

RESEARCH ARTICLE

Do the enlarged hind legs of male thick-legged flower beetles contribute to take-off or mating?

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ABSTRACT

The volume of the hind femora in the adult male flower beetle *Oedemera nobilis* is 38 times greater than in adult females. To determine what advantage limbs with swollen femora might provide, the behaviour of these insects was analysed with high-speed videography. First, because large hind legs are often associated with jumping and take-off, the performance of this behaviour by the two sexes was determined. Take-off was generated by a series of small-amplitude wing beats followed by larger ones, with the hind legs contributing little or no propulsion. The mean acceleration time to take-off was not significantly different in males (46.2 ms) and females (45.5 ms), but the mean take-off velocity of males was 10% higher than in females. Second, to determine if enlarged hind legs were critical in specifically male behaviour, interactions between males and females, and between males were videoed. The male mounted a female and then encircled her abdomen between the enlarged femora and tibiae of both his hind legs. The joint between these leg parts acted like a mole wrench (vice grip) so that when the tibia was fully flexed, a triangular space of 0.3 mm² remained, in which a female abdomen (cross-sectional area 0.9 mm²) could be compressed and restrained firmly without inflicting damage. The flexor tibiae muscle in a male hind femur was 5.9 times larger than the extensor. In interactions between males, attempts to achieve a similar entrapment were frequently thwarted by the pursued male extending his hind legs vertically.

KEY WORDS: *Oedemera nobilis*, Jumping, Mating, Locomotion, High-speed imaging

INTRODUCTION

Large hind legs are frequently an indicator that jumping is a notable feature of the behaviour of certain species of insects. This is particularly true for bush crickets (Orthoptera, Tettigoniidae) (Burrows and Morris, 2003), grasshoppers (Orthoptera, Acrididae) (Bennet-Clark, 1975), flea beetles (Coleoptera, family Chrysomelidae) (Brackenbury and Wang, 1995; Nadein and Betz, 2016) and some weevils (Coleoptera, family Curculionidae) (Nadein and Betz, 2018). All propel their impressive jumps with muscles in the enlarged femora of their hind legs. This correlation between the size of hind legs and jumping does not hold, however, for insects that use muscles within the thoracic cavity to propel jumping. The propulsive hind legs in such species do not have to accommodate large muscles, and are light so that they can be accelerated rapidly. For example, the champion jumping insects as

judged by their take-off speed are certain planthoppers (Hemiptera, Fulgoridae) (Burrows, 2009) and froghoppers (Hemiptera, Cercopidae) (Burrows, 2003; Burrows, 2006), which have small propulsive hind legs. Furthermore, in some beetles, jumping does not rely on propulsion by the legs at all; in the family, Histeridae, some may jump by sudden folding movements of their hard front wings (elytra) (Frantsevich, 1981), while click beetles (Elateridae) jack-knife their body (Evans, 1973; Sannasi, 1969).

Legs fulfil many different functions even though in life-threatening situations the rapidity and power of jumping may be paramount in propelling the insect to safety. Legs are used in walking, running and swimming in very different habitats. They may also be used as visual signals in mate attraction, as active weapons in encounters with conspecifics and predators, as mechanical implements in mating, and for mate guarding. Enlarged hind legs might enhance any of these roles. Male *Sagra* beetles (Coleoptera, Chrysomelidae) that apparently do not jump, have enlarged hind legs which they use to hold on to plant stems while they feed. Females, however, have thinner hind femora but feed in the same habitat (Becky Crew, Running Ponies blog, Scientific American, 2013), suggesting additional actions for the enlarged hind legs in males. In a clade of monkey beetles (Coleoptera, Scarabaeidae), males also have enlarged hind legs, which they use as weapons in combat with other males (Colville et al., 2018). The different usage of the hind legs of particular beetles has been analysed at the level of the tendons of their femoral muscles (Furth and Suzuki, 1990); jumping species have large hind femora with complex extensor tendons and large extensor tibiae muscles, while those that grasp vegetation for feeding have complex flexor tendons and large flexor tibiae muscles.

Here, two questions about the use of enlarged hind legs were asked in a species of thick-legged flower beetle (Coleoptera, Oedemeridae). First, do the enlarged femora of the hind legs of male *Oedemera nobilis* enhance take-off performance? High-speed videos of this behaviour in males and females were analysed and the possible mechanisms and performance compared. Second, do the enlarged femora of the hind legs of males play a role during natural interactions between males and females, and between males? Videos were again analysed to determine if and how the hind legs were used in these encounters.

MATERIALS AND METHODS

Adult male and female thick-legged flower Beetles, *Oedemera nobilis* (Scopoli 1763), were collected in Girton, Cambridge, UK between late May to late June of 2016–2019 while they fed on the pollen of white and yellow flowers of the Asteraceae family. This species is also called colloquially the false oil beetle, the swollen-thighed beetle, or simply just a flower beetle. It belongs to the order Coleoptera, superfamily Tenebrionoidea and family Oedemeridae which contains ~500–1500 species worldwide. Of the four species of the genus *Oedemera* in the UK, males of *O. nobilis* have the

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largest hind femora. Males of *Oedemera lucida* do not have enlarged hind femora and males of the remaining two species *Oedemera femoralis* and *Oedemera virescens* have hind femora intermediate between these two extremes.

Males and females had a bright green metallic colouration. Both had long antennae and a slender body over which a pair of hard elytra (modified front wings) extended almost to the tip of the abdomen and which gradually narrowed posteriorly so that the gap

between them at the midline widened to expose a greater area of the hind wings beneath (Fig. 1A–C). The shapes and lengths of the legs (Table 1, Fig. 1D,E) were examined in live insects and in those fixed in 50% glycerol or 70% alcohol. Images were captured with a GX CAM 5-C camera (GT Vision Ltd, Stansfield, UK) mounted on a Leica MZ16 microscope (Wetzlar, Germany). Leg lengths were measured with a ruler to an accuracy of 0.1 mm from these images displayed on a monitor. Body masses were determined to within

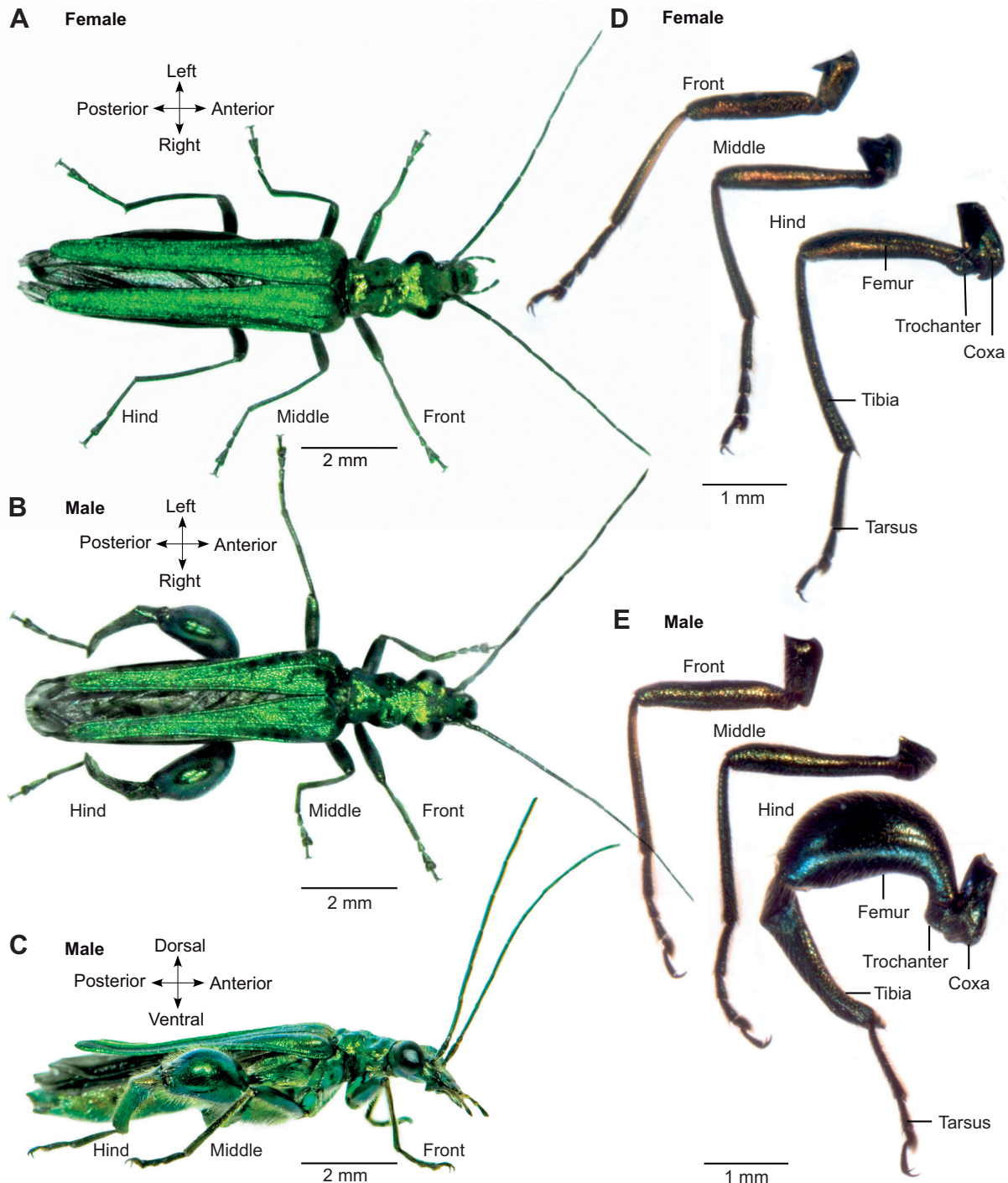


Fig. 1. Body and leg structure of male and female thick-legged flower beetles, *Oedemera nobilis*. (A) Dorsal view of an adult female. (B) Dorsal view of an adult male. (C) Side view of an adult male. (D) Lateral views of the right front, middle and hind legs of a female. (E) The same legs of a male. The hind femur is enormously enlarged.

