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Intraspecific interaction of *Neobrettus tibialis*, a spartaeine jumping spider from Malaysia

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Abstract. *Neobrettus tibialis* (Prószyński, 1978) is a small spartaeine jumping spider (3–4 mm) commonly found in curled, dried banana leaves across South-east Asia. The species exhibits pronounced sexual dimorphism: females are hairier and more brightly coloured, whereas males are comparatively duller. Here we provide the first detailed description of intraspecific interactions in *N. tibialis*. We identified 38 distinct behavioural elements across inter- and intrasexual encounters. During intersexual encounters, males consistently initiated courtship, expressing a diverse repertoire of displays that closely resemble those of other salticids. Females were usually passive observers or decamped but occasionally chased or pounced at males. In male-male and female-female encounters, fewer behavioural elements were expressed, and no direct physical contact was observed. Despite the female's distinctive, hairy, mould-like appearance, the intraspecific behavioural repertoire of *N. tibialis* closely resembles that of other salticids. These findings establish a behavioural baseline for *N. tibialis*, contributing to our understanding of courtship and agonistic displays in Spartaeinae and offering broader insights into the evolution of intraspecific communication in jumping spiders.

Key words. agonistic displays, courtship displays, intraspecific interactions, *Neobrettus tibialis*

INTRODUCTION

Jumping spiders (Araneae: Salticidae) constitute the largest spider family, comprising more than 690 genera and approximately 7,000 described species worldwide (World Spider Catalog, 2026). Unlike most spiders, salticids possess exceptionally acute vision (Harland et al., 2012; Land & Nilsson, 2012). Their anterior median eyes (AMEs) enable colour discrimination, including ultraviolet (UV), green and red wavelengths, through multiple photoreceptors and retinal filters, conferring high spatial acuity (De Voe, 1975; Harland et al., 2012; Zurek et al., 2015). The remaining three pair of eyes (anterior lateral, posterior median, posterior lateral) are specialised for motion detection (Zurek & Nelson, 2012). In addition, slit sensilla on their legs allow sensitivity to substrate-borne vibrations (Barth, 2004). This integration of visual and vibratory inputs enables salticids to be proficient at detecting prey, avoiding predators, and assessing potential mates (Land, 1969; Barth, 2004; Lim et al., 2007; Rößler et al., 2022).

These sensory capabilities have underpinned the evolution of complex multimodal communication in salticids. Male courtship and intrasexual contests typically involve combinations of visual signals, such as body colouration and coordinated leg and palp movements, and vibratory signals transmitted through the substrate. Such displays play key roles in mate choice and intrasexual competition (Richman & Jackson, 1992). For example, males of *Cosmophasis thalassina* (Koch, 1846) integrate UV reflections as a signal with substrate-borne vibrational signals during courtship (Zeng et al., 2019), while peacock spiders (genus *Maratus* Karsch, 1878a) are renowned for their elaborate colour displays and vibratory courtship signals that are strongly preferred by females (Girard et al., 2015). In *Phidippus clarus* Keyserling, 1885, males use both visual and vibratory signalling to assess competitors during agonistic encounters (Elias et al., 2008). Collectively, these studies illustrate how sexual selection may have shaped diverse and sophisticated signalling strategies in salticids.

Spartaeinae is a basal subfamily within Salticidae (Wanless, 1984; Su et al., 2007; Maddison, 2015), best known for araneophagic (specialised spider-eating) species (Harland et al., 2012). However, detailed descriptions of intraspecific interactions in spartaeines are currently restricted to species from only three genera (see Table 2). Species of *Portia* Karsch, 1878b, in particular, exhibit remarkably complex courtship and agonistic repertoires (Jackson & Hallas, 1986a). Nevertheless, there remains a clear need to extend behavioural studies of intraspecific interactions to a broader range of spartaeines genera.

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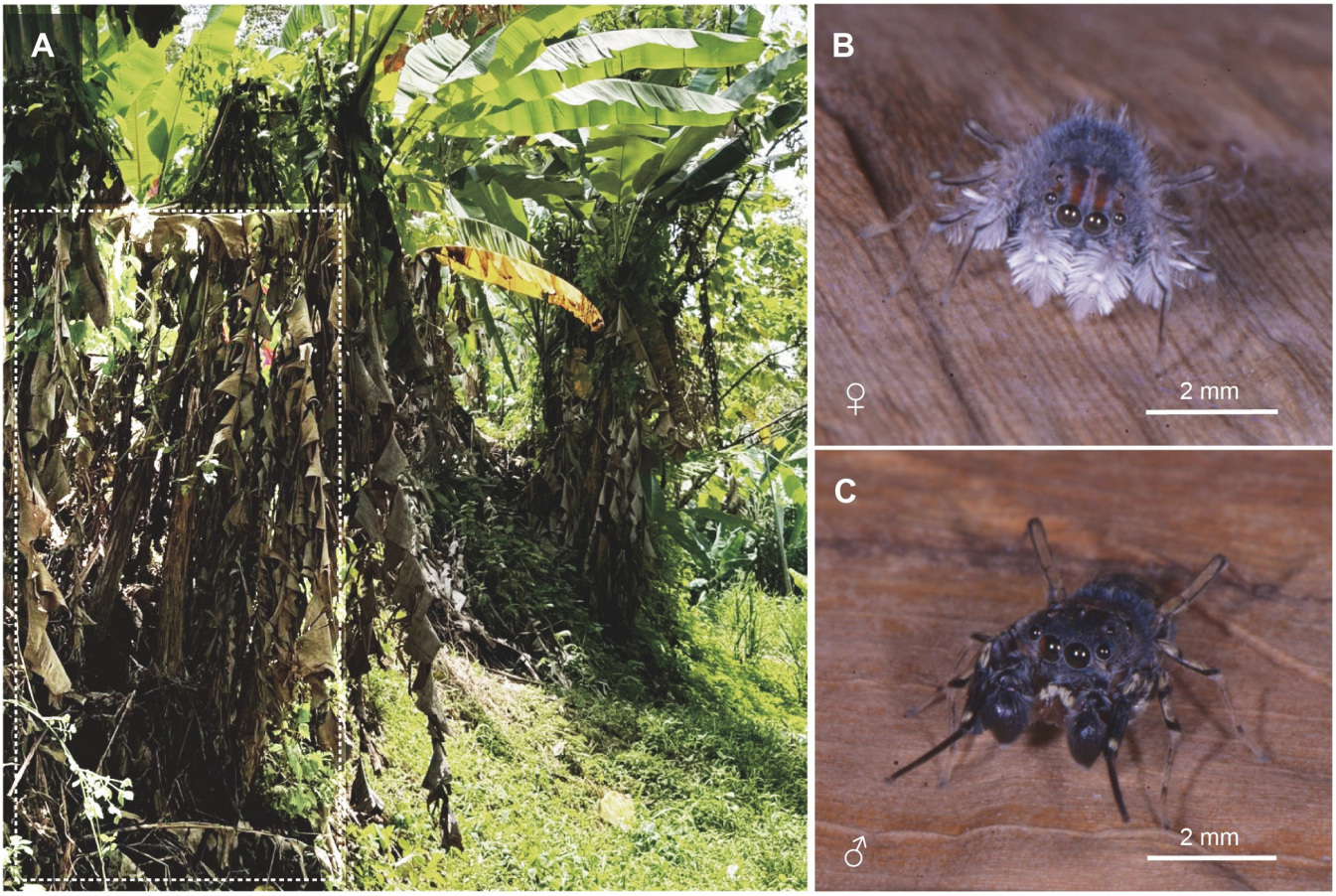

