Dugesiana, Año 27, No. 2, julio 2020-diciembre 2020 segundo semestre de 2020), es una publicación semestral, editada por la Universidad de Guadalajara, a través del Centro de Estudios en Zoología, por el Centro Universitario de Ciencias Biológicas y Agropecuarias. Camino Ramón Padilla Sánchez # 2100, Nextipac, Zapopan, Jalisco, Tel. 37771150 ext. 33218, http://148.202.248.171/dugesiana/index.php/DUG/index, glenusmx@gmail.com. Editor responsable: José Luis Navarrete-Heredia. Reserva de Derechos al Uso Exclusivo 04-2009-062310115100-203, ISSN: 2007-9133, otorgados por el Instituto Nacional del Derecho de Autor. Responsable de la última actualización de este número: José Luis Navarrete-Heredia, Editor y Ana Laura González-Hernández, Asistente Editorial. Fecha de la última modificación 1 de julio 2020, con un tiraje de un ejemplar.

Dugesiana 27(2): 109-114
Fecha de publicación: 1 de julio 2020

ISSN 1405-4094 (edición impresa)
ISSN 2007-9133 (edición online)

Artículo

Courtship and mating behavior in four Pachytroctidae species (Psocodea: 'Psocoptera': Troctomorpha: Nanopsocetae: Pachytroctidae)

Cortejo y apareamiento en cuatro especies de Pachytroctidae (Psocodea: 'Psocoptera': Troctomorpha: Nanopsocetae: Pachytroctidae)

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ABSTRACT

Courtship and mating behavior were investigated in four species, representing three different genera, in the family Pachytroctidae. All exhibited a lengthy courtship in the male-above position followed by brief copulation in the female-above position with both facing in the same direction. This courtship behavior has not previously been observed in 'Psocoptera' and may be unique to Pachytroctidae. In three of the species in this study, the spermatophore remnant protruded from the tip of the male's abdomen after copulation, and was immediately deposited on the surface of the experimental enclosure. Differences in courtship behavior of the two closely related and sympatric *Tapinella* species, described in this report, may represent reproductive isolating mechanisms. Under experimental conditions, we observed a male of each *Tapinella* species mount, court, and attempt to mate with a virgin female of the other species. In each case the female rejected the male and failed to mate. Implications relative to these behaviors are discussed. DOI links to videos are provided for easy access.

Key words: *Nanopsocus oceanicus*, *Peritroctes bengalensis*, *Tapinella maculata*, reproductive isolation, antagonistic coevolution, tremulation.

RESUMEN

Se investigó el cortejo y el comportamiento de apareamiento en cuatro especies de la familia Pachytroctidae. Este comportamiento de cortejo no se ha observado previamente en 'Psocoptera' y puede ser exclusivo de Pachytroctidae. Todos exhibieron un largo cortejo en la posición superior masculina seguido de una breve cópula en la posición superior femenina con ambos mirando en la misma dirección. En tres de las especies en este estudio, el remanente del espermatóforo sobresalía de la punta del abdomen del macho después de la copulación, y se depositó inmediatamente en la superficie del recinto experimental. Las diferencias en el comportamiento de cortejo de las dos especies de *Tapinella* estrechamente relacionadas y simpátricas, descritas en este informe, pueden representar mecanismos de aislamiento reproductivo. En condiciones experimentales, observamos que un macho de cada especie de *Tapinella* monta, corteja, e intenta aparearse con una hembra virgen de la otra especie. En cada caso, la hembra rechazó al macho y no pudo aparearse. Se discuten las implicaciones relativas a estos comportamientos. Se proporcionan enlaces DOI a vídeos para facilitar el acceso.

Palabras clave: *Nanopsocus oceanicus*, *Peritroctes bengalensis*, *Tapinella maculata*, aislamiento reproductivo, coevolución antagónica, tremulación.

Members of the family Pachytroctidae are small forms (0.7 to 1.5 mm) in which males are apterous and females either apterous or macropterous, with wings folded flat over the abdomen. The four pachytroctid species involved in this study have been recorded in central and south Texas. *Nanopsocus oceanicus* Pearman, 1928 is relatively cosmopolitan in distribution, having been recorded throughout North, Central and South America, Europe, Africa, Japan, and some South Pacific Islands (Mockford 1993). *Tapinella maculata* Mockford and Gurney, 1956 has a more limited distribution from central Texas south to Mexico, Guatemala and Belize. An un-described species of *Tapinella*, designated here as species #2, appears to be endemic to central Texas. The two *Tapinella* species occur together there in similar habitats and therefore appear to be sympatric. *Peritroctes bengalensis* Thornton and Wong, 1966 was described from apterous female specimens in the Botanical Gardens of Alipore, Calcutta, India. We recently described the male and macropterous female of this presumably introduced species (Mockford and Young 2019).