Table 1. Body form of male and female *Oedemera nobilis* flower beetles

	Body mass (mg)	Body length (mm)	Hind leg			Ratio of leg lengths			Middle leg (%BL)	Hind leg (%BL)	Hind leg length (mm)/body mass ^{1/3} (mg)
			Femur length (mm)	Femur volume (mm ³)	Tibia length (mm)	Front	Middle	Hind			
Male	19.7±1.04 (N=21)	9.3±0.31 (N=7)	2.5±0.07	2.0	2.1±0.08	1	1.1	1.3	64	73	2.6
Female	18.1±1.90 (N=24)	8.8±0.54 (N=7)	1.7±0.09	0.053	1.9±0.14	1	1.2	1.3	61	66	2.3

Body length (BL) and mass, and lengths of the hind femora and tibiae (means±s.e.m.) of male and female *O. nobilis*. The ratios of leg lengths are given relative to the front legs. The length of the middle and hind legs are also expressed as a percentage of BL and the hind legs also as a proportion of body mass^{1/3} (mg).

0.1 mg with a Mettler Toledo AB104 balance (Beaumont Leys, Leicester, UK).

Sequential images of take-offs were captured at a rate of 1000 s⁻¹ and an exposure time of 0.2 ms, with a Photron Fastcam SA3 high-speed camera (Photron Ltd, High Wycombe, UK) fitted with a 100 mm macro Tokina f/2.8 lens. The camera pointed at the centre of a chamber, which measured internally 80 mm wide, 80 mm tall and 25 mm deep. The floor, sides and ceiling of the chamber were made of 12 mm thick, closed cell foam (Plastazote, Watkins and Doncaster, Leominster, UK) and the front wall of 1.8 mm thick glass. Take-offs occurred spontaneously from these surfaces without any overt stimulus, but only those from the floor were analysed so that the effects of gravity were the same. If the body contacted any surface of the chamber during take-off, then that recording was excluded from the analysis. Changes in joint angles and distances moved were measured from selected take-offs that were parallel to the image plane of the camera, or as close as possible to this plane. Deviations of up to ±30 deg were calculated by trigonometry to result in a maximum error of 10% in the measurements of joint or body angles. Take-offs that deviated by more than ±30 deg were rejected. Tracks of the movements of particular body parts were made manually frame by frame with Tracker software (<http://physlets.org/tracker/>) and then in Canvas X

2019 (ACD Systems International, Seattle, WA, USA). To align and compare different take-offs, the time at which a beetle lost contact with the ground and became airborne was designated as $t=0$ ms. The time at which the wings first started to beat was also recorded and the interval between these two events defined the period over which the beetle was accelerated to take-off. Peak velocity was calculated as the distance moved in a rolling 3 point mean of successive frames. A point on the body that could be recognized in successive frames and was close to the centre of mass (determined by balancing an insect on a pin) was selected for measurements of the trajectory. The angle subtended by a line joining these points after take-off, relative to the natural horizontal, gave the trajectory angle. The body angle was defined as the angle at take-off subtended by the longitudinal axis of the beetle relative to the natural horizontal. The results are based on 210 take-offs by 11 male and 11 female flower beetles at temperatures of 20–25°C (Table 2). Measurements are given as means±s.e.m. for each individual beetle and as mean of means (grand means) for males and females analysed.

Videos of the spontaneous behavioural interactions between males and females, and between males, were also captured using the same protocols and the same chamber as for take-off, but at a frame rate of 250 s⁻¹ with an exposure time of 0.2 ms on the Photron camera. Colour videos of these interactions were also made in

Table 2. Take-off performance of male and female *O. nobilis* flower beetles

A		Time to take-off	Take-off velocity	Take-off angle	Body angle at take-off	No. small wingbeats	No. large wingbeats	Total no. wingbeats	Frequency of large wingbeats
Formula	Body mass								
Units	<i>m</i> mg	ms	<i>v</i> m s ⁻¹	deg	deg				cycles s ⁻¹
Male									
Mean	19.74±1.0	46.2±5.2	0.33±0.005	52.4±12.4	17.6±7.6	3.5±0.5	4.8±0.5	8.2±0.7	26.0±2.5
Best	18.5 (<i>N</i> =21)	59.0 (<i>N</i> =11)	0.43	13.9	14.6	3.0	6.5	6.5	38.9
Female									
Mean	18.05±1.9	45.5±2.2	0.29±0.01	58.8±6.3	37.8±6.3	3.0±0.8	5.1±0.3	7.5±0.5	24.8±2.7
Best	19.4 (<i>N</i> =24)	42.0 (<i>N</i> =11)	0.37	54.5	42.1	3.0	4.0	7.0	13.8
B	Acceleration	<i>g</i> force	Energy	Power	Force	Power kg ⁻¹			
Formula	<i>f</i> = <i>v</i> / <i>t</i>	<i>g</i> = <i>f</i> /9.81	<i>E</i> =0.5 <i>mv</i> ²	= <i>E</i> / <i>t</i>	= <i>mf</i>	=power/(0.1 m)			
Units	m s ⁻²	<i>g</i>	μJ	mW	mN	W kg ⁻¹			
Male									
Mean	7	1	1.0	0.02	0.1	12			
Best	8	1	2.1	0.04	0.1	20			
Female									
Mean	6	1	0.8	0.02	0.1	9			
Best	7	1	1.3	0.03	0.1	13			

Data in A are the grand means (±s.e.m.) for the measured take-off performance of males and females; the best performance (defined by the fastest take-off velocity) of a particular individual is also given. The values in B are calculated from the means of the measured data. N=number of males or females that were analysed.

parallel with a Nikon D7200 camera operating at 30 frames s^{-1} and fitted with a 105 mm Nikon macro lens. Still photographs of live males and females were taken with the same Nikon camera (Fig. 1A–C). Both males and females were taken from their natural habitat in the wild so that their previous encounters with other members of the same species were unknown. Once in the laboratory, individual beetles were kept separately in containers with their natural host plants for a maximum of 1–2 days before observations were made of their interactions with other members of the same species.

RESULTS

Females had a body mass of 18.05 ± 1.9 mg and a body length of 8.83 ± 0.54 mm ($N=24$) and were lighter and shorter than males, which had a body mass of 19.74 ± 1.0 mg and a body length of 9.26 ± 0.31 mm ($N=21$) (Table 1). Both mean values were significantly different between the two sexes (Student's t -test mass: $t_{43}=3.541$, $P=0.001$; length: $t_{43}=2.762$, $P=0.008$). The length of the legs had a ratio of 1 (front):1.2 (middle):1.3 (hind) in females and 1:1.1:1.3 in males. The striking difference in the hind legs of the two sexes was in the size and shape of the femora and tibiae (Fig. 1D,E).

In females, a hind femur had a similar tubular shape to the femora in the other legs and had a volume of 0.053 mm³. In males, by contrast, a hind femur was notably enlarged in both width and length. Its overall length was 2.54 ± 0.05 mm ($N=7$) compared with the length of the female femur of 1.71 ± 0.09 mm ($N=7$). The male hind femur is thus significantly longer (Student's t -test: $t_5=8.59$, $P<0.001$). It was also curved particularly at its proximal end where it turned through almost 90 deg before its joint with the trochanter. This is in marked contrast to the straight femora of all the other legs and in particular the almost straight hind femur of a female (Fig. 1D,E). The enlarged hind femur in males meant that the overall length of their hind legs was significantly greater than in females (mean male, 4.64 ± 0.08 mm; mean female, 3.69 ± 0.18 mm, $t_{12}=5.74$, $P=0.00005$). This difference meant that the hind legs of males were 73% of body length while in females they only represented 66%. The most dramatic difference was that the male femur had an overall volume of 2.0 mm³ making it almost 38 times greater than that of the female.

The hind tibia in females and males was not significantly different in length (mean female, 2.0 ± 0.15 mm; mean male, 2.1 ± 0.04 mm; $t_5=1.02$, $P=0.326$), but a male hind tibia was broader than that of a female and differed in shape (Fig. 1D,E). Close to the femoro-tibial joint it was 380% wider than in a female and although tapering distally, it was still 34% wider than in a female close to the tibio-tarsal joint (Fig. 1D,E). Moreover, at its extreme distal end, a male tibia had a flattened zone which when the femoro-tibial joint was fully flexed could be directly opposed onto an indented surface of the trochanter.

Take-off movements

In males, spontaneous take-offs from the horizontal were revealed in high-speed movies to be preceded by the following sequence of wing movements (Fig. 2, Movie 1). The first movement was an opening of the front wings (elytra) and hind wings. In the example shown, these movements occurred 90 ms before take-off and were often followed by a pause of 20–40 ms before the front wings were fully opened and the hind wings partially elevated. This was then followed by a series of small amplitude elevation and depression movements of the hind wings with an amplitude of about 20 deg, accompanied by up and down movements of the elytra (Fig. 2). The start of the first, small amplitude wing movement was taken to be the start of the acceleration phase of take-off. These wing movements then increased in amplitude until they reached an excursion of about

125 deg and continued after take-off so that a smooth transition into flapping flight occurred.