Fig. 1. Female (B) and male (C) *N. tibialis* on their natural habitat of dried banana leaves (A).

Neobrettus tibialis (Prószyński, 1978) (Fig. 1) is a small spartaeine species distributed across Malaysia, India, China, and Bhutan (World Spider Catalog, 2026), where it typically inhabits curled, dried banana leaves (Wanless, 1984; Murphy & Murphy, 2000; Banerjee et al., 2019; Lin et al., 2023). Females exhibit a dark blue, densely hairy appearance, and strong ultraviolet reflectance (wavelength < 400 nm) on the palps and legs I bristles, whereas males appear dull and weakly UV reflective (pers. obs.).

Despite its intriguing dimorphism, the courtship and agonistic behaviours of *N. tibialis* have not been formally studied. Here we provide the first detailed description of intraspecific interactions in this species, including male-female, female-male, male-male, and female-female encounters. These observations establish a behavioural foundation for future research on sexual selection in *N. tibialis* and offer broader insight into the evolution of signalling strategies in Spartaeinae and Salticidae.

MATERIAL AND METHODS

Neobrettus tibialis were collected from curled, dried banana leaves in Genting Sempah, Malaysia (3°21′09.2″N, 101°47′18.7″E; Fig. 1) and transported to the National University of Singapore for laboratory experiments. Subadults were reared to adulthood under controlled conditions (25±1°C; 80±5 % relative humidity; 12 h:12 h light-dark cycle) following established salticid rearing protocols (Kwek et al., 2023; Tan et al., 2024). To ensure virginity, individuals were housed singly in plastic containers (6 × 5 × 5 cm), separated by opaque black dividers to prevent visual contact (Zeng et al., 2019; Kwek et al., 2023). Spiders were fed four *Drosophila melanogaster* Meigen, 1830 twice weekly and provided with water ad libitum.

Owing to limited availability of individuals, behavioural assays were conducted with six female-male pairs, two male-male pairs, and six female-female pairs (see below for definitions of behavioural elements). Each spider was used only once to avoid pseudo-replications and had no prior interaction with conspecifics after collection. Trials were performed on a dried banana leaf fixed in a place and illuminated with full-spectrum lighting to simulate natural conditions. A male and a female (two males, or two females) were introduced simultaneously onto the leaf. If an individual decamped, it was gently guided back to the arena using a soft brush. Each trial ended when (i) courtship culminated in a pre-mount or copulation, or (ii) one individual decamped more than five times. The terms “usually” or “generally”, “sometimes” or “occasionally”, and “rarely” were used to describe behaviours occurring in >80%, 20–80% and <20% of trials, respectively, following conventions used in previous studies (Jackson & Hallas, 1986a; Lim & Li, 2004). All interactions were recorded using an iPhone 15 Pro Max.

RESULTS

Normal locomotion. Consistent with previous descriptions (Wanless, 1984), *N. tibialis* adopted a characteristic squat resting posture, with the abdomen pressed against the substrate and the legs bent laterally. In rest, legs I were either held parallel to or in touch with the substrate, or slightly lifted and waved or tapped with low amplitude. During locomotion, spiders usually paused, extended legs I parallel to the substrate and waving them up and down, while the palps occasionally brushed the surface. Failed jumps were usually followed by climbing up the dragline, or less often by cutting the silk and dropping back onto the substrate. When disturbed, spiders fled by running or jumping. No marked differences in locomotory behaviour were observed between males and females.

Intraspecific interactions. We identified a total of 38 distinct behavioural elements during intraspecific encounters (Table 1). Male-female interactions involved 26 males and 19 female behavioural elements, while male-male and female-female encounters involved 14 and 15 elements, respectively. During intersexual interactions, males and females performed 14 and 6 behavioural elements that were unique to these encounters, respectively. In intrasexual contests, males and females performed 4 and 5 unique behavioural elements, respectively.

Behavioural elements.

1. Body raising
   The body is elevated above the normal locomotion height (approximately ¼ to 1 body height), with the cephalothorax usually held higher than the abdomen. During courtship displays, males elevate the body to approximately one body height (Fig. 2), whereas females respond by raising the body to about ½ body height (Fig. 3). In male-male contests, males raise the body by approximately ¼ body height (Fig. 5). During female-female displays, females raise the body to about ½ body height (Fig. 6).
2. Abdomen twitching
   Rapid upward and downward movements of the abdomen, occurring in three distinct forms:
   Type 1: Very rapid twitching preceding dancing displays (Element 7, type 1), with a duration of approximately 0.03–0.1 s per twitch.
   Type 2: Slower twitching during approaching, with a duration of approximately 0.5–1 s per twitch.
   Type 3: Twitching directed toward another female during female-female interactions, occurring at approximately 0.5 s per twitch.
3. Abdomen bending
   The abdomen is lowered by downward displacement at the pedicel relative to the cephalothorax, forming an angle of approximately 30°–45º, and often contacting the substrate.
4. Legs spread
   Extend all legs laterally, elevating body; legs II aligned parallel to legs I. Tibia, metatarsus and tarsus of all legs are directed sideways.
5. Legs arched
   Extend legs II–IV outward and downward in an arch-like stance, nearly perpendicular to substrate; legs II parallel to legs I.
6. Legs hunched
   Fold legs II–IV laterally against body rather than extending (Fig. 4).
7. Dancing
   Stepping movements performed while oriented toward a conspecific, expressed in two forms:
   Type 1: Rapid stepping movements (5–9 steps/s) by moving to the side, on a diagonal or in arc-shaped steps while remaining oriented toward the female; each step accompanied by waving of legs I or brief contact with the substrate. During arc-shaped stepping, the male progressed along a shallow curved path to one side and occasionally reversed direction without pausing.
   Type 2: Slower stepping movement (1–2 steps/s), consisting of small-radius arc movements during withdrawal.
8. Legs II-abdomen rubbing
   Repeated lateral movements of the male legs II tarsi across the ventral surface of the female's abdomen in a side-to-side motion (~6 Hz). During pre-mount, legs II reach beneath the female from the anterior direction, often eliciting elevation of one of the female's legs IV.
9. Leg IV raising
   Elevation of one of the female's legs IV in response to male stimulation; the femur is raised approximately 70°–80°, the tibia 10°–20°, and the metatarsus ~45° relative to the substrate.
10. Palps downward
    Palps are extended ventrally, nearly perpendicular to the substrate, with dorsal surface facing forwards.
11. Palps parallel
    Palps are extended forward, parallel to the substrate, with the tips directed anteriorly.
12. Palps forward
    The dorsal surface of the palpal tarsus (Fig. 2) is oriented anteriorly; the tibia-tarsus joint of each palp is flexed, positioning the tarsus to be nearly perpendicular to the substrate, while the more proximal segments (from the tibia proximally) remain straightened.
13. Palps spread
    Palps are spread diagonally outward, exposing the clypeus; the femora are aligned with legs I; palps may either contact or hover just above the substrate (Fig. 2).
14. Palps extended
    Palps are projected horizontally forward, nearly parallel to the substrate; the dorsal surface of the palpal tarsus is oriented anteriorly or dorsally.
15. Palps waving
    Moving palps up and down at low frequency (~6 Hz) without contacting the substrate; observed in females.
16. Palps drumming
    Type 1: Palp repeatedly contact the substrate rapidly (15–20 drums/s).
    Type 2: Palp repeatedly contact the substrate slowly (~6–8 drums/s).

