hair inhibited the smooth operation required when transferring the fleas, as well as hindered observation of mating behavior. In addition, for humidity balance and air exchange on cats, the microcell was sealed with a plastic cap that had the same nylon screen as the bottom of the cylinder. For observing off-host mating behavior, the screen of the cap was replaced by a transparent plastic pad. Room temperature was maintained at $\approx 27^{\circ}\text{C}$ by an air conditioner.

Effects of a Blood Meal. For harvesting the virgin fleas, larvae were individually reared in small glass vials. A series of tests were performed to determine whether consumption of a blood meal was a necessary trigger for the male to attempt to mate with females. Application of microcells on cats for the blood meal of fleas followed the approach of Hsu and Wu (2000). Approximately 25–30 newly emerged males and females (1 d old) were separated by sex in microcells and placed on a cat for a 3-d blood feeding period. The unfed and fed virgin males were combined with unfed and fed virgin females (fed virgin fleas were 4 d old, whereas the unfed virgin fleas were 1 d old) in a crossover design in which each microcell contained a pair of fleas, with 50 pairs per combination. The microcells with fleas were placed on a 38.5°C (typical cat skin temperature) digital hot plate and observed for 3 h. The number of mating pairs was recorded, and the number of males that displayed mating attempts (a male raised the antennae and claspers when approaching a female) was also recorded.

Effects of Surface Temperatures. Results of the above blood meal experiments indicated that unfed males did not attempt to copulate with females. Therefore, individually maintaining flea larvae or pupae to obtain virgin adults was deemed unnecessary. Approximately 25–30 newly emerged fleas (1 d old) were separated by sex in microcells, and then placed on a cat for a 5-d blood feeding period. Next, the range of temperatures required for the mating behavior was

determined by placing 25 pairs of 6-d-old fed fleas at each temperature controlled by the digital hot plate. Each microcell contained a pair of fleas. The temperatures tested were 27, 30, 34, 38, 42, and 44°C . The observation period was 3 h, and the numbers of mating pairs and males that displayed the mating attempt were recorded.

Observations of Mating and Postmating Behaviors.

Ten pairs of male and female fed fleas were put together in each microcell. These fleas were fed with blood on cats for 5 d, and thus they were 6 d of age, as were the fleas in the above surface temperature experiment. Eight microcells were placed on a 38.5°C digital hot plate, and some of the couples mated. The mating fleas within six of these microcells were examined under a stereomicroscope, and the complete process and duration of copulation in 15 pairs were recorded by a color video camera (SONY, SSC-S20, Tokyo) CCD system for repeated examination. After 10 min on the hot plate, another two of these microcells with mating fleas inside were carefully transferred to a china bowl already containing liquid nitrogen, and the mating pairs were quickly frozen (Fig. 1 A and B). This method generally preserves the natural relationships of the interlocking terminalia. Specimens were soaked in 10% KOH, dehydrated with alcohol, and mounted in Canada balsam for preparing permanent slides (Figs. 1C and 2 A–C). Some of the mating pairs were carefully pulled apart before they were soaked in KOH solution, allowing easy examination of the exposed aedeagus under a light microscope (Fig. 3A). Finally, the detailed structure of the thin penis rod was observed by pulling the rod out of the male flea (Fig. 3 B and C).

Results and Discussion

Effects of a Blood Meal and Surface Temperatures on Mating. Although without access to a blood meal, cat fleas on a hot plate could copulate completely once mating behaviors were triggered. In our experience, fed fleas in a microcell did not take a blood meal during copulation. In contrast, both sexes of *T. penetrans* took blood meals during copulation (Suter 1964). It is possible that mated cat fleas do not feed while copulating to reduce the likelihood of predation by host animals during grooming. Females of *Tunga* embed into the host skin to avoid the predation of hosts.