The hind legs of males showed no progressive movements that suggested a contribution to propulsion leading to take-off. The angle of the enlarged femur relative to the long axis of the body did not change, indicating a lack of depression of the trochanter about the coxa (Fig. 2). Similarly, the angle of the enlarged tibia remained at about 90 deg relative to the huge hind femur throughout the acceleration phase leading to take-off. Only after take-off, when the hind legs were not supporting the weight of the insect, did these joint angles change and this could be explained by passive gravitational effects. By contrast, the same joints in the front legs did show progressive changes that accompanied the head and front of the body being raised higher and higher above the ground. The continuing positions of these joints after take-off indicated that they were more involved in controlling posture than in applying propulsive forces for take-off. The middle and front legs also showed no consistent angular changes of their joints that indicated they were contributing thrust to take-off.

Tracking the positions of the different legs emphasised their paths during a take-off (Fig. 3A) and revealed the sequence in which they lost contact with the ground (Fig. 3B). Middle legs lost contact first as much as 30 ms before take-off and in this example, during the second large amplitude movement of the hind wings. The middle legs were then raised above the body and in front of the elytra so that they did not interfere with the increasing amplitude of the wing movements. This posture also meant that during most of the acceleration phase of take-off they could not apply propulsive forces to the ground. The hind legs were the next to lose contact with the ground, frequently as much as 4–5 ms before take-off. They could not therefore contribute to the forward and upward thrust in the latter stages of the acceleration phase of take-off. This sequence resulted in the outstretched front legs being the last to leave the ground and thus to mark the end of the acceleration phase and the point of take-off at which the insect became airborne.

High-speed movies of spontaneous take-offs by females revealed a similar pattern of wing movements and the same sequence in which the legs left the ground to those seen as in males (Fig. 4, Fig. 5A,B, Movie 2). A contribution of the legs to the forward and upward propulsion was again not obvious. The angle of hind femur relative to the body did not change during acceleration to take-off, but the hind femoro-tibial angle did increase just before take-off and still further after take-off (Fig. 4).

In both sexes, the sequence in which the legs left the ground depended on the angle subtended by the longitudinal axis of the body relative to the ground. For example, if the angle was greater, the front of the body was then higher, with the result that the front legs left the ground before the hind legs. The middle legs remained the first to leave the ground so that the loss of contact by the hind legs indicated take-off. In this example, a take-off was preceded by eight complete cycles of small amplitude wing movements followed by four cycles of increasing amplitude movements that reached their peak at take-off (Fig. 5B).

The elytra and the hind wings maintained a stable phase relationship with each other such that all four appendages were elevated and depressed at the same time in the acceleration phase to take-off (Fig. 6A,B). The gradual changes in amplitude of the hind wing movements leading to take-off were also reflected in parallel changes by the elytra. Overall, however, the movements of the elytra were of smaller amplitude reaching an excursion of 70 deg compared with the full excursion of the hind wings which reached 120 deg, visible both in the tracks and graphs of a take-off (Fig. 6A,B).

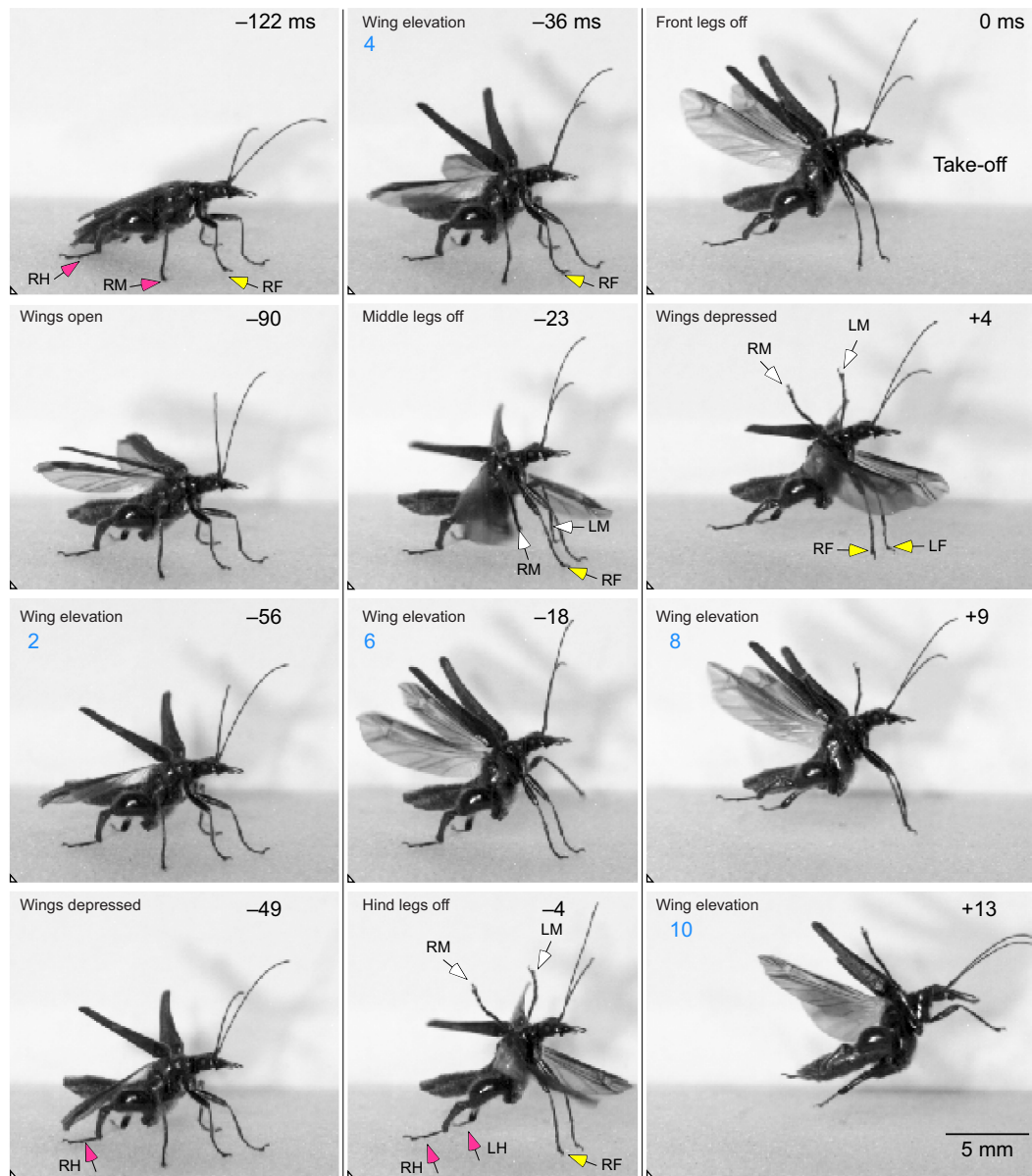


Fig. 2. Take-off by a male *O. nobilis*. Selected images (frames) of a spontaneous take-off, captured at 1000 s^{-1} and each with an exposure time of 0.2 ms, are arranged in three columns. The sequence starts with the beetle standing on a horizontal surface with its wings folded and ends with it in free flight. The triangles in the bottom left hand corners of each image, here and in Fig. 4, indicate a constant spatial reference point and the timings at the top right are given relative to take-off (0 ms). In this and Figs 3–5, the front legs (LF, left front; RF, right front) are indicated by arrows with yellow heads, the middle legs (LM, RM) by arrows with white heads, and the hind legs (LH, RH) by arrows with pink heads. The numbers in blue here and in Fig. 4 indicate the number of wing elevations that have occurred since the start of the recording.

Take-off performance

From the preceding analysis of the kinematics of the legs and wings during take-off, the data on the performance of males and females could be determined and compared for any significant differences between the two sexes (Table 2). The mean acceleration time of take-offs (measured from the first propulsive movement of the wings until the legs lost contact with the ground at take-off) by 11 males was $46.2 \pm 5.2 \text{ ms}$ and by 11 females was $45.5 \pm 2.2 \text{ ms}$. There was no significant difference in these take-off times between males and females (Student's t -test: $t_{20}=0.738$, $P=0.469$). The mean take-off velocities reached by males was $0.33 \pm 0.005 \text{ m s}^{-1}$ and in females was $0.29 \pm 0.01 \text{ m s}^{-1}$. The 10% difference between males and females in these take-off velocities was significant (Student's t -test:

$t_{20}=2.5$, $P=0.022$). It could not, however, have been generated by the enlarged hind legs, which showed no movements indicating that they were contributing to propulsion. The wing movements of males and females before take-off showed no significant difference in either the number of small (males, 3.5 ± 0.5 ; females, 3.0 ± 0.8 ; Student's t -test: $t_{20}=0.684$, $P=0.502$) or large (males, 4.8 ± 0.5 ; females, 5.1 ± 0.3 ; $t_{20}=-0.376$, $P=0.711$) amplitude movements. The power required for a given mass of muscle indicated that a take-off could easily be met by the direct contractions of muscle. This estimation (Table 2) was made on the basis that the propulsive muscles comprised 10% of total body mass; this is likely to be an underestimate given the participation of all the wings and thus makes it even more likely that direct muscle contractions are sufficient.