The few descriptions of courtship and mating in the suborder Troctomorpha are limited to studies in Liposcelididae. Broadhead (1952) investigated reproductive behavior in Liposcelis and found that initial courtship involves antennal vibration alternating between male and female. Male courtship also involved jerking motions of the body and active running movements near the female. Receptive females play an active part by raising the anterior part of their body to allow the male to move backwards underneath them. Copulation duration was lengthy—lasting 30-60 min. Courtship patterns among the 8 species he studied were similar. Immediately after the genitalia join, the male twists

so that the pair face in opposite directions. Males courted non-conspecific females, but mating did not occur. Broadhead noted that the male and female genitalia in this genus are remarkably similar and therefore could not provide a mechanical barrier to inter-specific mating. He also noted that mating behavior is very similar in these eight species but nevertheless reproductive isolation is complete. Broadhead was not able to determine the specific cues that cause a female to reject a male of the inappropriate species.

The present study was inspired by a chance observation by DWY while collecting pachytroctids from dead palm leaves. Males were occasionally observed mounted on a female's back for extended periods of time. We then confirmed this same behavior in all four pachytroctid species found in central Texas and determined that the behavior observed was courtship and not post-copulatory mate guarding.

MATERIAL AND METHODS

Four pachytroctid species were collected from dead leaves of *Washingonia filifera* (Washington palm), *Sabal mexicana* (Sabal palm) and *Panicum virgatum* (switch grass). Specimens were cultured in 9 cm plastic petri dishes lined with 100% cotton paper and provided with several strips of dead palm leaf with a patina of black mold and one piece of Cheerios®. Dishes were placed in a desiccator over saturated potassium chloride solution to provide a relative humidity of approximately 85%. Individual nymphs were transferred from cultures and reared in 21 x 70 mm cotton plugged shell vials provided with a 1.5 x 5 cm strip of dead palm leaf. This procedure provided virgin males and females for courtship and mating studies.

Individual virgin females were placed in a 9 cm paper-lined petri dish with a strip of palm leaf and a small piece of cotton moistened with distilled water. A single conspecific male was introduced and videotaping begun with focusing on the female. Videos were made with a Meiji Techno zoom stereo microscope, a Canon Rebel T1i SLR camera with a Martin Microscope Company MDSLR adapter, Canon ACK-E5 Adapter Kit and a Schott ACEI tungsten halogen light source. Elapsed time for male to approach female and for courtship was recorded for each pair. Time elapsed for courtship climax and copulation was determined using the timeline on Microsoft Movie Maker. Still images were made with Canon MP-E 65 mm lens and a Canon Macro Ring Lite MR-14EX flash unit. To view videos, open FigShare (https://figshare.com/) then type in the DOI code. All DOI links to videos in this work contain the initial code: "10.6084/m9.figshare.1188" one then adds the last four digits provided in the text to access the video. After viewing one video, simply use back arrow, then change the last 4 digits to the next video.

RESULTS

Courtship and mating behavior observed in the four species in question can best be discussed as the following sequential phases: 1) "attraction"—begins with the introduction of the male into the petri dish and continues as the male locates and approaches the female; 2) "initial courtship"—begins when the male mounts the female and continues until an abrupt change in the male's behavior; 3) "courtship climax"—occurs as the male exhibits a dramatic increase in activity seconds before dismounting and backing under the female and 4) "copulation"—begins as the male and female genitalia make contact and ends as their genitalia separate.

Behavioral traits common to all four species

The time interval between introduction of the male and the initiation of courtship was lengthy and variable in all four species (Table 1). During this time, the male often approached the female briefly but retreated. In some cases, males mounted females for a considerable time but were rejected by females as they attempted to mate (data not shown).