Table 1. Behavioural elements observed in *N. tibialis* during intraspecific interactions. "Male–female" refers to male behaviours directed toward females, and "Female–male" refers to female behaviours directed to males. "P" = presence; "A" = absence.

Behavioural elements	**Male-female**	**Female-male**	**Male-male**	**Female-female**
Body raising (1)	P	P	P	P
Abdomen twitching (2) (type 1)	P	A	A	A
Abdomen twitching (2) (type 2)	A	A	P	A
Abdomen twitching (2) (type 3)	A	A	A	P
Abdomen bending (3)	P	P	A	P
Legs spread (4)	P	P	P	P
Legs arched (5)	P	P	A	A
Legs hunched (6)	P	A	A	A
Dancing (7) (type 1)	P	A	A	A
Dancing (7) (type 2)	P	A	A	A
Legs II-abdomen rubbing (8)	P	A	A	A
Leg IV raising (9)	A	P	A	A
Palps downward (10)	A	P	A	A
Palps parallel (11)	A	P	P	A
Palpal bulbs forward (12)	P	A	P	A
Palps spread (13)	P	P	P	P
Palps extended (14)	A	A	P	A
Palps waving (15)	A	P	A	A
Palps drumming of substrate (16) (type 1)	A	P	A	A
Palps drumming of substrate (16) (type 2)	A	P	A	P
Palps drumming of substrate (16) (type 3)	P	A	P	A
Palp retracting (17)	P	A	A	A
Palps raising (18)	A	A	A	P
Palp-to-palp contact (19)	P	P	A	A
Legs I raised (20) (type 1)	A	P	P	A
Legs I raised (20) (type 2)	P	P	A	A
Legs I raised (20) (type 3)	A	A	A	P
Legs I folding (21)	P	A	A	A
Legs I opening/closing (22)	P	A	A	A
Legs I straightening (23)	P	A	A	A
Legs I pushing (24)	A	A	P	A
Legs I waving (25) (type 1)	P	A	A	A
Legs I waving (25) (type 2)	P	A	A	A
Legs I waving (25) (type 3)	A	P	A	A
Legs I waving (25) (type 4)	A	A	A	P
Legs I tapping on female (26)	P	A	A	A
Legs I spreading (27) (type 1)	A	P	P	A

Behavioural elements	Male-female	Female-male	Male-male	Female-female
Legs I spreading (27) (type 2)	A	P	P	P
Legs I spreading (27) (type 3)	A	A	A	P
Legs I extending (28)	P	A	A	A
Legs I stroking (29)	P	A	A	A
Legs I tapping (30) (type 1)	P	A	A	A
Legs I tapping (30) (type 2)	A	P	A	A
Legs I striking substrate (31)	A	P	A	P
Pre-mounting contact (32)	P	P	A	A
Decamp (33)	P	P	P	P
Retreat (34)	P	A	P	P
Chasing (35)	A	P	A	P
Pounce (36)	A	P	A	P
Side-to-side arcing (37)	A	A	P	A
Mounting (38)	P	A	A	A

Type 3: Palp repeatedly contact the substrate in short bursts (~0.1s), each consisting of 3 to 5 contacts, with the palpal bulbs oriented perpendicular to the substrate.

17. Palps retracting
    Palps move inward toward the midline during dancing displays; palps may or may not contact each other.
18. Palps raising
    Palps are lifted simultaneously from the proximal joints and moved medially toward the midline until they contact each other, thereby obscuring the clypeus. The dorsal surfaces of the palps are oriented approximately 30-60° relative to the substrate.
19. Palp-to-palp contact
    Direct contact between the male and female palps during the pre-mount phase, without a fixed posture.
20. Legs I raised
    Elevation of legs from the resting position, expressed in three forms:
    Type 1: Elevate legs I about 30°–80° relative to the substrate; the tibia is held horizontally or angled upward at ~40° (Fig. 5).
    Type 2: Slightly elevated legs I with the tibia positioned alongside the cephalothorax and the distal segments from the metatarsus onward lifted approximately 45° relative to the substrate.
    Type 3: With legs I spread (Element 27, type 3), the tibia remain parallel or slightly elevated above the substrate, while the distal segments are raised approximately 30–40° relative to the substrate.
21. Legs I folding
    Bend tibia-metatarsus joints, placing metatarsus in front of cephalothorax without extending femur forward (Fig. 4).
22. Legs I opening/closing
    The distal tips of legs I are alternately brought together and spread apart with each step while dancing.
23. Legs I straightening
    Legs I are extended forward during approach, with the distal segments lifted approximately 20°– 45° relative to the substrate (Fig. 3).
24. Legs I pushing
    The femora change position from vertical to horizontal, thrusting legs I forward for ~0.5 s before returning to the raised posture (Element 20, type 1) (Fig. 5).
25. Legs I waving
    Up-and-down movements of legs I, expressed in four forms:
    Type 1: Legs I move up and down once per step during dancing displays (Element 7, type 1).
    Type 2: In males, legs I move up and down during pre-mount, with the tibiae raised ~45° relative to the substrate and the bristles contacting the substrate (6-8 Hz) (Fig. 3).
    Type 3: In females, raise legs I moves down, and then return to the raised posture (~1–2 s duration) (Fig. 3).
    Type 4: In females, with legs I spread (Element 27, type 3) and raised (Elements 20, type 3), legs I move up and down either alternatively or synchronously at a rate of ~5 waves/s, driven by lowering and raising the femora. Femora are oriented at approximately 40° and 20° relative to the substrate at the highest and lowest points, respectively.
26. Legs I tapping on female
    Contacting the female's palps (3 times at ~0.05 s intervals) and subsequently the cephalothorax (~5 times) with the bristles on legs I during pre-mount.
27. Legs I spreading
    Lateral positioning of legs I, expressed in three forms:
    Type 1: Legs I are positioned laterally at approximately 100°–120° relative to the body midline and held stationary, sometimes slightly lifted.