Numerous mating pairs appeared when both sexes were fed and a male cat flea needed a blood meal before mating (Table 1). Only fed males were found to mate with unfed and fed females. According to Dean and Meola (1997), the epididymis of the unfed male flea was blocked with folded columnar epithelial cells. Our data suggest that in addition to stopping sperm transfer, epididymis blockage also affects the mating attempts of males. We also used the 4-d-old unfed males and females to pair with the opposite sex in our preliminary experiments. Like the 1-d-old unfed males (Table 1), the 4-d-old unfed males did not attempt to mate with either unfed or fed females. We observed that 13/50 of 4-d-old fed males attempted to

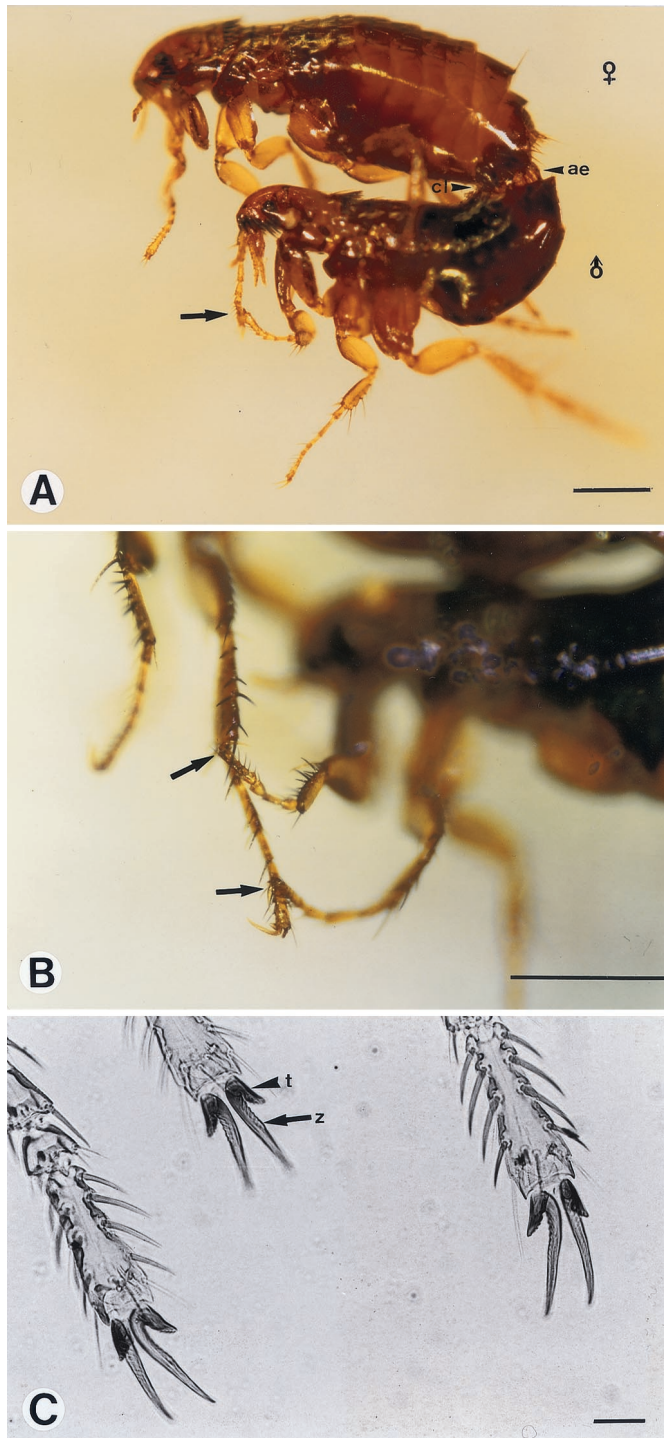


Fig. 1. (A) Lateral view of a mating pair. The male is under the female's abdomen during mating. The male attaches the claspers (cl) to the abdomen of the female. The arrow indicates that the male is grasping the female's right mesothoracic leg by his right prothoracic leg during copulation. ae, aedeagus. Bar = 100 μ m. (B) The left pro- and mesothoracic legs of the male simultaneously grasp the left mesothoracic leg of the female. Arrows indicate that the claws of the male are hooked on the spines of the female. Bar = 100 μ m. (C) The teeth (t) on the claws and the serrated surface (z) on the main part of claws. Bar = 10 μ m.