All four pachytroctid species investigated were characterized by lengthy courtship behavior with the male mounted on the back of the female followed by brief copulation in the female-above position with both facing in the same direction. Males mounted females without any prior behavior that could be interpreted as courtship and secured a firm grasp with their middle legs. The male's hind legs rested on the female's abdomen or forewings. Pairs remained in this courtship position for an extended period of time (Table 1, Fig. 1) during which females would occasionally relocate. Otherwise, females remained motionless except for slight movements described below. Courtship climax of varied duration (Table 1) involved intense movement of the male's front legs, antennae, and body. Males then backed under the females and attempted to mate. Females raised the anterior part of their bodies and in some species assisted the males by movement of their front legs. Copulation was brief (Table 1) and, except in the case of *Peritroctes bengalensis*, the spermatophore remnant was temporarily attached to the end of the male's abdomen after the pair separated. Males quickly deposited the spermatophore on the surface of the experimental enclosure. There was no obvious difference in male courtship behavior between macropterous versus apterous females (Table 1).

Courtship and mating in *Nanopsocus oceanicus* (Video 1: 2754, Video 2: 2793)

Minutes before the onset of male courtship, macropterous females on two occasions were observed to vibrate the body vigorously for 14 -21 times at approximate 10 sec intervals. This behavior was not consistent and did not occur with apterous females. During the entire initial courtship, the males brushed the proximal tibiae and sides of the female's head with their front legs and jerked their head forward over the front of her head, actively brushing their maxillary palps over the anterior part of her head while making contact with her palps (Video 3: 6915). These

movements continued for the entire courtship. Courtship climax was brief (Table 1) and involved vigorous movement of the male's front legs, followed by a rocking left and right motion, raising the tip of the abdomen and rapid antennal movement. As the males dismounted, the females raised the anterior part of their bodies to accommodate the male as he backed underneath them. In two observations, macropterous females consumed the spermatophore remnant.

Courtship and mating in *Tapinella maculata*
(Video 4: 2853, Video 5: 6495)

During initial courtship, males subtlty jerked their bodies every 3-6 seconds and females, in response, showed a slight simultaneous movement. During this initial phase of courtship, the males did not move their legs. Courtship lasted approximately 1 hour (Table 1). Later, male body-jerking ceased, and their antennae began jerking approximately once every second. The climax of courtship began as males lifted the tip of their abdomen and lowered their front legs, sometimes pressing them against the front tibiae of the females at the same frequency as the antennal jerking. The climax phase of courtship was very brief (Table 1) and involved rapid vigorous side-to-side movements of the body, rapid movement of the antennae and slight sweeping movements of the front legs. As males dismounted, the females lifted their bodies and moved their front legs to accommodate the male backing underneath. Copulation lasted longer in this species than in the other species of this study (Table 1). During this time the male jerked his body several times in a "pumping" motion. Neither males nor females made an attempt to consume the spermatophore remnant.

Courtship and mating in *Tapinella* sp. #2.
(Video 6: 6285, Video 7: 6996)

In two instances, macropterous females exhibited repeated body jerks as the male approached. As in *Nanopsocus oceanicus* (noted above), this behavior was not consistent and did not occur with apterous females. During initial courtship males did not move their front legs. Males remained mounted on the females' back with front tibiae along the sides of the female's head, between her antennal sockets and compound eyes. Initially, males jerked their body every 3-5 seconds, with head positioned directly over that of the female. Finally, males raised the tip of their abdomen and a relatively lengthy courtship climax (Table 1) began as they vigorously swept their front legs along the sides of the female's head while moving slightly side to side. Males then dismounted and with the female's assistance, backed underneath. Copulation was brief (Table 1) and during this time males did not move their antennae considerably or exhibit any pumping action of their abdomen. As in *T. maculata*, the spermatophore remnant was not consumed.

On two occasions, we observed males of *T. maculata* court and attempt to mate with virgin females of *T.* sp. #2 (Video 8: 7011). We also recorded a male of *T*. sp. #2 court and attempt to mate with a virgin female of *T*. maculata (Video 9: 6708). Individual males were placed in the same petri dish with a non-conspecific female of an age known to be sexually receptive. An exceptionally long time elapsed before males mounted the females (5-7 hrs.). Courtship in two of the three cases lasted much longer than in con-specific pairings. In each case the female refused to mate. These same females were placed with conspecific males the following day and typical male courtship resulted in copulation.