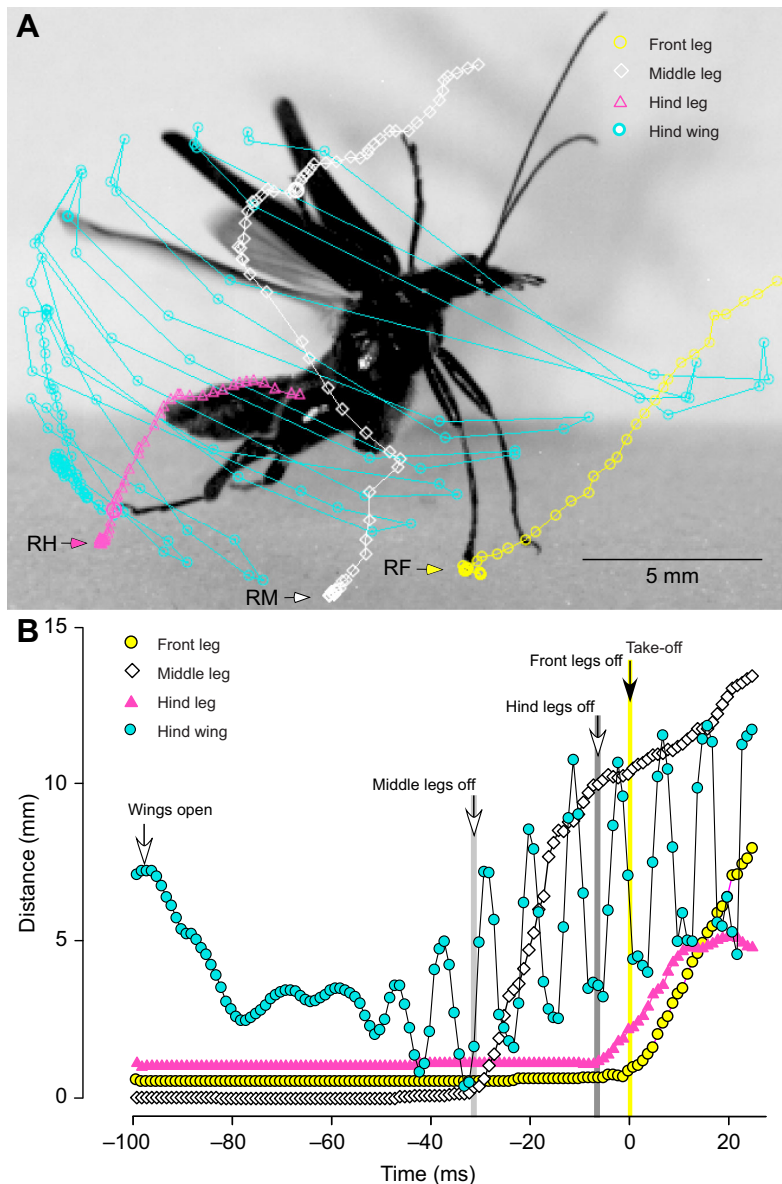


Fig. 3. Tracks of movements of the right legs and hind wing during a take-off by a male *O. nobilis*. (A) Tracks of the tip of the right hind wing (cyan circles), and of the tarsi of the front (yellow circles), middle (white diamonds) and hind legs (pink triangles) are superimposed on the image at take-off taken from a high-speed video (1000 images s^{-1}). (B) Plots of the position in the y-axis of these leg and wing points against time. The hind wings are first opened, then depressed before executing a sequence of depression and elevation movements of increasing amplitude. The legs lose contact with the ground in the sequence middle, hind and finally front legs.

Musculature of male hind femora

The conclusion from the preceding analysis is that the take-off performance of males was not enhanced by their large hind femora. To seek clues as to the function of the enlarged femora, the action of their femoro-tibial joints was examined and the relative sizes of the extensor and flexor tibiae muscles of male femur were measured (Fig. 7). When fully flexed the distal end of the tibia abutted against an indented surface on the trochanter preventing a close juxtaposition of the femur and tibia along their lengths and thus enclosing a triangular space with an area of $0.3 \pm 0.01 \text{ mm}^2$ ($N=5$ males) (Fig. 7A,B). The enclosed space could not be further reduced, implying that anything that fitted snugly within it could be held firmly without being squashed and thus damaged. The force that could be applied to a restrained object was thus limited by a mechanical stop. A structure that might be grasped in this space is the abdomen of a female of the same species. The cross-sectional area of the female abdomen at its mid-point was $0.9 \pm 0.03 \text{ mm}^2$ ($N=5$ females). The dorsal surface of the abdomen had a marked longitudinal depression which occupied most of its width and length. This was the space into which the hind wings fitted when

folded and covered by the elytra, giving it a bowl-like profile in transverse section. A grasping male would only need to compress the female abdomen by 50% to ensure a tight fit in the space between each of his hind femora and tibiae. Holding both hind tibiae flexed would thus apply two contact areas to the female abdomen with sufficient force to restrain her firmly. This applied force would not have to be closely controlled because the engagement of the stop between a distal tibia and a trochanter ensured that it could not exceed a certain level which would potentially damage the female. It is also notable that the femur and tibia of a male hind leg did not have any inwardly pointing spines, which could inflict damage on something that is grasped. Such spines are present on the equivalent parts of the hind legs of some beetles which are used as weapons (Colville et al., 2018).

The interior of a male hind femur was tightly packed with muscle (Fig. 7C,D) with the flexor 5.9 times the mass of the extensor (Fig. 7E), leading to the inference that flexion was the movement requiring the most power. A contribution to take-off would demand an extension of the femoro-tibial joint, leading to the contrary expectation that the extensor muscle would be larger than the flexor.

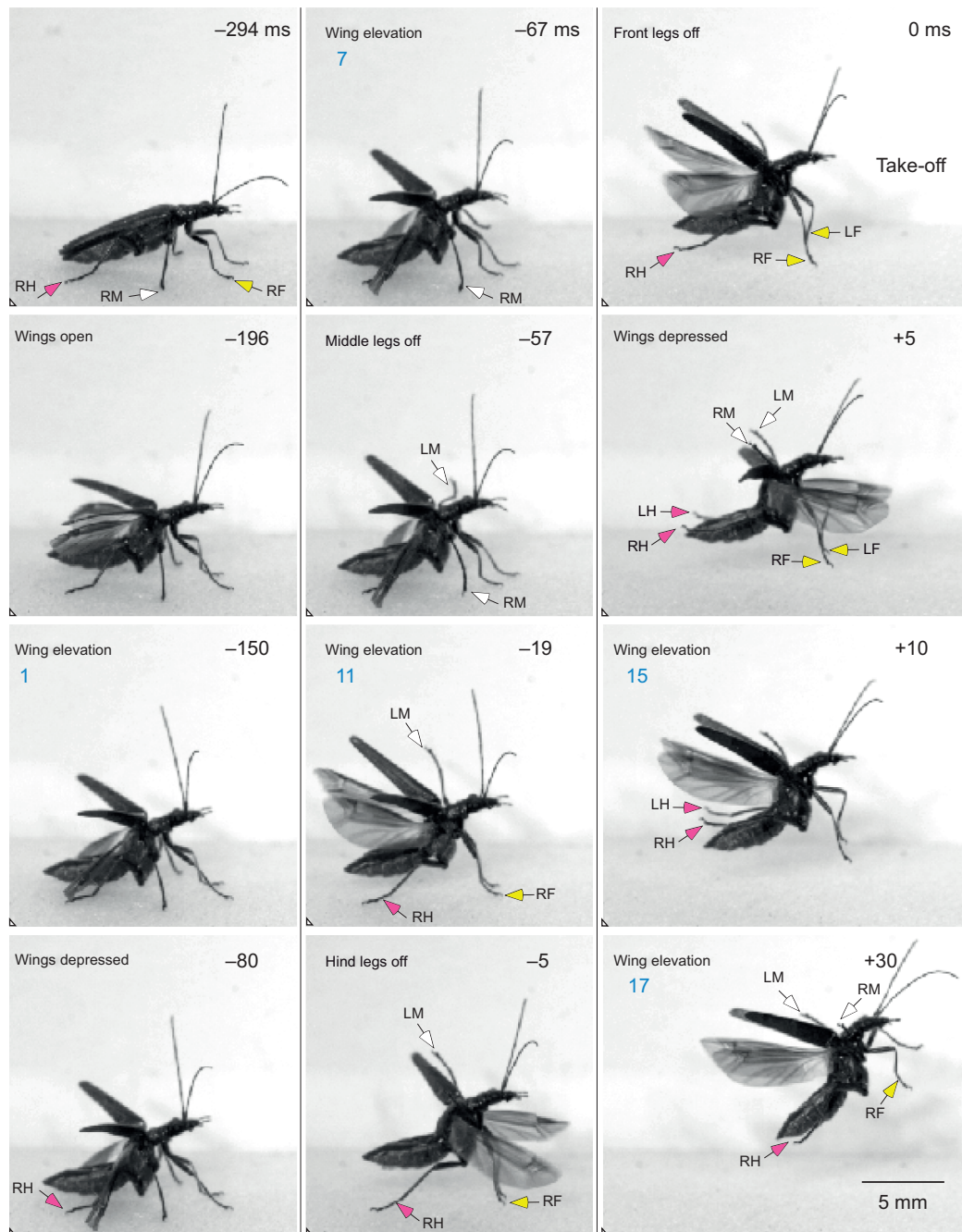


Fig. 4. Take-off by a female *O. nobilis*. Images at the times indicated of a take-off from the horizontal and viewed from the side are arranged in three columns. The wing beat cycles are counted from the peaks of elevation.

This implies that grasping might be an important role for the enlarged femora of male hind legs. To test whether these predictions from anatomy were found in normal behaviour, two experimental paradigms were adopted following preliminary observations of the behaviour of these beetles in their natural habitat.