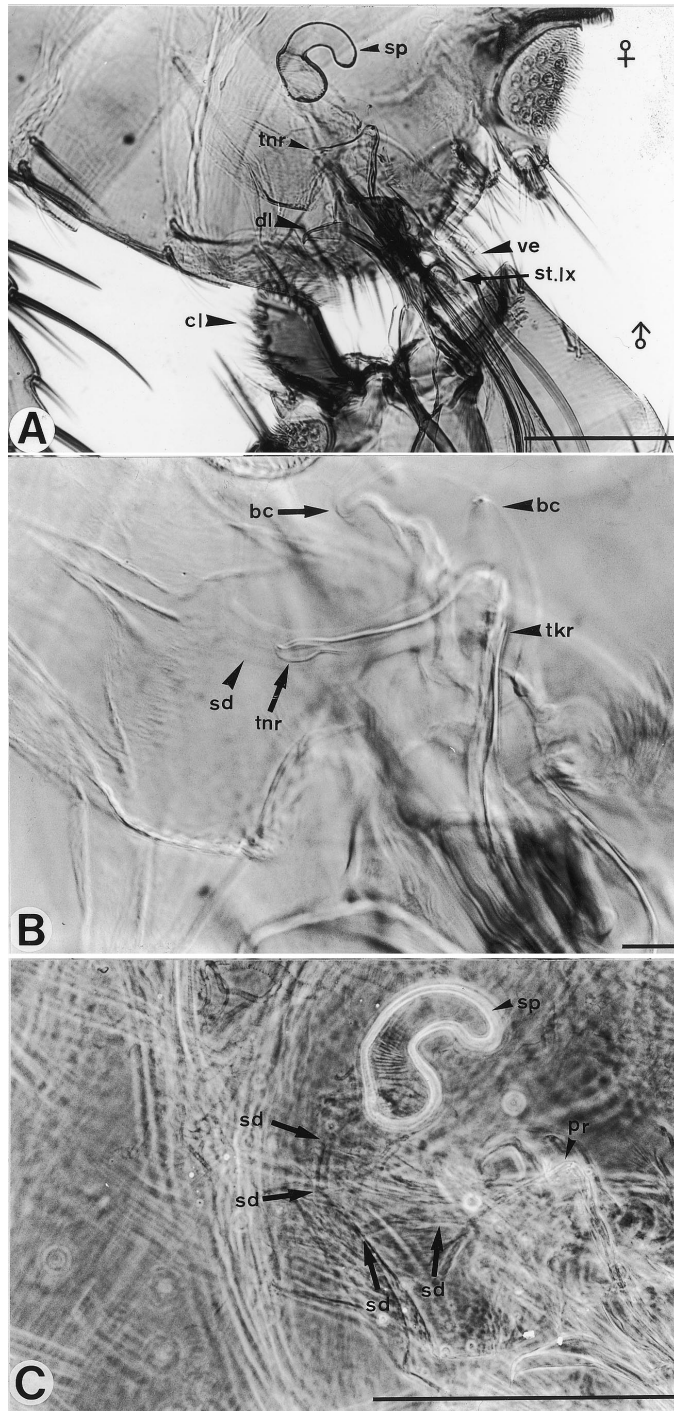


Fig. 2. Linked terminalia in mating pair. (A) The male claspers (cl) gripping female's sternum, and the thin penis rod (tnr) inserting deep into female body. The vesicle of phallosome (ve) and the sternum IX (st. IX) do not enter the female body. The dorsal lobe of the aedeagus (dl) enters the vagina. Bar = 100 μ m. (B) The thick rod (tkr) enters the bursa copulatrix (bc), and the thin rod enters the spermathecal duct (sd). Bar = 10 μ m. (C) Showing the spermathecal duct near the spermatheca (sp) that the thin rod does not reach. pr, penis rods. Bar = 100 μ m.

mate with the 4-d-old unfed females, but no mating pair appeared. However, 7/50 of mating pairs appeared when a 1-d-old unfed female was paired with

a fed male (Table 1). The abdomen of a 4-d-old unfed female shrinks because of starvation, and the shape of this small abdomen is not the same as that of a well-fed