Courtship and mating in *Peritroctes bengalensis*
(Video 10: 6783, Video 11: 7020)

During lengthy courtship (Table 1) the male and female were essentially motionless except for occasional relocation movement by the female. The males were positioned directly over the females' bodies with front tarsi touching the sides of the females' heads. Courtship climax lasted for less than 1 min. (Table 1) and at this time the male moved both his front and hind legs vigorously then dismounted and backed under the female. Copulation was brief (Table 1) and differed from the other pachytroctid species in that no spermatophore could be seen protruding from the tip of the male's abdomen as the pair separate.

DISCUSSION

The unusual courtship behavior observed in the four pachytroctid species involved in this study is unique among 'Psocoptera'. Ours is the first report, in this taxon, of lengthy courtship during which the male remains mounted on top of the female. Previous studies in the suborders Trogiomorpha (Broadhead 1961, Sommerman 1956, Wearing-Wilde 1996), Troctomorpha (Broadhead 1952) and Psocomorpha (Betz 1983, Sommerman 1944) all depict brief courtship involving rapid movements of the male near or in contact with the female—his antennae or palps often touching her. In *Trichadenotecnum alexanderae* Sommerman, 1948 (Psocidae) essential courtship behaviors are a "sideways gait" and rapid wing fanning as the male approaches the female (Betz 1983). "Vigorous flicking of the wings is a characteristic feature of courtship in many winged species. In apterous species, such as *Liposcelis*, these are replaced by a similar pattern of flicking of the antennae" (Broadhead 1961).

Pachytroctid courtship begins as the male quickly mounts the female and firmly grasps her with his middle legs. There is little movement by the male during the roughly hour long initial phase of courtship except for occasional jerking of the male's body. In *Nanopsocus oceanicus*, however, the male strokes the female's head with his palps throughout courtship. "Courtship climax" begins in all four species as the male raises the tip of the abdomen, sweeps his front legs vigorously along the side of the female's head and moves his body vigorously side to side. The male then backs under the female and brief copulation begins. The lengthy courtship described in this report would seem to

place the pachytroctid pair at greater risk from predators since the female becomes essentially motionless and the pair constitute a larger visible target (Fig. 1). The selective advantage of this behavior is not clear.

In several groups of insects, the male genitalia have evolved to allow male-above copulation allowing the male to gain more control by use of the legs, palps and antennae to stimulate and hold the female (Huber 2010). The courtship behavior of the pachytroctid species investigated here, may represent a unique strategy allowing the male more control—not through the mating position but by the lengthy male-above courtship position. The lengthy courtship outlined here could represent yet another strategy in what Huber calls the "antagonistic coevolution scenario" as males, in an evolutionary sense, struggle to outwit female choice.

Our observation of cross-species courtship in *Tapinella* was unexpected. When non-conspecific pairs were tested, the male mounted the female after several hours and courtship began. The courtship was unusually long (up to 4 hours) and the female repeatedly tried to shake off the male. After courtship climax, the male dismounted but copulation did not occur. The next day the same females were paired with conspecific males and courtship resulted in copulation (Video 8: 7011, Video 9: 6708). Engelmann (1970) enumerated the mechanisms by which closely related sympatric species of insects might remain reproductively isolated by difference in mating behavior. These included acoustic, olfactory, visual, tactile, and temporal aspects of courtship and copulation. *T. maculata* and *T*. sp. #2 are sympatric in central Texas and occur in similar habitats, especially on dead palm and grass leaves. We found significant differences in the courtship behavior of these two species. Initial courtship behavior was similar in these two species in terms of duration, the lack of movement of the male's legs, and body jerking by the male. Differences in the "courtship climax" phase were significant. In the brief courtship climax of *T. maculata*, the male jerks violently side-to side with only minimal movement of the front legs. Courtship climax lasts longer in *T*. sp. #2 and involves more vigorous and lengthy sweeping movements of the front legs and less side-to-side movements. These differences in initial and climax courtship behavior could serve as isolating mechanisms between the two species.

Cross-species courtship has been also reported in booklice (Broadhead 1952) which belong to the suborder Troctomorpha. Sommerman (1956) recorded remarkable cross-species male courtship behavior while working with *Psoquilla marginepunctata* Hagen, 1865 and *Rhyopsocus bentonae* Sommerman, 1956 (Trogiomorpha: Psoquillidae). Males of each species attempted to court females of the other genus. This is perhaps the only recorded example of cross-genus courtship in insects. As expected, the males' advances were rejected. This tendency of males to court non-conspecific females may occur sporadically within the suborders Troctomorpha and Trogiomorpha.