Behavioural interactions between males and females

One or two males and one female were introduced into the same chamber as used for recording take-off. This was repeated with different individuals so that 115 sequences of interactions between the two sexes were videoed and analysed (Fig. 8). The interactions took the following general form (Fig. 8B,C). A male vigorously

chased a female by attempting to follow her every evasive twist and turn with zig-zag running assisted by flapping movements of his wings. This pursuit usually lasted a few seconds, but after a pause of variable length, could then be repeated. Sustained chases could last for 10 s and then be repeated or interspersed with shorter chases. If the male came close enough to the female then he attempted to mount her dorsal surface, with lift provided by flapping movements of his hind wings with the elytra also moving, but with a smaller amplitude (Fig. 8A). The initial grasping of the female was made by the front and middle legs with both hind legs assuming a seemingly more dominant role the closer the male got to the abdomen of the female and the more they encircled her abdomen. Wing flapping

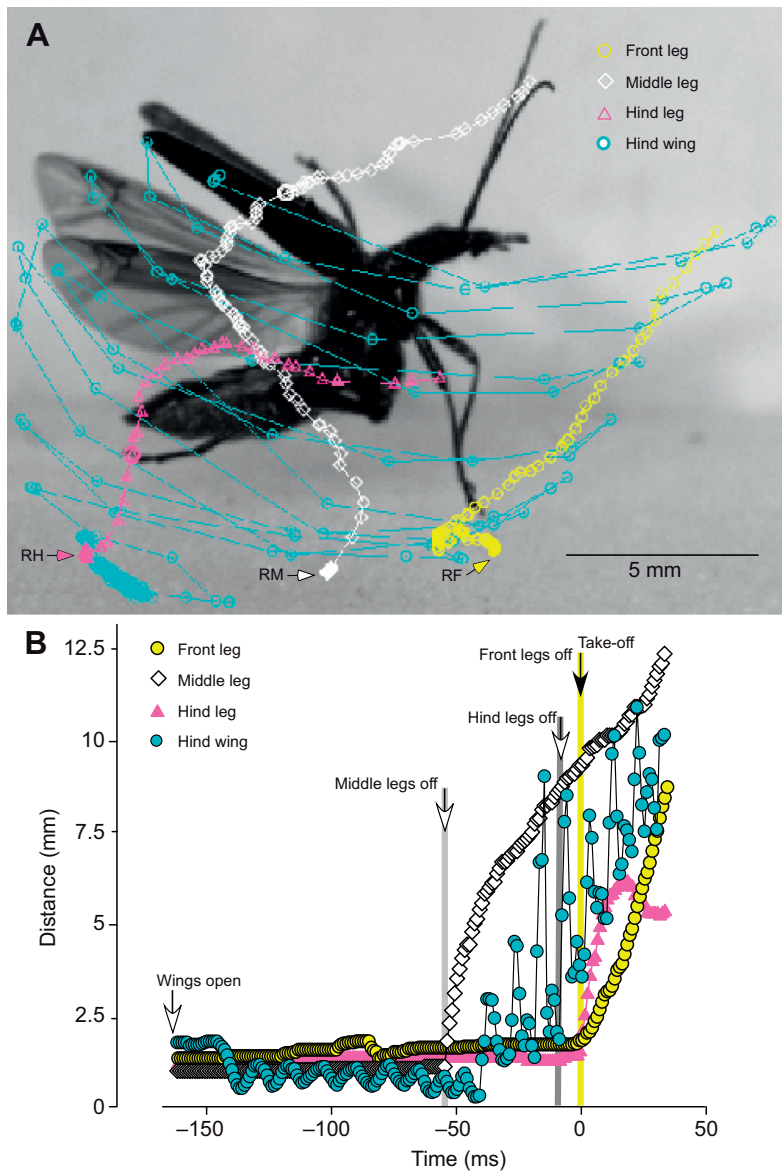


Fig. 5. Tracks of movements of the right legs and hind wing during a take-off by a female *O. nobilis*. (A) Movements of the tip of the right hind wing (cyan circles), and of the tarsi of the front (yellow circles), middle (white diamonds) and hind legs (pink triangles) are superimposed on the image at take-off taken from a high-speed video (1000 images s^{-1}). (B) Plots of the position in the y-axis of these points against time.

could continue in this process. The subsequent movements during an interaction varied, dependent on whether the female was quiet and stationary or executed a series of rapid bucking and turning movements to dislodge him from her back. Attempts by the male to encircle her with both his hind legs were sometimes repelled by pushing movements of her hind legs. If he was thrown off, his pursuit of the female could then either be repeated or abandoned. If he managed to hang on and the mounting was secure, he would then tighten his hind legs around the middle of her abdomen so that it became indented (Fig. 8C,D). This firm grasp on the female was then followed by twisting and searching movements by the tip of his abdomen until the two sets of genitalia became engaged. The success of these mating encounters was judged by an often lengthy engagement and from an often prolonged disengagement that could involve eversion and stretching of the genitalia of the participating individuals (Fig. S1).

Behavioural interactions between males

Three or four males were introduced into the same chamber and in a series of experiments with different individuals, 40 sequences of their interactions were videoed and analysed. Males would attempt

to mount other males (Fig. S2), again propelled by flapping movements of the hind wings, although the frequency of attempted mountings appeared to be less than with male–female interactions. The pursued male would attempt to push away the advancing male with his hind legs. If the advancing male attempted to mount the pursued male, the latter often responded by raising his hind legs vertically above his body with the enlarged hind femora impeding a close contact (Fig. S2A,B). The hind legs of the advancing male could not therefore encircle the abdomen of the pursued male so that his grip was less secure, with the result that these encounters were of shorter duration than those with females. Females did not raise their smaller hind legs in this way when males attempted to mount them.

DISCUSSION

Do the enlarged hind femora of males play a role in propelling take-off?

High-speed videos of the take-off mechanisms in both males and females showed that the legs performed no consistent movements that would indicate a substantial contribution to the generation of the necessary forces. The first question posed by this paper was whether their enlarged hind femora gave males an improved jumping

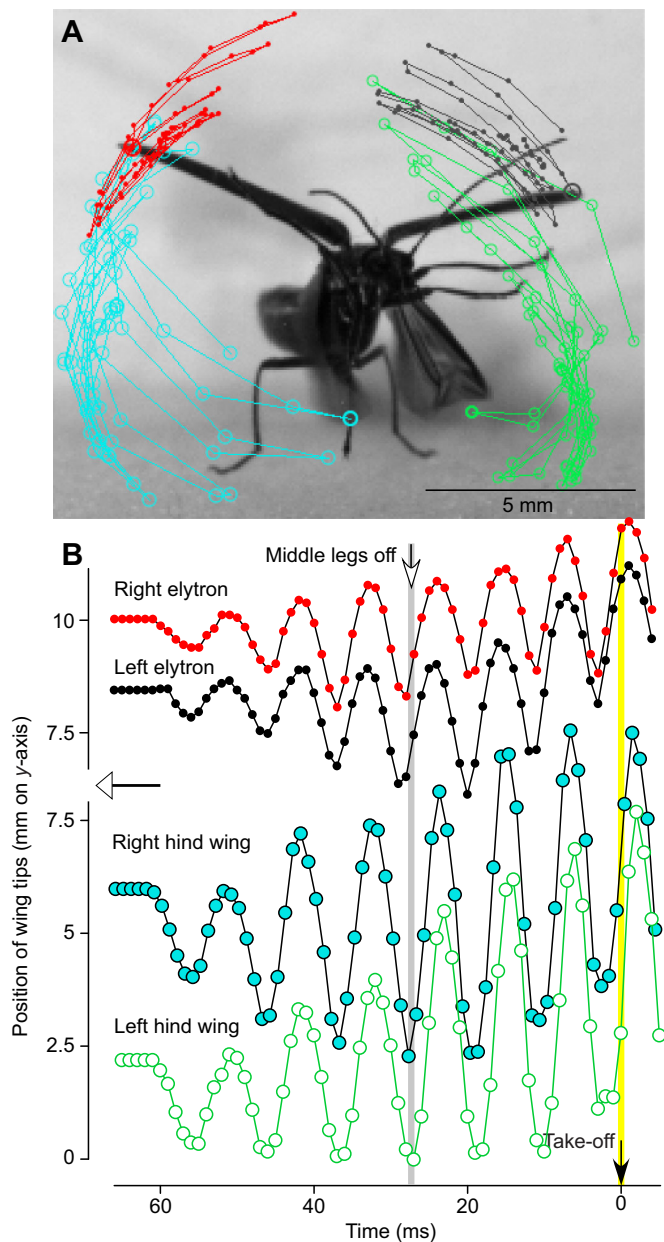


Fig. 6. Elytra and wing movements during take-off by a female *O. nobilis*. (A) Tracks of the movements of the right (red) and left (black) elytra and hind wings (right, cyan; left, green) during take-off of an insect facing the camera. The tracks are superimposed on an image of this female at take-off. (B) Plot of the position on the y-axis of the four wing tips. The time when the middle legs left the ground (grey bar) and when take-off occurred (yellow bar) are indicated. For clarity, the separation of the elytra and hind wings has been increased by a shift of the vertical axis as indicated by the horizontal arrow.

performance over females. The findings showed that the hind legs were not involved in take-off. The coxo-trochanteral and femoro-tibial joints of the hind legs did not change in a way that would be expected if they were contributing to propulsion. This was observed in both males with enlarged hind femora and in females with smaller ones. Instead, movements of the hind wings consistently preceded take-off. The flexible hind wings executed a mean of 3.5 small (20 deg) amplitude flapping movements followed by a mean of 4.8 fuller (125 deg) amplitude ones that propelled take-off. Once the beetle was airborne, these movements translated into a smooth transition to flapping flight. Quantitative measurements of the

take-off performance showed that the mean acceleration times to take-off in males were 46.2 ms and 45.5 ms in females, values that were not significantly different. The mean take-off velocities in males were 10% higher than in females. The hind legs, however, contributed little toward take-off in either sex, so the slightly better performance of males is not explained by the size of their hind legs (their femora have 38 times the volume of those in females). The calculations of other aspects of take-off performance indicate that wing movements powered by direct muscle contractions can generate the lift and propulsive forces measured during take-off. The required power output of the muscles for take-off is only a twentieth of what normal muscle can produce, indicating that power does not need to be amplified and energy does not need to be stored.