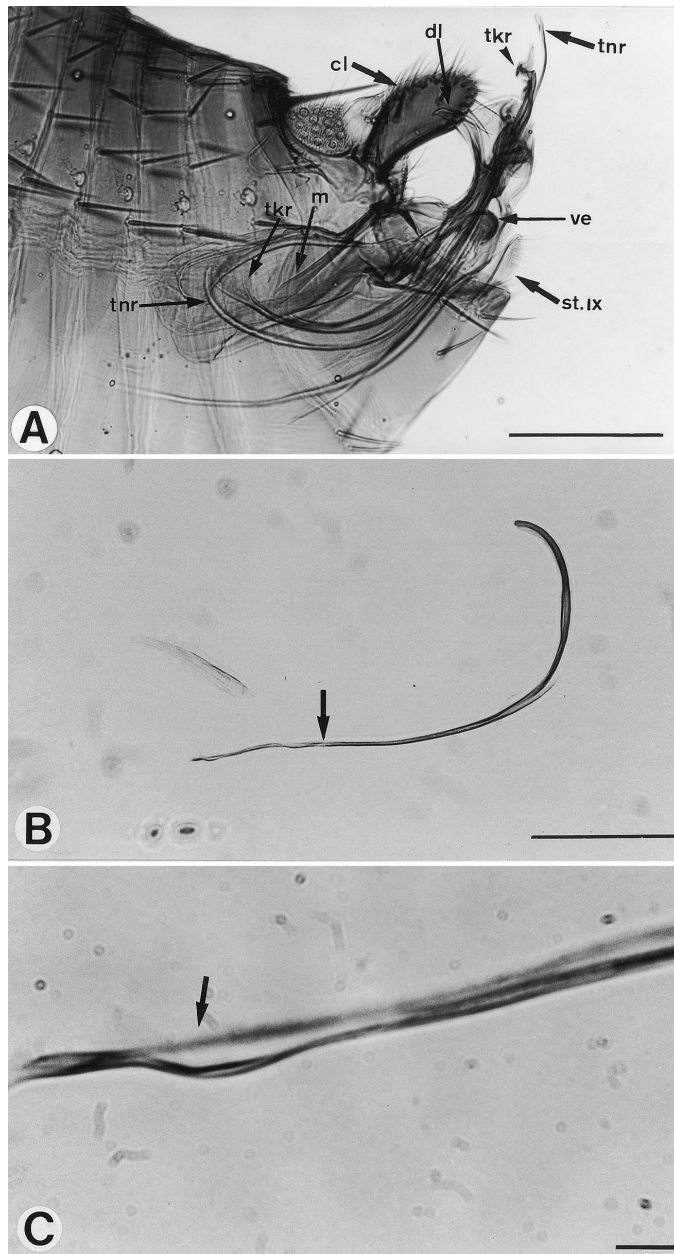


Fig. 3. (A) Exposed terminalia of the male cat flea, showing that anterior ends of the manubria lower, elevating the claspers. The anterior ends of these two penis rods push backwards and their tips enter the female body. Bar = 100 μ m. (B) The thin penis rod. The arrow indicates that the point where the groove begin. Bar = 100 μ m. (C) The tip (arrow) of the thin penis rod is like the cobra's hood. Bar = 10 μ m.

female or a newly emerged female. Thus, the extension level of the female's abdomen may affect whether a male successfully copulates with her.

Cat fleas mated when the temperatures of the hot plate ranged between 34 and 42°C, and the majority of copulation occurred at 38°C (Table 2). The male fleas walked fast at 42°C and many mating attempts to females were observed. No mating attempts were found at 44°C. According to Iqbal and Humphries (1970), fed male

northern rat fleas, *Nosopsyllus fasciatus* (Bosc), did not attempt to mate with unfed females at 23°C, but both sexes of unfed *N. fasciatus* mated if subjected to higher temperatures of 30–35°C. In contrast, the newly emerged unfed European chicken fleas, *Ceratophyllus gallinae* (Schrank), mated readily on a surface of room temperature (Humphries 1967b).