Fig. 2. Male (right) raising body and extending legs I, with palps positioned laterally. Female (left) usually remains stationary during the male's display. The male's palpal bulb is indicated by a black circle.

Type 2: Legs I are positioned laterally for 1–2 s and then returned to the resting position in a brief spreading motion.

Type 3: Femora of legs I are extended laterally away from the body axis by approximately 40°, resulting in the two legs I forming an inter-leg angle of ~140°.

28. Legs I extending
    In males, legs I are positioned anteriorly at an angle of approximately 90°–110° relative to the body midline; the tibia are angled ~20° downward, and tibial bristles may contact the substrate (Fig. 2).
29. Legs I stroking
    After mounting, the male performs repeated linear movements along the lateral surface of the female's abdomen using one of his legs I, often eliciting elevation of one of her legs IV (Element 9).
30. Legs I tapping
    Contact of legs I with the substrate, expressed in two forms:

    Type 1: Legs I contact on the substrate once per step during courtship dancing (Element 7, type 1).

    Type 2: Legs I contact on the substrate in short bursts of 4–5 taps at ~0.2 s intervals.
31. Legs I striking substrate
    In females, raised legs I are rapidly brought down onto the substrate once or twice while facing or chasing another spider.
32. Pre-mounting contact
    Lower body and straighten legs I within 1–2 body lengths of the female; legs I wave and contact both the palps and cephalothorax, while legs II rub the abdomen (Element 8), often inducing legs IV raising (Element 9); lasts approximately 4–6 s and is followed by mounting or termination.
33. Decamp
    The individual moves away from a conspecific by walking, running, or jumping, while facing away from the other spider.
34. Retreat
    The individual withdraws while maintaining orientation toward the conspecifics.
35. Chasing
    The female raises the body, waves legs I, and drums the palps (~15–20 Hz) while pursuing another spider, causing it to retreat or decamp.

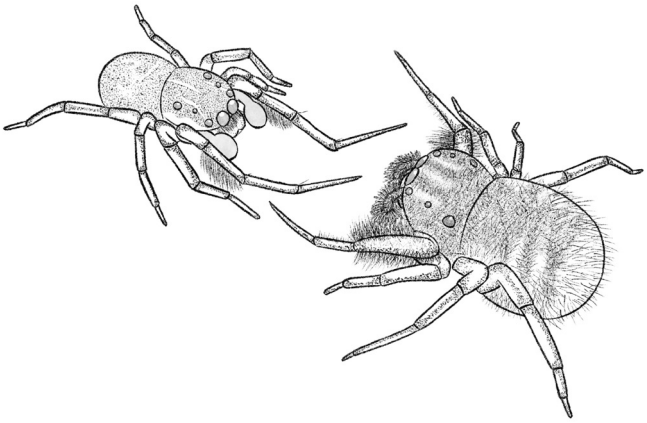

Fig. 3. Male (left) straightening and waving legs I during pre-mount. Female (right) may respond by raising its body and legs I, waving the palps, and pouncing on the male.

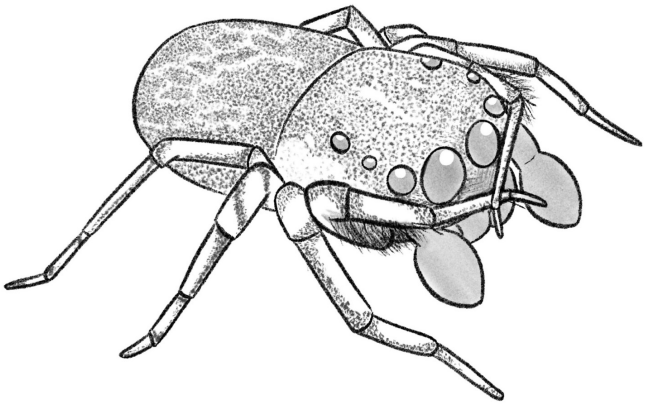

Fig. 4. Male folds legs I in front of the clypeus and hunches the remaining legs while observing a female.

36. Pounce
    The stationary female rapidly leaps forwards towards the other spider with legs I raised, often preceded by body raising and abdomen bending (Fig. 3).
37. Side-to-side arcing
    Individuals move laterally in alternating arcs lasting 3–5 s each during male-male displays; legs I sometimes perform pushing movements without contact (Fig. 5).
38. Mounting
    Following pre-mount (Element 32), the male moves onto the dorsal surface of the female from the anterior direction and initiates copulation.

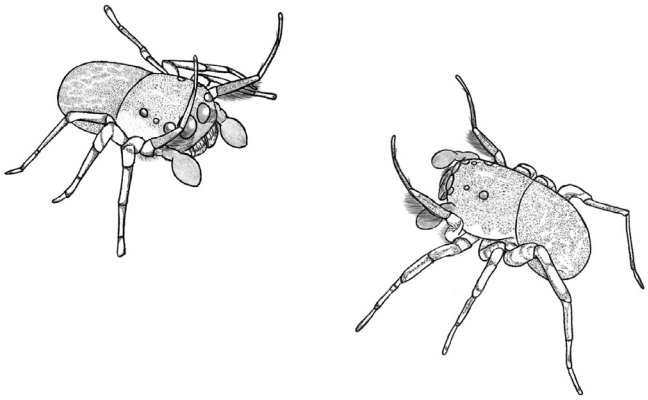

Fig. 5. Two males facing each other during a contest, raising their body and legs I, pushing forwards, and moving in side-to-side arcs. The males have spread their palps, which exposed their clypeus.