Where do these analyses place the take-off performance of *O. nobilis* relative to other insects? The acceleration time of flower beetles is much longer than for insects that use either legs alone or a combination of leg and wing movements for take-off. The champion jumping insects, defined by their take-off velocity, use only their legs to propel take-off. Planthoppers (Hemiptera, Fulgoridae) (Burrows, 2009) and froghoppers (Hemiptera, Cercopidae) (Burrows, 2006) can accelerate in less than 1 ms (a time almost 58 times shorter) to take-off velocities of 5.5 m s^{-1} (18 times faster). The take-off velocity of flower beetles matches the slowness of some small wasps (Hymenoptera) that may also only use wings to propel take-off (Burrows and Dorosenko, 2017b). The velocity is below that of the slowest mirid bugs that combine leg and wing movements for take-off (Hemiptera, Miridae) (Burrows and Dorosenko, 2017a) and is half that of lacewings, which are propelled by movements of the middle and hind legs (Neuroptera, Chrysopidae) (Burrows and Dorosenko, 2014). It is also slower than that of some small moths (Lepidoptera) that can be propelled by the legs alone or in combination with the wings (Burrows and Dorosenko, 2015). The performance of insects that use the movements of the wings alone to propel take-off have rarely been systematically measured, with the exception of butterflies (Lepidoptera) (Bimbard et al., 2013; Sunada et al., 1993), but here some contribution of the legs may also be implicated.

The conclusion to be drawn from the analyses here is that the huge increase in the volume of the femora of male hind legs does not endow them with any greater prowess at jumping or taking-off over females.

Are the enlarged hind femora of males functionally involved in mating?

The second question posed was whether the enlarged femora and greater overall length of male hind legs of males serve a functional role in mating. In their study of tendons in the legs of four families of beetles with enlarged hind femora, Furth and Suzuki (1990) concluded in their discussion that in '*Oedemera*, where only the males have distinctly enlarged metafemora, the large and complicated (five part) tibial flexor tendon with its associated musculature is certainly concerned with the male's ability to grasp and hold the female during copulation'. No evidence was provided and no references were given to support this conclusion. Reflecting on the paucity of evidence for the enlarged hind femora of *Oedemera*, in 2018, Ray Cannon asks on his Nature Notes website: 'It is possible that they are used by the males during courtship or mating? Perhaps in competition with other males, or as an exaggerated feature favoured by females when they choose their mates?' The evidence presented in my paper is that a major use is to grasp a female during mating and to ensure the stability and hence

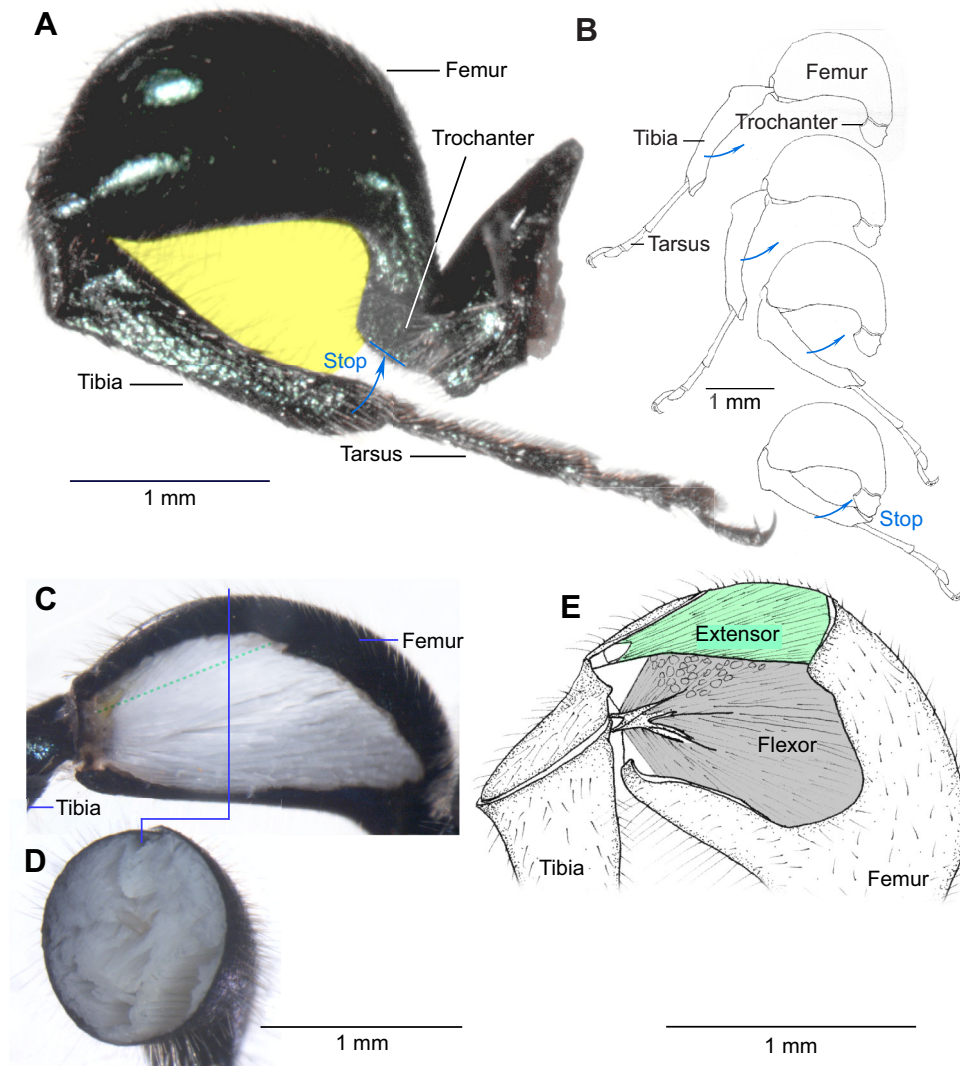


Fig. 7. Anatomy of the hind femur of a male *O. nobilis*. (A) Hind leg with the tibia almost fully flexed about the femur. The enclosed triangular space is tinted pale yellow and the stop between the distal tibia with the trochanter is indicated. (B) Drawings of the right hind leg with the tibia at four different angles about the femur. Contact of the distal tibia with the trochanter prevents apposition of the femur and tibia along their lengths. (C) Photograph of a lateral view of the hind femur with some lateral cuticle removed and a green dashed line indicating the demarcation between the extensor and flexor tibiae muscles. (D) Cross section of the femur at the level indicated by the blue line in C to show muscle filling the whole internal space. (E) Drawing of a dissection to show part of the large flexor muscle (tinted grey) relative to the much smaller extensor muscle (tinted green).

success of the process. The enlarged hind femur contains a flexor muscle with 5.9 times the mass of the extensor, emphasising the importance of grasping. The shape of the hind femur and tibia emphasises their use as a mole wrench in holding a female during mating. The male may pounce on the female and attempt to grasp her. Often this is resisted by rapid movements of the body of the female in different directions. The challenge for the male is to maintain his position and this is achieved by holding the female tightly with both hind legs, so that the two sets of genitalia can engage. The males often seem to be somewhat unselective in their choice of a partner and will mount another male. The pursued male will then hold his large hind legs vertically and extended above his elytra to thwart the encirclement of his abdomen by the hind legs of the advancing male. This emphasises that legs must do many things in different circumstances and their final shape and actions may result from several evolutionary pressures. The conclusion from the evidence presented is that a major action of the male hind legs is to grasp the female firmly for mating.

Male hind legs as mole wrenches (vice grips)

The unusual curved shape of the male hind femora means that when a femoro-tibial joint is fully flexed the apposition of a small area on the distal tibia against the trochanter encloses a triangular space into

which the middle region of the female abdomen can be squeezed and restrained to prevent escape while mating. Videos of mating show that when the male is positioned on top of the female (Movie 3), both of his enlarged hind legs completely encircle the abdomen of the female and noticeably compress it. The shape of the male hind leg and its use has an action reminiscent of a mole wrench (vice grip) with a stop that prevents compression beyond a set point. This means that high forces can be applied in a controlled way because the joint cannot be closed beyond the stop; the enclosed space is protected so that there is no danger of excessive force being applied that might inflict damage to the enclosed abdomen of a female. If the objective is mating, then it becomes of paramount importance not to impede or prevent the fertilisation of the eggs, their maturation and final deposition. The shape and action of this joint prevents such undesirable outcomes.

Are enlarged hind legs used as visual signals?