The differences in requirements for a blood meal and a rising temperature before mating may be due to

Table 1. Numbers of pairs (out of 50) that mated (showed mating attempts) when fed and unfed fleas were variously combined and placed on a 38.5°C digital hot plate

	1-d-old unfed males	4-d-old fed males
1-d-old unfed females	0 (0)	7 (16)
4-d-old fed females	0 (0)	35 (41)

various life histories in these three species of fleas. The rat fleas are likely to mate in an occupied nest when the rats are inside, thus providing them with easy access to a blood meal. They may mate nearby, but not on the host, after a meal. Rats are quite skillful at ridding their bodies of fleas. Thus, this mating strategy reduces the likelihood of flea predation by their hosts. Marshall (1981) indicated that bird fleas (except for sticktight fleas) were seldom removed from hosts captured away from nests, but could occur in great numbers in the nests. Both sexes of *Ceratophyllus gallinae* emerged nearly simultaneously, stimulated by a mechanical disturbance, and did not require the triggering signal of a rising temperature or a blood meal for mating, and they might mate in or near the occupied nest regardless of the bird's presence (Humphries 1967b). These bird fleas could complete one to two generations in blue tit nests within the nesting period of the host's breeding cycle (Tripet and Richner 1999). According to Suter (1964), males of *Echidnophaga gallinacea* (Westwood) mated immediately after emergence. In the remarkable *Tunga monositus* Barnes & Radovsky, the emerged male fertilized the female and died without feeding (Barnes and Radovsky 1969). The cat flea is a permanent ectoparasite on a wide range of hosts. It lives, feeds, mates, and oviposits on the host animal. We have never found cat flea mating occurring off-host in nature, even in proximity to a cat. In our experience, rising temperature was only a triggering signal. Once the mating pairs were stimulated, the mating process could be completed on a surface of room temperature.

Mating and Postmating Behaviors. *Initiation of Mating.* According to Rothschild (1965), the characteristic zigzag approach made by the male rabbit flea *Spilopsyllus cuniculi* Dale suggested that it followed some airborne scent trail. Humphries (1967b) and Iqbal (1973) pointed out that the mating pheromones received by the maxillary palps were on the cuticle of *Ceratophyllus gallinae* and *N. fasciatus*. However, the zigzag walking and the responses of maxillary palps were not observed during courtship of the cat flea. Exactly how the male cat flea found the female and

initiated the subsequent mating within the dense hairs of the host remained unclear.

Erection of Antennae and Claspers. The sequence of mating behavior began when a male approached a female and the antennae and the claspers of the male became erect. The manubria controlled the erection of the claspers. The proximal ends of the manubria depressed during the erection of the claspers (Fig. 3A). The male pushed underneath the female from behind and attached his antennae and claspers to the abdomen of the female. His dorsal curvature increased as he lifted the posterior part of his abdomen. In this manner, the distal ends of the genitalia were directed anteriorly over his back to touch the terminalia of the female. The aedeagus exposed outside then searched for the genital aperture for entering the female body. If linking failed to occur when the male raised his genitalia, he moved closer to the anterior end of the female abdomen and continuously searched for the opening of the vagina with his aedeagus. The male retracted the antennae back into the antennal grooves immediately after genitalia linkage (Fig. 1A). While in *Ceratophyllus gallinae* and *N. fasciatus*, males did not loosen their antennal clasp until termination of copulation (Humphries 1967b, Iqbal and Humphries 1974). The male cat flea raised his antennae again when disturbed by other individual fleas (especially other males) or when resisted by his mate. When the disturbance had passed, he immediately retrieved his antennae again. The solitary male may use his head to push the head of a copulating male from one side. A strong male may successfully displace the rival male and mate with the female. Like most fleas, the male cat flea attached its claspers to the female's sternum during copulation (Figs. 1A and 2A). Although the function of grasping by antennae during mating was crucial to *Ceratophyllus gallinae* and *N. fasciatus*, this is not true for *Ctenocephalides felis*. The grasping behavior of the male cat flea during mating was displayed in a different manner (Fig. 1 A and B). We found that the male cat flea used his legs to grasp the female while copulating (discussed below).

Rejection by the Female. The female cat flea may reject the male by directly walking or jumping away. The male occasionally gave up the attempt to mate with the female even though no rejection behavior was observed. The female *Ceratophyllus gallinae* rejected the male by kicking and moving away. These behaviors closely resembled cleaning actions (Humphries 1967b).