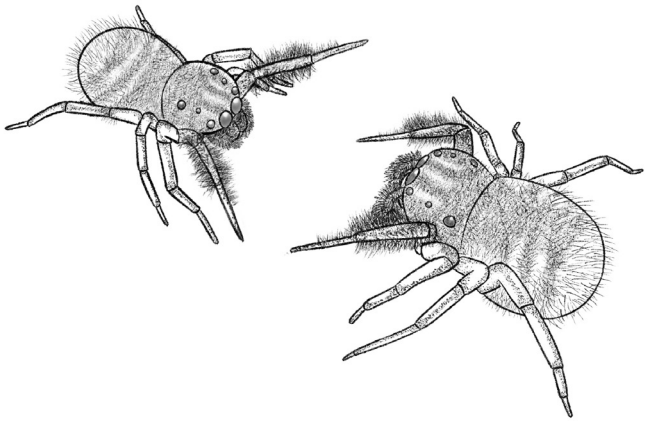

Fig. 6. Female (left) displays to another female (right) by raising her body, spreading, raising and waving her legs I while raising her palps. This female usually chases the other female, but may occasionally retreat and decamp. The recipient female generally retreats and decamps.

Male–female interactions. The sequence of male and female behavioural elements observed during intersexual interactions is summarised in Fig. 7. Upon detecting a female, males usually initiated courtship regardless of the female orientation. Courtship generally began with the male raising his body (Element 1), extending legs I (Element 28), spreading the palps (Element 13), and orienting the palpal tarsus perpendicular to the substrate (Element 12), thereby exposing the clypeus (Fig. 2). This elevated posture was further supported by spreading or arching the legs (Elements 4 and 5) (Fig. 2), constituting the male's courtship display posture. Occasionally, the male briefly retreated (Element 34) and raised legs I (Element 20) before resuming courtship. In some cases, the abdomen bent ventrally to contact the substrate (Element 3).

The male's display posture was often followed by rapid abdominal twitching (Element 2, Type 1), and subsequently by dancing (Element 7, Type 1) in sideways, diagonal, or in arc-shaped steps while maintaining orientation toward the female. Dancing occurred at ~5–9 steps/s and was sometimes accompanied by waving legs I (Element 25, Type 1), alternatively opening and closing legs I (Element 22), or tapping the substrate with legs I (Element 30, Type 1). During diagonal dancing, leg movements were often asymmetrical, with one leg I tapping the substrate while the other remained extended (Element 28). Palps were usually retracted during dancing (Element 17), with males resuming the display posture after each bout. Dancing (Element 7, Type 1) may function both to attract female attention and as an approach tactic.

Females usually remained passive towards male displays but they occasionally responded (Fig. 2). Responsive behaviours include raising legs I (Element 20) and waving them (Element 25, Type 3), drumming the palps against the substrate (Element 16, Type 2), or waving palps at low amplitude (Element 15) while holding them parallel to the substrate (Element 11). Females also occasionally spread the palps (Element 13) or struck the substrate with legs I (Element 31) while facing the male.

When males approached closely, females sometimes performed agonistic behaviours: raising the body (Element 1), spreading the legs (Element 4), waving the palps (Element 15), and rapidly drumming them (Element 16, Type 1 or 2) while holding them perpendicular to the substrate (Element 10). Abdominal bending (Element 3) often accompanied these displays, which were frequently combined with forward movement or decamping (Element 33). In other instances, females showed no response and decamped (Element 33) without displays. Occasionally, they re-oriented to face the male after decamping (Element 33), leading to renewed interactions.

Males occasionally adopted an alternative display posture by folding legs I in front of the clypeus and palps (Element 21) while hunching the remaining legs (Element 6) (Fig. 4). This posture was sometimes followed by low-frequency dancing (Element 7, Type 2). Male palps occasionally drummed on the substrate (Element 16, type 3). Occasionally, males might gradually straighten legs I (Element 23) and resume the standard courtship display. Females generally responded by decamping (Element 33) or approaching; males retreated (Element 34) if females approached.

At ~1–2 body lengths from the female, males attempted pre-mounting behaviour (Element 32, Fig. 3). During pre-mount, the male lowered the body, straightened legs I (Element 23), and waved them rapidly (Element 25, Type 2) while contacting the female's legs I and cephalothorax (Element 26). Palp-to-palp contact sometimes occurred (Element 19). Pre-mount (element 32) could occur with or without prior display and typically ended either in mounting or female decamping.

Females might reject pre-mounting males through agonistic behaviours, including chasing (Element 35). During chasing, females might raise legs I (Element 20, Type 1 or 2) and wave (Element 25, Type 3), tap them against the substrate (Element 30, Type 2), drum the palps (Element 16, Type 1), and raise the body (Element 1). Males usually retreated

