Role of locust *Locusta migratoria manilensis* claws and pads in attaching to substrates

WANG LiXin, ZHOU Qiang* & XU ShuYan

Department of Mechatronic Engineering, China Agricultural University, Beijing 100083, China

The present study attempts to investigate the role of rigid claws and smooth adhesive pads in the locust *Locusta migratoria manilensis*, when attaching to various substrates. We measured the attachment forces on sandpaper and silicate glass plate of locusts with intact attachment system, and those with either the pretarsal claws or the tarsal pads having been entirely destroyed, to explore the role of pads and claws when a locust is walking on various substrates. To obtain information about morphological characteristics and material properties of the claws, we examined the intact and fractured claws by scanning electron microscopy, and tested the fractural force in a fracture experiment. We proposed a mechanical model for locust climbing on a slanting surface to analyze the conduction and final result of the attachment forces generated by the attachment organs on the fore-, mid- and hindlegs. Attachment forces generated by locusts with destroyed pads were similar to those generated by locusts with intact attachment system on both substrates, which presumably indicated that the claws have a significantly important role when attaching to various substrates. The result of the fracture experiment demonstrated that the claws are made of relatively stiff material, and their shear strength ranged between 39–45 MPa. Mechanical analysis of locust climbing on slanting surface showed that the force generated by the hindlegs suspended the whole body of locust up from the surface and pushed the body forward, while the midlegs steadily suspended the centre of gravity and the forelegs pulled the suspended body forward. The results obtained contribute to the further interpretation of the interaction mechanisms between insect attachment system and substrates, and supply information for designing and manufacturing slippery plates for trapping plague locusts.

locust, pads, claws, attachment force, mechanical model

In the course of biological evolution, insects have optimized their attachment organs to adapt to various substrates. Two distinguishable mechanisms, namely mechanical interlock and adhesive attachment, have developed to serve the functions of walking, jumping and climbing on a diverse range of substrates [1,2]. The first mechanism is generated by rigid claws interacting with surface irregularities of macroscopically rough substrates [3]; the second involves adhesive pads, including hairy adhesive structures and smooth flexible pads, to maximize the contact area and guarantee the acquisition of attachment force on smooth surfaces [4]. It has been previously demonstrated that insects can stand or move on vertical substrates using their claws to generate mechanical interlock, when the diameter of macroscopic surface irregularities is much larger than the diameter of the claw tip [5–7]. In this case, insects generally use the surface irregularities as solid anchorage points for their claws to grasp. When the surface roughness is comparable with, or smaller than the claw tip diameter, no effective anchorage site can be provided to generate the mechanical interlock. For reliable attachment to smooth surfaces, the majority of insects have evolved specialized tarsal devices namely adhesive pads, whose function depends on two different mechanisms: hairy adaptable structures and smooth flexible pads [8]. Hairy pads, of insects such as flies and beetles, consist of relatively long deformable setae, which can bend

*Corresponding author (email: zq@cau.edu.cn)

freely and form independent contacts with substrates at numerous points [9,10]. The other type of insect pads, occurring in ants and grasshoppers, are covered by rather soft deformable structures with an extremely flexible cuticle [10–12]. Regardless of the discriminations in such microstructures, both hairy pads and smooth pads duplicate the unevenness of the surface profile at different scales to guarantee a maximum real contact area, and thus achieve sufficient attachment force [9,12,13]. Measurements of the friction force of insects on polishing papers and other artificial surfaces have demonstrated that the microscopic roughness alone can minimize insect attachment, and a correlative model showed that surface roughness with a certain scale can prevent adhesion by restricting pads but not claws [13]. Therefore, insects depend on claws to generate mechanical interlock and pads to cause flexible attachment for walking or standing freely on substrates.

The locust bears smooth adaptable pads and rigid claws, and can attach to a variety of substrates during walking, standing and jumping using similar attachment mechanisms as the other insects. Previous experimental studies have demonstrated many interesting phenomena about locust pads, including the mechanism of its attachment to substrates, the chemical composition and physical properties of its secretions, and the measurement of adhesion force generated by the pads on substrates [14–17]. However, the claws are more important when locust is standing or walking especially on macroscopically rough surfaces. In the present study, experiments were designed and conducted to investigate which part of the locust attachment system has a more important role when attaching to various substrates. Information on material properties and morphological characteristics of locust claws was obtained by a fracture experiment and SEM examination. We also proposed a mechanical model to analyze the conduction and final result of the attachment forces generated by attachment organs in the fore-, mid- and hindlegs. Results obtained from these approaches will contribute to the further interpretation of the interaction mechanisms between the insect attachment system and substrates, and supply information for designing and manufacturing slippery plates for trapping plague locusts.