Could the large hind legs of males act as visual signals of enhanced fitness to impress other members of the same species, in much the same way that exaggerated jodhpurs once extended their function in horse riding to a fashion statement by humans? If the reason for enlarged hind legs was to make them more visible and attractive to females then this could be achieved by, for example, simply having

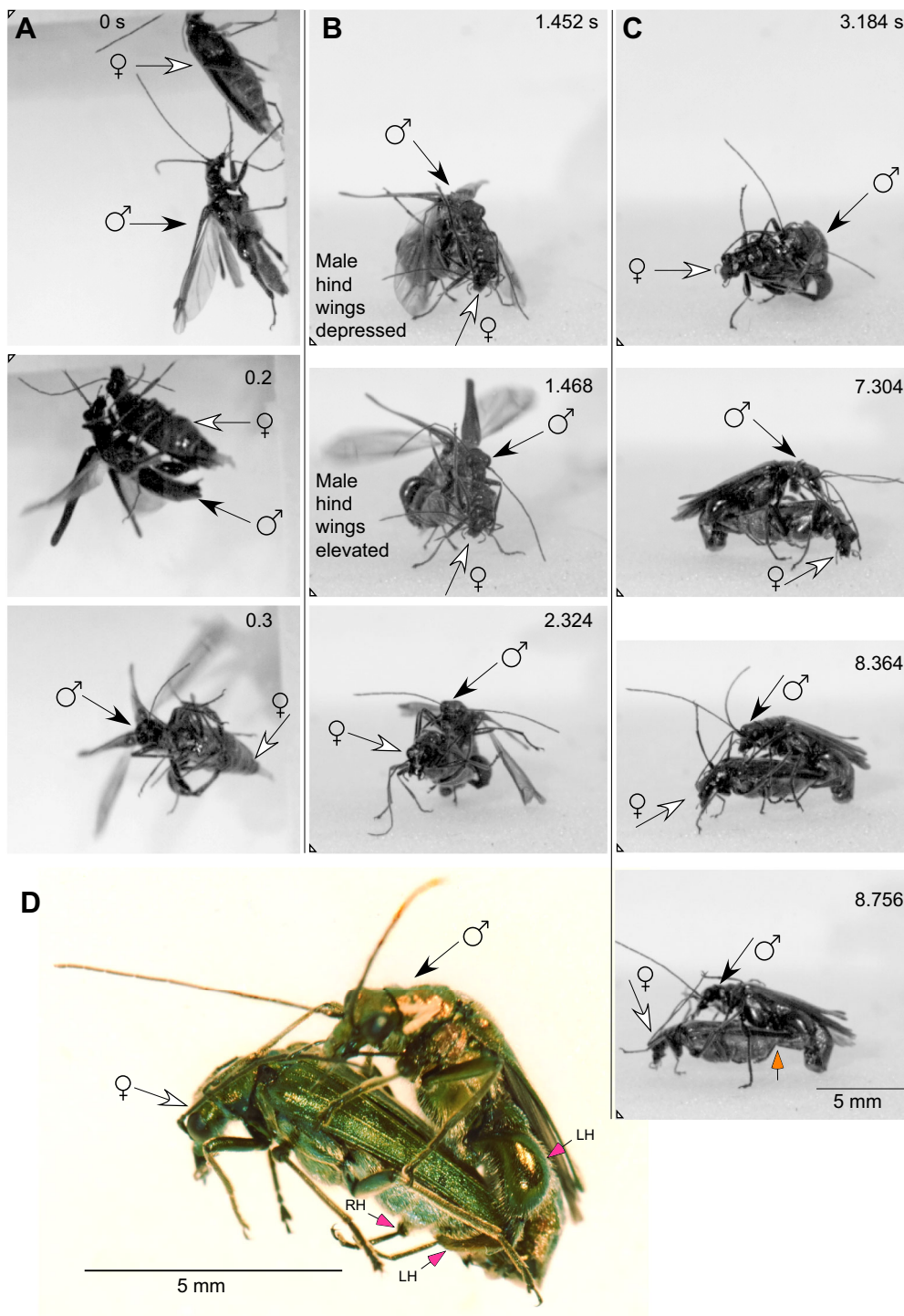


Fig. 8. The male uses its enlarged hind femora to grasp and hold a female when mating. (A–C) Three excerpts from a continuous sequence of a male grasping a female. Images were captured at 250 frames s^{-1} at the times indicated (0 ms represents the start of the sequence), and are arranged in three columns. At the start, a female on a vertical surface is stalked by the male who then mounts her. There then follows a rapid series of movements by the female during which the male hangs on, eventually holding her tightly by compressing her abdomen (orange arrow) with the grip of his hind legs. (D) Enlarged photo of a mating pair; the male is on top with his hind legs (pink arrows) encircling and squeezing the abdomen of the female.

flattened outgrowths rather than a complex shape and filling the expanded volume with muscle. A more satisfying explanation, which is backed by the evidence presented here, is that the huge expansion of the male hind femora is to accommodate more muscle that enables particular strong actions of the hind legs in grasping females and ensuring reproductive success. The enlarged and complex shape of the femur and tibia also fits with their action as a mole wrench operated in *O. nobilis* by a large flexor muscle and a much smaller extensor muscle and that delivering a constrained flexion in grasping a female is a key function.

Other insects with enlarged hind legs

Further functions for enlarged hind legs have been proposed in other insects. In *Sagra* beetles, the specific actions of the larger hind legs of males may be useful in contests with other males as they do not appear to be used for grasping females in mating (Katsuki et al., 2014; O'Brien and Boisseau, 2018) or used to propel jumping. It is suggested that these interactions between males have been the evolutionary driving force behind the enlargement of the hind legs (Katsuki et al., 2014). Male to male wrestling matches with their enlarged and flattened hind legs also occurs in the passion vine bug

Leptoglossus australis (Coreidae, Hemiptera) (Miyatake, 1993, 1997), and in the same family of bugs, male *Acanthocephala declivis* have been observed reversing into each other abdomen first and reaching backwards to grasp the abdomen of an opponent with their enlarged hind legs (Eberhard, 1998). In monkey beetles (Coleoptera, Scarabaeidae), a clade that feeds and mates at fixed sites (within flower heads), enlarged hind legs are used as weapons in combat with rival males and in mate guarding. By contrast, another clade that feeds on unpredictable resources (it forages on widely distributed flowers) has smaller hind legs, indicating an ecological driver of this sexual dimorphism (Colville et al., 2018). These authors also noticed several males in the wild with the severed hind leg of another male clamped in their femoro-tibial joint. There have been no reports to indicate that the male hind legs are used to grasp females during mating, and indeed the common presence of an inwardly pointing tibial or femoral spine would suggest the potential for causing damage were they to be used in this behaviour. This contrasts with flower beetles in which the hind legs of males do not have prominent spines that could inflict damage in this way. Flower beetles, instead, have hind femora with an unusual design like a mole wrench that ensures that no injury can be inflicted on a female when she is clasped tightly during mating.

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Competing interests

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Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.212670.supplemental>

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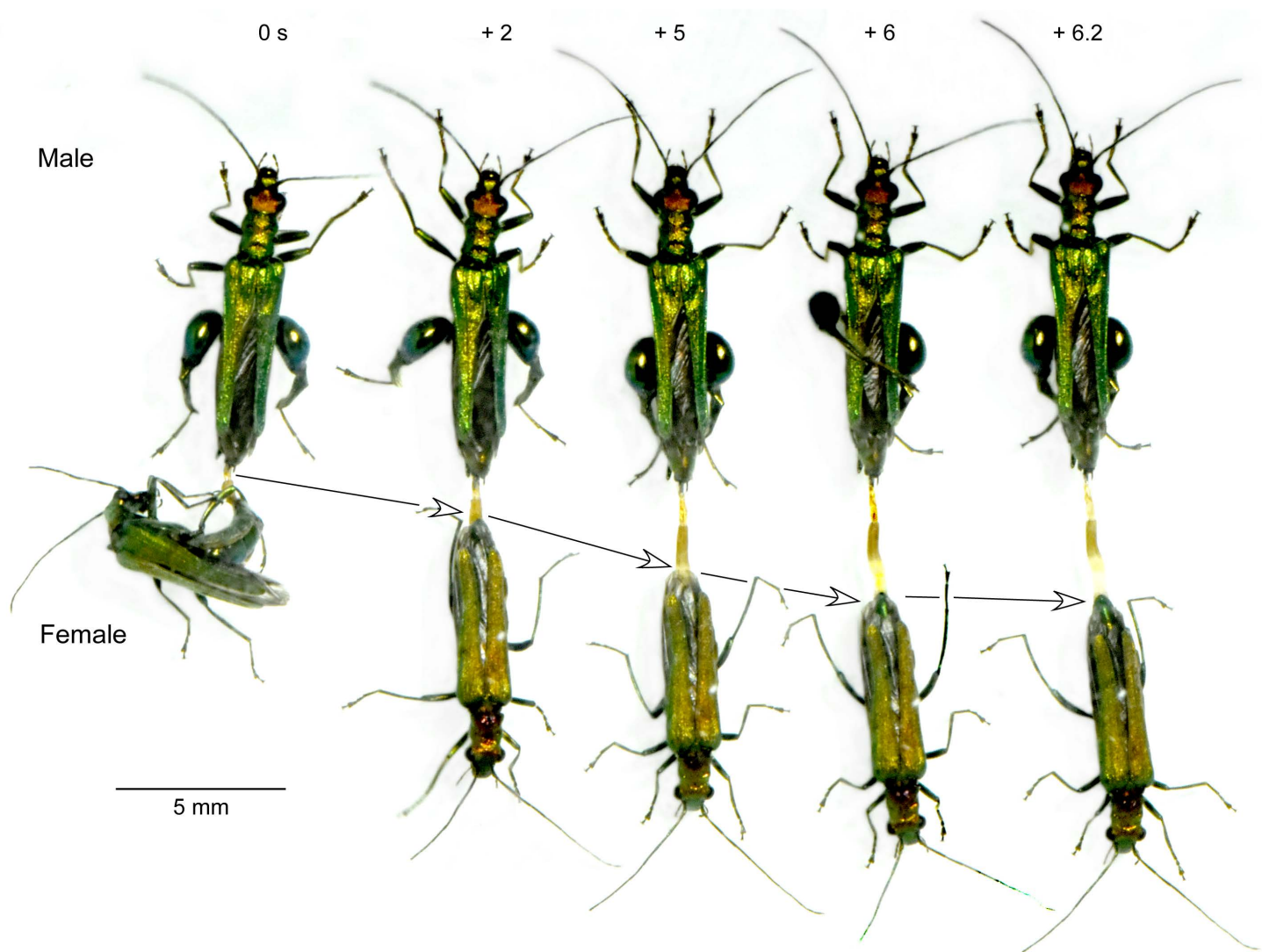


Fig. S1 . Disengagement after mating. Sequence of still images taken with a Nikon D7200 camera from the start (time = 0 ms) of disengagement after mating on a vertical surface. The images are arranged from left to right. As the male (top) and female (bottom) gradually separate, the genitalia of both are progressively extended.