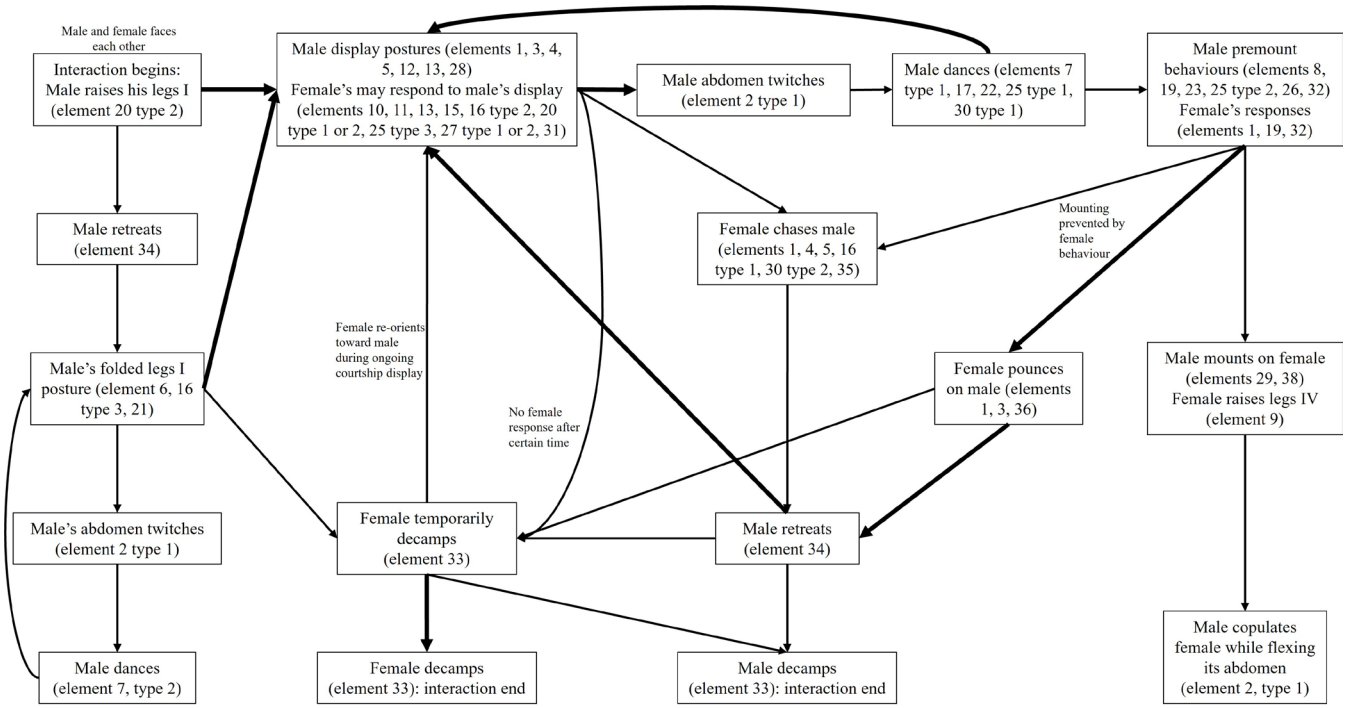

Fig. 7. Sequences of male and female behavioural elements during male-female interactions. Bold arrows indicate elements that occurred more frequently.

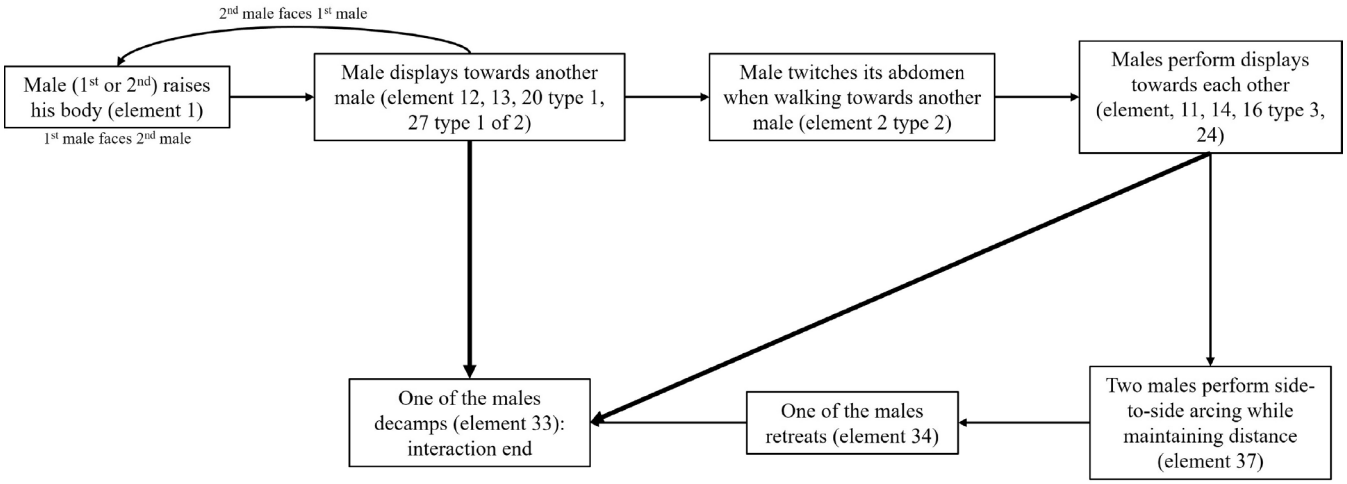

Fig. 8. Sequences of male behavioural elements during male-male interactions. Bold arrows indicate elements that occurred more frequently.

(Element 34) and reinitiated courtship displays. Occasionally, females raised legs I and II and pounced (Element 36), forcing the male to decamp (Element 33).

Successful pre-mount behaviour led to further tactile courtship. Males tapped the female with legs I (Element 26), extended legs II to stimulate her ventral abdomen (Element 8) and raised one leg IV (Element 9) while tilting her abdomen. The male then mounted (Element 38) as the female lowered her body. While mounted, males stroked the female's dorsal abdomen with legs I (Element 29), sometimes leaning sideways while continuing to the strokes. These behaviours were repeated until the female raised her legs IV and tilted her abdomen. Finally, the male applied his palps into the female's epigynum while continuing abdominal twitching (Element 2). Females typically remained still during copulation and showed no aggression.

Male-male interactions. The sequence of behavioural elements observed during male-male encounters is shown in Fig. 8. Upon encountering another male, individuals typically raised the body (Element 1), raised legs I (Element 20, Type 1), and spread them (Element 27, Type 1). The femora of legs I shifted from a vertical to a horizontal orientation, causing the legs I to adopt a pushing posture (Element 24) (Fig. 5). In some cases, legs I spread laterally without being raised (Element 27, Type 2) (Fig. 5). Palps were often spread (Element 13), with palpal bulbs perpendicular to the substrate (Element 12) to expose the clypeus or were extended forward (Element 14) and held parallel to the substrate (Element 11) (Fig. 5). Palpal drumming (Element 16, Type 3) and slow abdomen twitching (Element 2, Type 2) were sometimes incorporated.