1 Experimental methods

1.1 Locusts and surfaces used in experiments

Male and female (about 50:50) imagines of the locust *Locusta migratoria manilensis* were used in measuring the attachment forces on different substrates. These locusts were acquired commercially from Cangzhou, Hebei Province and selected for similarity in size (values are means± S.D., male: length=38.65±1.87 mm, female: 48.92±2.09 mm, N=30) and weight (male: mass=1.13±0.11 g, female: mass=1.92±0.21 g, N=30). Pads of one third of the locusts

were very cautiously destroyed with a razor blade, the claws of another third of the locusts were carefully cut with shear cutters, and the remaining locusts were left with an intact attachment system. Males and females of the treated locusts were kept in separate cages with sufficient food (various grass species) for more than 5 d before the force measurement experiments to ensure complete recovery. The temperature and humidity of the cages were maintained at 25–30°C, and 35%–50%, respectively.

The silicate glass plate and sandpaper (being covered by Al_2O_3) used for the attachment force measurement experiment were obtained from the market in Beijing. Data of surface roughness (glass: R_a=0.01 μm; sandpaper: R_a=8.50 μm) were acquired from the supplier.

1.2 Attachment force measurement of treated locusts on substrates

Attachment force measurement experiments with locusts (including those with intact attachment systems, those with claws being cut entirely and those with pads being destroyed completely) were carried out to explore the influence of claws and pads on locust attachment to the substrates. To measure the attachment force, a force sensor (load cell force transducer, 1-PW4C3, 300 g capacity; Hottinger Baldwin Measurement Co., Ltd, Suzhou, China) was utilized. This was fixed on a stand connected to a platform (Figure 1(a)). The force sensor was connected to a signal conditioning system, a computer-based data-acquisition system, and a data processing and displaying software. The sampling frequency could be adjusted by the software, and was set at 10 Hz in this experiment.

Prior to experiment, the experimental locusts were made incapable of flying by cutting their wings off. Sandpaper and silicate glass plate (each 10 cm×16 cm) were connected with double-sided adhesive tape to the platform. Following a similar method previously introduced in detail [18], the experimental locust was attached to the force sensor (along the load direction) using a thin thread (about 10 cm long) fastened to the locust neck, and then was put on the substrate. To make the force sensor precisely obtain the information of the locust attachment force, the height of the force sensor was adjusted so the thin thread was horizontal to the platform. Also, the position of the locust was adjusted and controlled so the thread lay precisely along the load direction (perpendicular to the load point) of the force sensor. The attachment force we measured was the force generated when the locust was desperately crawling away from the force sensor over the substrate. Force-time curves, which were generated by the data processing system, show changes in the force in real-time (Figure 1(b), (c)). For each measuring experiment, the value of maximal attachment force could be acquired by the data processing software and displayed on the screen. For all groups of locusts, eight samples with two repetitions per individual were conducted.
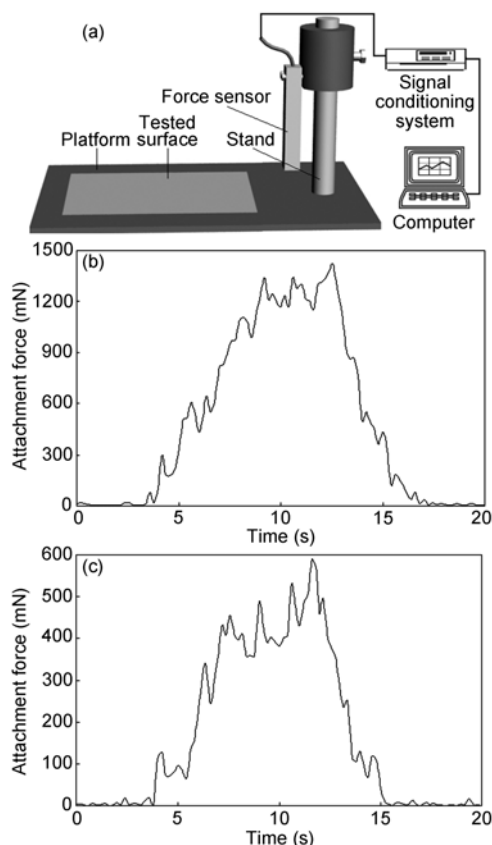
Figure 1 System for measurement of attachment force of locusts on substrates (a); typical attachment force-time curves on sandpaper (b) and on silicate glass plate (c) showing real time changes of attachment force. The system consists of a platform covered by substrates being tested, a force sensor, a signal conditioning system, and a computer-based data-acquisition and processing system.

All the experiments were carried out under the ambient conditions: temperature about 28°C, relative humidity about 45%.