Based on our observations, sperm transfer was by means of a compact spermatophore. In our video recordings, the outer covering of the spermatophore is clearly visible protruding from the tip of the male's abdomen immediately after copulation except in the case of *P. bengalensis.* Within seconds the spermatophore is cast off by the male. In *Rhyopsocus bentonae*; *Rhyopsocus eclipticus* Hagen, 1876; and *Psoquilla marginepunctata* (Psoquillidae); as well as *Psocatropos microps* (Enderlein), 1903 (Psyllipsocidae); the male was observed to deposit a transparent spermatophore immediately after mating (Sommerman 1956). "Almost immediately after separation the male deposited on the substrate a transparent, slightly curved (upward) carrot-shaped sac, which was drawn to a fine tip at the posterior end". This observation in psoquillids and psyllipsocids is similar to our report that sperm transfer in pachytroctids is by spermatophores which are briefly retained by the male after copulation. Mockford cleared up possible confusion by distinguishing between "plug spermatophores" which are sperm-containing structures produced in the male reproductive tract and transferred to the female during copulation and "ampule spermatophores" which are sperm containing ampules formed within the spermatheca of the female after copulation (Mockford and Wynne 2013).

Sommerman (1956) observed both males and females of the three species in her study consuming the spermatophore remnant after mating. On two occasions, we observed this same behavior in macropterous females of *Nanopsocus oceanicus*. In other groups of insects, especially orthopterans, females routinely consume the spermatophore remnant which can contain nutrients, enhancers of ovarian development, and even anti-aphrodisiacs (Mann 1984). How widespread this phenomenon is in pachytroctids and what significance it has on reproduction is not known.

The repeated body vibrations observed with some macropterous females of *N. oceanicus* (2 of 5) and *T*. sp. #2 (2 of 6), preceding the approach of the male, could be more common under natural conditions. Pachytroctids lack the coxal organ, therefore this behavior cannot involve stridulation. It could represent what Duelli and Johnson (1981) refer to as "tremulation"—which is propagated by the substrate as opposed to percussion which is propagated through air. It is tempting to associate these body movements with courtship behavior as this behavior only occurred with the approach of males. Such body movements were not observed in all four species and in none of the apterous females in this study. The interpretation of this behavior, therefore, is unclear.

ACKNOWLEDGEMENTS

The authors would like to dedicate this work to our colleague and friend, Alfonso García Aldrete, who has made major contributions to psocid research not only by his own work but also by recruitment of other investigators in Central and South America.

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Recibido: 21 enero 2020
Aceptado: 20 febrero 2020

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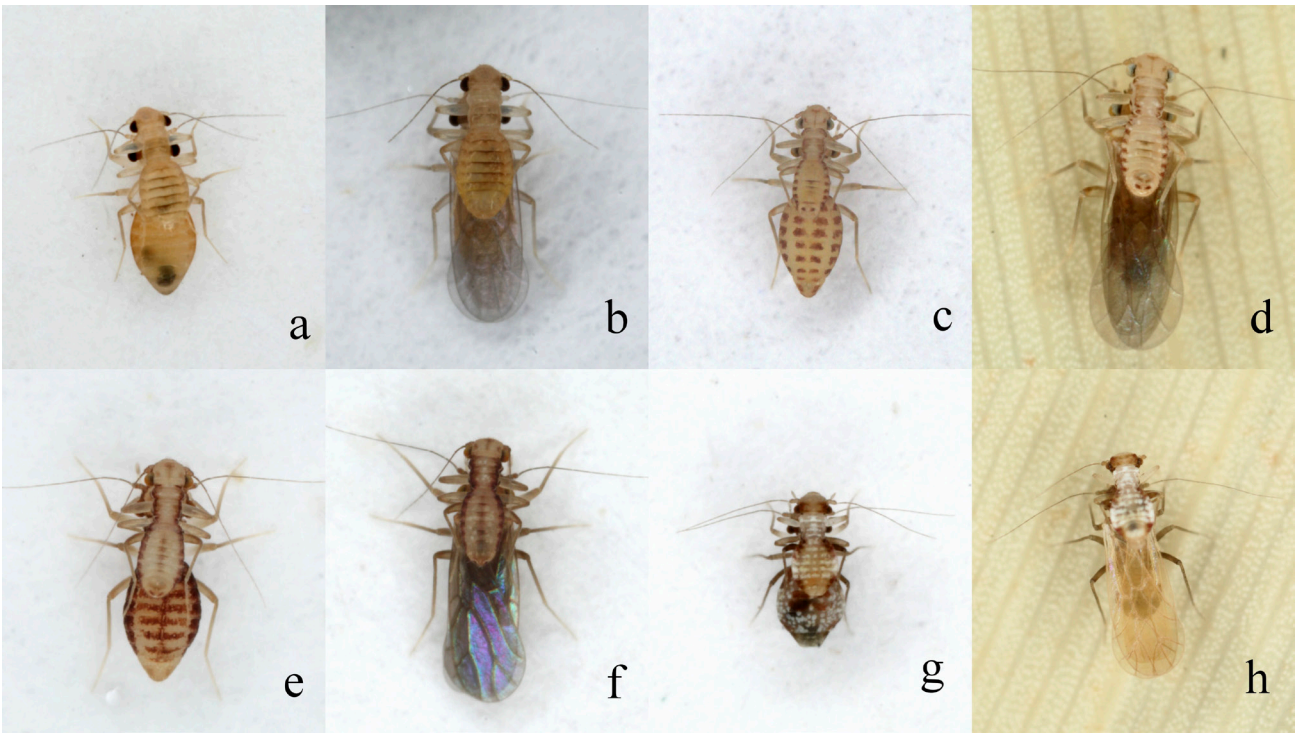