Claw Grasping by the Male. During cat flea mating, all of the males grasped the females by their tarsal claws (Fig. 1 A and B). Two claws are on each leg, with one prominent tooth on each claw (Fig. 1C). The inner surfaces of the claws are serrated (Fig. 1C). Spines on the female's tarsi generally interlocked tightly in the inner surfaces between the tooth and the main part of the claw (Fig. 1B). Thus, although some of the mating pairs lay down, the male's claws still tightly grasped the female's leg that was free in the air. Frequently, the male grasped either the female's mesothoracic legs by his prothoracic legs (Fig. 1 A and

Table 2. Numbers of pairs (out of 25) mated when 6-d-old fed fleas were placed on the digital hot plate of various surface temperatures (room temp. 27°C)

	Temp. °C					
	27	30	34	38	42	44
No. mating pair	0	0	8	17	13	0
Mating attempt	0	3	10	20	20	0

B) or female's metathoracic legs by his mesothoracic legs. The appendage interlocking typically continued to the end of mating. If the female disentangled during copulation, the male usually grasped her legs again. However, in *Ceratophyllus acutus* Baker, males were held securely by the tarsal spurs of the female interlocking with the tibial spines of male's pro- and mesothoracic legs (Mitzman 1910).

In contrast, the teeth on claws in *T. penetrans* and *E. gallinacea* are quite reduced or are only remnants (Hopkins and Rothschild 1953). The female of *T. monositus* attached to the skin surface of the host immediately after adult emergence, and the volume of the female swelled 1,000 times into the neosome that lost a variable number of leg segments. *Tunga caecigena* Jordan & Rothschild also lost some leg segments but this typically did not occur in *T. penetrans* (Marshall 1981). Therefore, the claws of these male pulicid fleas do not need to grasp the sessile females while copulating.

Linkage of Genitalia. If the female did not reject the courting male, the male might successfully insert his penis rods and dorsal lobe of aedeagus into her body. The dorsal lobe only reached the vagina, and two penis rods penetrated deeper during copulation: the thicker of the two rods only reached the bursa copulatrix, while the thinner one entered the spermathecal duct (Fig. 2 A and B). This finding agrees with observations of copulation in *Ceratophyllus idius* Jordan (Holland 1955). Rothschild (1965) pointed out that the thicker penis rod of the male *S. cuciculi* acted as a guide to the thinner one, thus enabling it to pass beyond the bursa copulatrix. During copulation the male cat flea performed regular strokes of his terminalia against the terminalia of the female by rhythmic abdominal contractions and relaxation. However, in contrast to *N. fasciatus* as described by Iqbal and Humphries (1974), the male cat flea did not make the coiling and uncoiling movements of the aedeagal tendons during copulation. The vesicle of phallosome and the sternum IX did not enter the female body during mating, and therefore the functions of these two structures remained unclear (Figs. 2A and 3A). In this study, the conveyance of sperm was not observed in cat fleas. However, we have found that there is a groove on the terminal portion of the thin rod, and the length of the groove is approximately a quarter of the length of the thin rod (Fig. 3 B and C). The tip of the thin rod is like an expended cobra's hood (Fig. 3 A and C). When a male *Ceratophyllus gallinae* was decapitated during copulation and separated from the female, the tip of the pointed penis rod twitched from side to side with a snake-like motion; however, the proximal parts of the rod did not move (Humphries 1967a). If the function of the groove on the thin rod of the male cat flea is to convey the sperm to the spermatheca, then how is the sperm conveyed to the groove? According to Hsu and Wu (2000), the female cat flea mates multiply. Thus, the other possible function of the groove or the cobra's hood of the thin penis rod is to remove sperm of the rival males from the spermatheca during copulation. The latter possibility was still not confirmed because

the thinner rod that entered the spermatheca was not observed in our slides. The permanent slides were made of the frozen mating pairs that mated <10 min, and the thin penis rod of the male flea only reached the point at approximately two-sevenths the distance of the spermathecal duct from the turning point inside the bursa copulatrix leading to the spermatheca (Fig. 2C). A longer time may be required for the thinner rod to reach the spermatheca during mating.