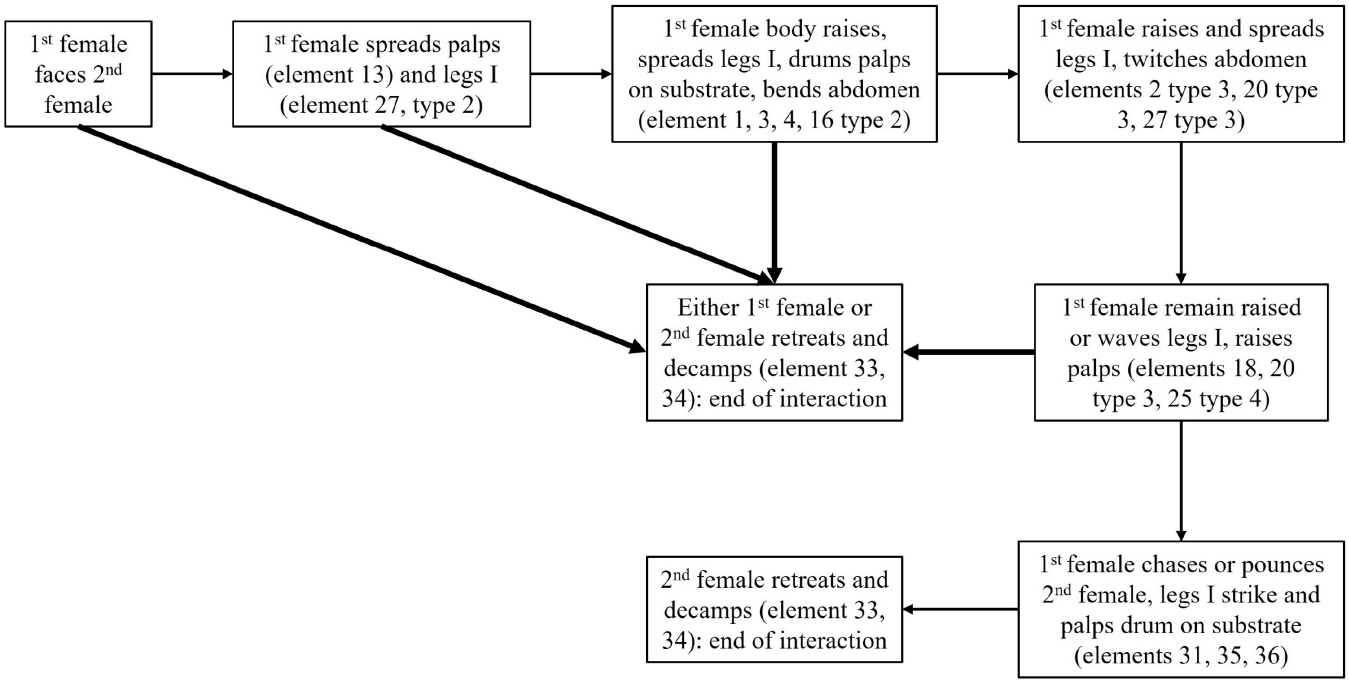

Fig. 9. Sequences of female behavioural elements during female-female interactions. Bold arrows indicate elements that occurred more frequently.

Other legs were occasionally spread (Element 4), slightly elevating the body. The opposing male either retreated, decamped, or performed similar displays as the other male (Elements 31and 32) (Fig. 5). Mutual displays often escalated into side-to-side arcing (Element 36), with each male moving approximately one body length to either side of the original position along lateral arcs lasting 3 – 5 seconds each (Fig. 5). Although both males pushed their raised legs I forward each other (Element 24), direct contact was rare, and no physical combat (e.g., grappling or biting) was observed.

Female-female interactions. The sequence of behavioural elements observed in female-female interactions is shown in Fig. 9. When two females encountered each other, they usually remained stationary or decamped (Element 33). Occasionally, a female displayed toward another female (Fig. 6), spreading her palps (Element 13) and legs I (Element 27, type 2). Further displays rarely occurred, as the other female usually decamped (Element 33). If the other female did not decamp, the displaying female escalated her behaviour by raising her body (Element 1), spreading her legs (Element 4), drumming the substrate with her palps (Element 16, type 2) and occasionally bending her abdomen (Element 3). She then raised and spread her legs I (Element 20, type 3; Element 27, type 3) while twitching her abdomen (Element 2, type 3). Legs I were either maintained in a raised position (Element 20, type 3) or waved (Element 25, type 4), alternately or simultaneously, while palps were raised (Element 18). These behaviours occurred as she chased (Element 35) or pounced (Element 36) towards the other female, striking the substrate with legs I (Element 31). Throughout, her palps either remained raised (Element 18) or drummed on the substrate (Element 16, type 2). The other female usually responded by retreating (Element 34) and decamping (Element 33). Rarely, the displaying female instead retreated (Element 34) and decamped (Element 33). Both females were never observed to simultaneously raise, spread, and wave their legs I toward each other (Elements 20 type 3; 25 type 4; 27 type 3).

DISCUSSION

In this study, we documented 38 major behavioural elements in the intraspecific interactions of *N. tibialis*. Some elements occurred in multiple variants (e.g., palp drumming, legs I waving), yielding a total of 51 distinct actions. Males exhibited 26 elements in intersexual interactions compared to 19 in females, suggesting that male displays are more elaborate. This sexual asymmetry is consistent with predictions of sexual selection theory, which posit that females typically exert stronger mate choice than males while males evolve to be more active in advertising their quality (Andersson, 1994; Candolin, 2003). In contrast, males and females expressed only 14 and 15 elements, respectively, during intrasexual interactions, reflecting a more limited agonistic repertoire.

Across Spartaeinae and other salticid lineages, the number of behavioural elements varies widely, from as few as 13 in *Brettus cingulatus* Thorell, 1895 (Jackson & Hallas, 1986b) to over 35 in *Evarcha culicivora* Wesołowska & Jackson, 2003 (Cross et al., 2008), and *Servaea incana* (Karsch, 1878a) (McGinley et al., 2015). The 38 elements recorded in *N. tibialis* place it toward the upper end of this spectrum, suggesting a relatively complex behavioural repertoire compared with other salticids (Table 2).

Male-female interactions. Courtship in *N. tibialis* is male-driven, with males adopting conspicuous postures, extending legs I, spreading palps, and occasionally twitching the

Table 2. Reported number of major behavioural elements and notable features in intraspecific interactions across selected salticid species. Species were selected based on phylogenetic relevance, shared signalling traits, or contrasting strategies representing alternative approaches to intraspecific interactions in salticids.

Species	Subfamily	No. of elements	Notable features (courtship/agonistic)	Reference(s)
Brettus cingulatus	Spartaeinae	~13	Limited repertoire; ritualised displays	Jackson & Hallas, 1986b
Cyrba algerina	Spartaeinae	>20	Leg I extension; aggressive females	Jackson & Hallas, 1986b; Jackson, 1990
Neobrettus tibialis	Spartaeinae	38	Rich repertoire; non-contact male and female contests; female UV reflectance	This study
Portia fimbriata	Spartaeinae	>25	Cryptic displays; female aggression; complex courtship	Jackson & Hallas, 1986a
*Cosmophasis thalassin*a	Salticinae	~18	UV cues; vibrational signalling	Lim & Li, 2004; Zeng et al., 2019
Evarcha culicivora	Salticinae	~35	Rich repertoire; female aggression; sexual cannibalism	Cross et al., 2008
*Jacksonoides queenslandic*a	Salticinae	~20	Escalated male fights; sexual cannibalism	Jackson, 1988a
*Servaea incan*a	Salticinae	>35	Palp drumming; courtship dancing	McGinley et al., 2015

abdomen. Elevated or extended-leg displays are widespread among salticids (e.g., *Portia*, *Cyrba* Simon, 1876, *Asemonea tenuipes* O. Pickard-Camridge, 1869, *Servaea* Simon, 1888), though the specific configurations vary among species (Jackson & Hallas, 1986a, b; Lim & Li, 2004; Tay & Li, 2010; McGinley et al., 2015). Courtship dancing, often accompanied by abdominal movements, occurs in *N. tibialis* and many other taxa (Jackson & Hallas, 1986b; Jackson, 1988b; Jackson & Whitehouse, 1989). Interestingly, males occasionally fold legs I across the face (Fig. 4), resembling defensive or cryptic postures described in *Portia* when mildly disturbed and the forward-hunched posture of male *Brettus* Thorell, 1895 when courting potentially aggressive females (Jackson & Hallas, 1986a, b). This behaviour is typically observed after the male has retreated and maintained distance from the female, suggesting that it may serve as a defensive or risk-reducing posture.