Figure 1. Pairs in courtship position. *Nanopsocus oceanicus*: a, b; *Tapinella maculata*: c,d; *Tapinella* sp. # 2: e, f; *Peritroctes bengalensis*: g. h.

Table 1. Duration of time interval for attraction, courtship, courtship climax, and copulation in four species of Pachytroctidae with YouTube video links for each species.

TABLE 1 Courtship and copulation in four pachytroctid species

Species	Female aptery	Attraction	Courtship duration	Courtship climax	Copulation duration	YouTube video
		mean ± s. d. in min.	mean ± s. d. in min.	mean ± s. d. in sec.	mean ± s. d. in sec.	unique search ID
Nanopsocus oceanicus	macropterous	33.8 ± 30.3 n=4	59.5 ± 13.6 n=4	8.6 ± 3.8 n=3	26.4 ± 6.5 n=5	c3R-N0_9z3s
		(range 5-70)	(range 47-78)	(range 4.2-10.8)	(range 21.8-37.7)	
	apterous	12 n=1	50.0 n=1	10.0 n=1	25.0 n=1	Kpq5SA5QA-FM
Tapinella maculata	macropterous	96.0 ± 62.3 n=4	50.5 ± 12.5 n=4	7.5 ± 0.5 n=4	42.0 ± 12.8 n=4	A4p_a_F69nE
		(range 30-127)	(range 39-68)	(range 6.9-7.9)	(range 31.7-59.5)	
	apterous	59.3 ± 52.8 n=4	61.5 ± 15.2 n=4	9.4 ± 1.6 n=3	55.9 ± 12.7 n=3	Jbg0sNFEl4
		(range 15-125)	(range 41-74)	(range 7.5-10.5)	(range 41.6-65.6)	
Tapinella sp. Type 2	macropterous	45.8 ± 31.1 n=4	45.3 ± 6.1 n=4	111.8 ± 38.9 n=4	18.3 ± 7.9 n=4	6oU4z7S2TUU
		(range 26-92)	(range 39-53)	(range 64-158)	(range 11.4-28.3)	
	apterous	96.5 n=2	52.5 n=2	156.0 ± 17.0 n=4	16.8 ± 3.4 n=4	mr1aObf0ikQ
		(range 57-136)	(range 46-59)	(range 137-178)	(range 12.3-20.2)	
Periroctes bengalensis	macropterous	96.0 ± 80.5 n=3	66.8 ± 13.9 n=4	28.7 ± 8.1 n=4	12.3 ± 6.2 n=3	sWGTv3IcxwA
		(range 8-169)	(range 54-85)	range (23.1-40.6)	(range 8.7-12.3)	
	apterous	70.7 ± 43.7 n=3	66.7 ± 7.2 n=3	29.9 ± 7.6 n=3	8.8 ± 0.6 n=3	tW3thZValgc
		(range 37-120)	(range 62-75)	(range 21.3-35.7)	(range 8.2-9.3)	