Termination of Mating. We found that the female terminated copulation when disturbed, as by other fleas or disruptive conditions such as the deep breath of an observer or disturbance of the microcells by an observer. First, the female flea's head waved laterally. She then pulled forward by her prothoracic legs, and the meso- or metathoracic legs escaped from the male's grasp. Finally, the copulation was terminated after the genitalia separation. The abandoned male attempted to resume copulation with either the same female or another.

The male could terminate the mating as follows. First, he waved his head laterally and loosened the grasps of the female by his pro- or mesothoracic legs. He then lowered the abdomen, unlinked the genitalia, and walked forward or laterally. Finally, he returned the claspers to a normal position. Termination of mating by the male was 71.83 min (SE = 13.11 min). This was significantly longer than that terminated by the female 12.11 min (± 3.12 min) (F -test; $F = 11.78$; $df = 1, 13$; $P = 0.003$). Mating duration ranged from 25 to 110 min when terminated by the male. According to Humphries (1967b), *Ceratophyllus gallinae* matings lasting for 1 h or more were almost invariably terminated by the male; briefer matings were usually ended by the female rejecting the male. Thus, the termination behavior and the subsequent postmating behavior can be used to recognize that the mating proceeds smoothly under the male's control or suddenly is terminated by the female. The cryptic female choice may be involved during the female-terminated matings. We had reported that the relationships between mating duration and the number of eggs/viable eggs (fecundity/fertility) were not significant (Hsu and Wu 2000). However, in that study 55.56% of once-mated females produced no viable eggs. These impotent matings were significantly briefer than potent matings, and the data of such matings were excluded from calculations of the relationships between mating duration and the reproductive output. Most of the impotent matings were terminated by females (M.H.S., unpublished data). Therefore, mating process terminated by the female or the male may affect the fecundity and fertility of the female.

Postmating Behavior. A male that terminated the mating process would display a series of postmating behaviors. Based on the different parts of body involved, we divided postmating behavior into three different steps. Although some parts of the first and second steps were occasionally observed in male cat fleas when they were not mating, the third step of postmating behavior was specifically associated with mating.

The first step involved the terminalia cleaning by metathoracic legs. The rear half of the abdomen bent to the right, and the right metathoracic leg scratched the terminalia with tibial spines. The abdomen then bent to the left, and the process was repeated on the left side. Finally, both metathoracic legs stretched out under the terminalia to rub against each other. The male repeated the above-mentioned cleaning procedures several times. The second step was antennal cleaning in which both prothoracic legs simultaneously scratched the ipsilateral antennal grooves with antennae inside by using the claws. The third step was the aedeagus cleaning. The claspers were raised again after mating. The aedeagus then extended outside and drew back into the body. The male flea repeated this in-and-out behavior two to three times, and an unidentified transparent jelly-like object was finally left outside. The function of this aedeagus cleaning deserves further studying.

In conclusion, the sequences of mating events in mating of the cat flea were similar to those of *Ceratophyllus gallinae* and *N. fasciatus*. However, the cat flea and the other two species differed in many ways. In cat fleas, the male's antennae attached to the abdomen of the female generally before genitalia linkage. Thus, the antennae may not play the major role in the grasping of the female flea by the male during mating. However, according to our results, the legs played a prominent role in grasping of the female flea by her mate. This article documents the grasping and postmating behaviors displayed by the male cat flea. Requirements for a blood meal and a rising surface temperature were both important to male cat fleas in terms of triggering mating. Thus, a cat flea possibly has little likelihood of mating off-host in nature. Rothschild (1965) stated that the copulatory apparatus of the male flea is the most elaborate genital organ in the animal kingdom. This study of the structure of the male cat flea's genitalia during copulation may throw light on the function of this complicated organ.

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Appendix 1

Video files of mating and postmating behavior of cat fleas are as follows: (1) Mating attempts. (2) Rejection by female. (3) Grasping of female by male's legs. (4)

Male's antennae erect again because of disturbances and then retract after these interferences. (5) Postmating behavior displayed by a male.