Palpal drumming on the substrate was also observed in *N. tibialis*, a behaviour uncommon among salticids but known in *C. thalassina* and *S. incana* (McGinley et al., 2015; Zeng et al., 2019). This behaviour may attract the female's attention or signal male quality, potentially influencing mating success (Kotiaho et al., 1996; Girard et al., 2015; Zeng et al., 2019). Such vibrational cues are likely particularly effective in the dim, enclosed microhabitats of curled banana leaves, where visual signals may be limited.

Female-male interactions. Females were largely passive, often remaining stationary or decamping. When responsive, their actions were typically agonistic (e.g., leg raising, tapping, lunging), a pattern common among Spartaeinae and other salticids, where females may reject males or display aggression (Jackson & Hallas, 1986a, b; Lim & Li, 2004; Tay & Li, 2010; McGinley et al., 2015; Wee et al., 2017). The aggressive repertoire of female *N. tibialis*, including chasing and pouncing, resembles that of *Portia*, *Cyrba*, and *Brettus* (Jackson & Hallas, 1986a, b). Unlike in certain salticid species (*Evarcha culicivora*, *Jacksonoides queenslandica* Wanless, 1988, *Plexippus paykulli* Audouin, 1826), female sexual cannibalism was not observed in *N. tibialis*, possibly due to the limited sample size (Jackson, 1988a; Jackson & Macnab, 1989; Cross et al., 2008; Humbel et al., 2023).

Male-male interactions. Agonistic displays of *N. tibialis* were ritualised and non-contact, involving leg raising, abdominal twitching, palp spreading, and side-to-side arcing movements. These behaviours resemble contest displays in other salticids but contrast with species that engage in escalated physical fights (e.g., *Cosmophasis* Simon, 1901, *Thiania* Koch, 1846, *Jacksonoides* Wanless, 1988) (Jackson, 1982; Jackson & Macnab, 1989; Jackson & Whitehouse, 1989; Li et al., 2002; Lim & Li, 2004; Cross et al., 2008; Tay & Li, 2010; Lim & Li, 2013; Wee et al., 2017). Palp drumming during male–male contests, rare among salticids, may function as an honest vibrational signal facilitating mutual assessment and reducing the risk of escalation (Elias et al., 2008). The absence of grappling in *N. tibialis* suggests selection for non-injurious assessment strategies, potentially mediated by visual cues such as leg I extension or cheliceral colouration. However, as only two male-male contests were observed due to the small sample size, additional trials are needed to confirm whether *N. tibialis* consistently lacks escalated combat and to capture a more complete repertoire of agonistic behavioural elements.

Female-female interactions. Female-female encounters usually end with one individual decamping immediately. However, females often display to the other female, primarily by raising, spreading and waving their legs I, raising the palps, and twitching the abdomen. More aggressive behaviours were occasionally observed, including chasing or pouncing

on the other female and striking the substrate nearby. Similar behaviours have been reported in other Spartaeinae (Jackson & Hallas, 1986a, b). However, female *N. tibialis* appear less aggressive than *Portia* spp., likely reflecting differences in resource availability (Jackson & Hallas, 1986b). Female *Portia* may have evolved heightened aggression, including cannibalism, to compete for scarce oviposition sites (Jackson & Hallas, 1986b). In contrast, *N. tibialis* oviposits on dried, curled banana leaves, which are abundant in its natural habitat (Banerjee et al., 2019), potentially reducing the need for intrasexual competition. Behaviours such as abdomen twitching and raising, spreading, and waving of legs I during intrasexual interactions in *N. tibialis* resemble those observed in several other salticid species (Jackson, 1982; Jackson, 1988a; Jackson & Macnab, 1989). However, intrasexual cannibalism, reported in species such as *Evarcha culicivora* and *Jacksonoides queenslandica* (Jackson, 1988a; Cross et al., 2008), was not observed in *N. tibialis* (this study). Likewise, hunched-leg postures seen in *Asemonea tenuipes*, *Servaea incana* and *Cyrba algerina* (Lucas, 1846) (Jackson & Hallas, 1986b; Tay & Li, 2010; McGinley et al., 2015) were not observed in female *N. tibialis*.

Function of the morphological traits. Females are dark blue, have white bristles on legs I and palps, and a hairy body with white stripes on her abdomen. Males are generally dull, dark in colouration, and not hairy. The sexual dimorphism in colour and hairs may allow conspecifics to recognise the opposite sex. Males may recognise females based on their hairy white palps and legs I, while females may identify males via the darker and non-hairy appearance. In addition, the substrate-borne vibrations, possibly produced during palp drumming or legs I tapping on the substrate by *N. tibialis*, help to identify the opposite sex. Sexual dimorphism in *N. tibialis* may be caused by sexual selection (Lande, 1980). Female mate choice is common in jumping spiders, with females often selecting males based on vibration signals or colours (Lim et al., 2007; Zeng et al., 2019). Unlike other females, whose palps are slender and leg-like, *N. tibialis* females possess extremely hairy palps and legs I (Cordellier et al., 2020). The white colouration of these female appendages appears UV reflective (pers. obs.), while males are duller and only weakly UV reflective. This unusual reversal suggests that, unlike in many salticids, male *N. tibialis* may exercise mate choice based on female UV cues (Lim et al., 2007; Li et al., 2008). The female's hairy appearance may also function as a form of masquerade, resembling mould and potentially reducing predation risk (Murphy & Murphy, 2000). In contrast, the less hairy male may be more conspicuous to visual predators such as *Portia* (Li & Jackson, 1996; Li et al., 1997). Consequently, males may have evolved a darker appearance to better match the dark background of dried, curled banana leaves, reducing conspicuous to predators (Cuthill, 2019).

Limitations and future directions. The present study was constrained by a small sample size, the use of older individuals, and the artificial conditions of the laboratory, which may have limited the observed behavioural diversity, particularly in male-male interactions. Nevertheless, these results provide a robust baseline for understanding the courtship and agonistic behaviours of *N. tibialis*. Future work should investigate how the species' specialised habitat—dried banana leaves—shapes intraspecific interactions. Additionally, the roles of UV reflectance and vibrational signalling in mate choice warrant further exploration, as does whether the elaborate male repertoire primarily reflects female choice, male-male competitions, or an interplay of both.

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