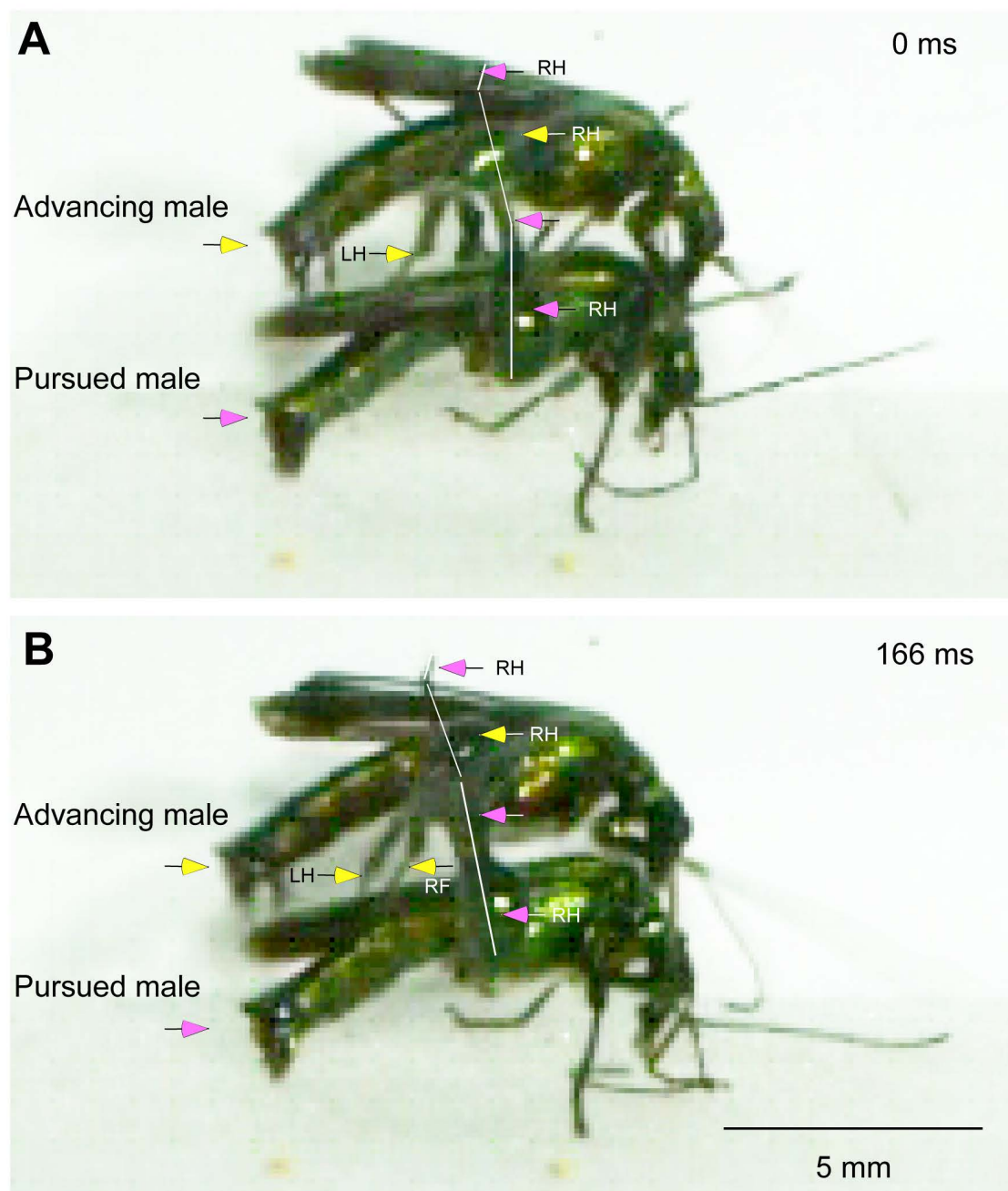
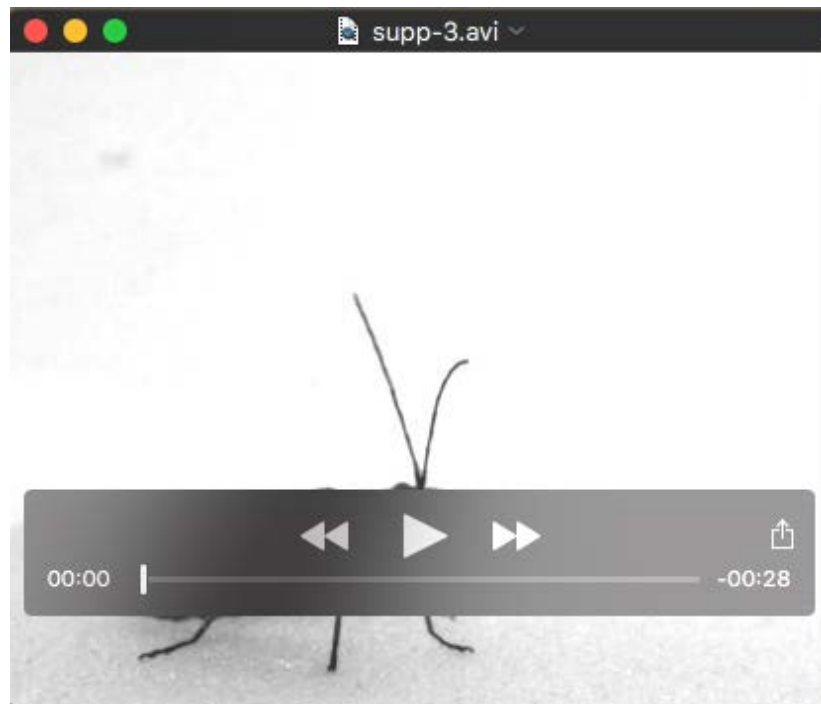


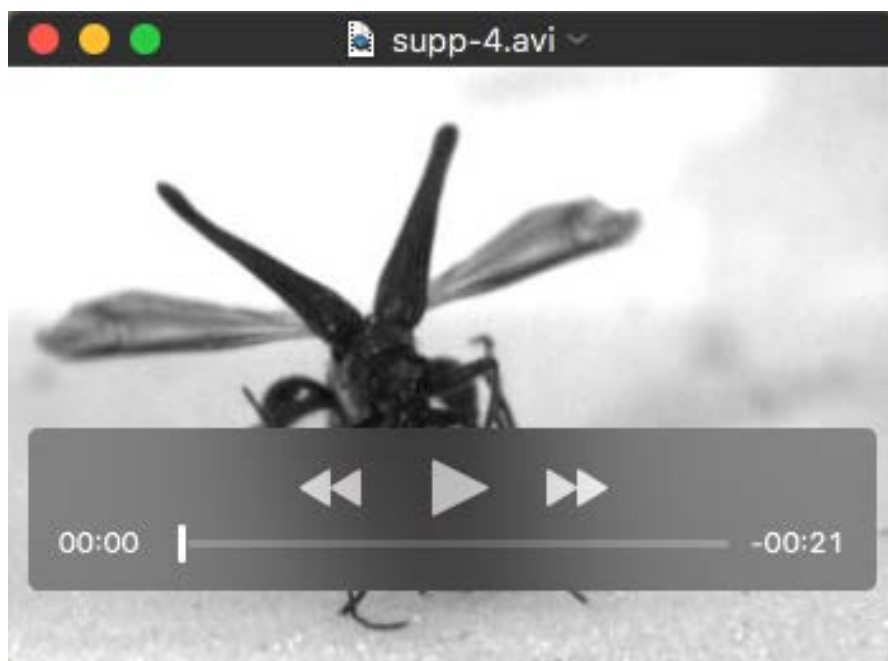
Fig. S2. Male to male interactions. (A, B) Two images separated in time by 166 ms from a video of an advancing male (yellow arrow heads) mounting a pursued male (pink arrow heads) but meeting resistance from his extended hind legs (white lines).



Movie 1. High speed movie with images captured at 1000 s^{-1} and replayed at 10 s^{-1} of a male *O. nobilis* taking-off as viewed from the side.



Movie 2. High speed movie with images captured at 1000 s^{-1} and replayed at 10 s^{-1} of a female *O. nobilis* taking-off as viewed from the side.



Movie 3. Video captured at 250 frames s^{-1} and replayed at 30 s^{-1} of a male mounting a female and grasping her with his enlarged hind legs during mating.