1.3 Fracture experiment of locust claw tips

Fracture experiments using locust claws from the fore-, mid- and hindlegs were carried out to investigate the maximum force at which the claw tip fractured. Freshly cut claws from locusts were glued to an alloy block. The block was then put on the platform of the attachment force measurement system (Figure 1(a)). The height of force sensor was adjusted to line up the claw tip and the sensor's load point. The alloy block was pushed towards the force sensor very slowly and carefully until the tip fractured. A similar method was introduced previously by Dai et al. [7]. The sampling frequency was set at 10 Hz by adjusting the data processing and displaying software. The force-time curves (Figure 2) and the maximum force were obtained by same method as described above. Twelve claws from the fore-, mid- and hindlegs of locusts were tested.
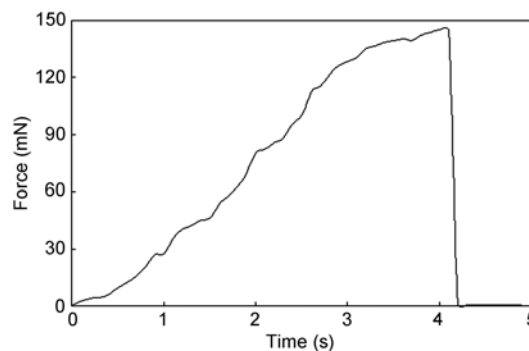

Figure 2 Typical force-time curve obtained in the claw fracture experiment used to evaluate the breaking stress of the claw.

1.4 Morphology studies of locust attachment system

To examine the morphologies and structures of locust attachment system, as well as calculate the section area of the fractured claws, intact attachment organs and the fractured claws obtained from the fracture experiment were air-dried for several days. They were then glued with conductive carbon double-side adhesive tape to alloy blocks, sputter-coated with gold-palladium (about 10 nm) (Bal-Tec SCD 005 Sputter Coater; 25 mA, 300 s; Balzers, Switzerland) and examined with SEM (Hitachi S-3400N, 20 kV: Hitachi, Japan). The section area of the fractured claws was acquired with the image processing software belonging to the SEM equipment.

2 Results

2.1 Attachment forces generated by treated locusts on the substrates

Values of the maximal attachment force generated by the treated locusts exhibited significant differences among the different treatment methods and the substrates used in this experiment (Figure 3). The effect of treatment methods on locust performances was the most significant. Compared with the attachment force generated by locusts with intact attachment system on sandpaper or the silicate glass plate, the force provided by locusts with pads being completely destroyed presented slightly lower (about 250 mN lower on the sandpaper, and 70 mN lower on the silicate glass plate), while the force caused by locusts with all their claws removed exhibited significantly lower values (about 850 mN lower on the sandpaper, and 200 mN lower on the silicate glass plate). Without consideration of the treatment methods, the attachment force generated on sandpaper was distinctively higher (presumably about 2–3 times) than the force caused on the silicate glass plate. On both of the substrates, there was no obvious difference between the values of attachment force provided by male and female locusts.
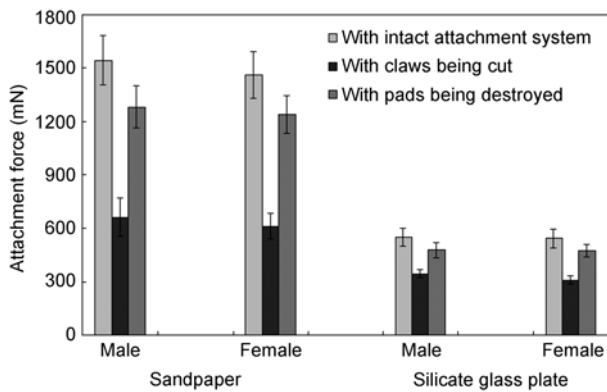
Figure 3 Maximal attachment forces generated by locusts with different treatments on different substrates.

Generally, on the two plates, male locusts with intact attachment system possessed the greatest attachment force (values are means±S.D., 1544.6±141.5 mN on the sandpaper and 549.6±50.8 mN on the silicate glass plate, n=16), while the female locusts with all claws being cut had the lowest attachment force (613.4±70.5 mN on sandpaper and 308.9± 22.4 mN on the silicate glass plate, n=16).

2.2 Fracture force of the claw tips

The fracture force of locust claws obtained from the fracture experiment was used to calculate the shear strength of the claw tips. During the fracture test, the claw was pushed to the force sensor carefully and slowly, so that the load increased almost linearly, then suddenly decreased to almost zero when the claw fractured. Values of the fracture force were significantly different among claws from different legs (Table 1). Claws from the forelegs had the greatest values for the fracture force (198.6±12.4 mN), while claws from the midlegs had the smallest values (176.5±13.6 mN).

Table 1 Fracture force of locust claws from the fore-, mid- and hindlegs of locusts[a]

	Forelegs	Midlegs	Hindlegs
Fracture force (mN)	198.6±12.4	176.5±13.2	190.3±13.6

a) Values are means±S.D., n=12.

2.3 SEM examinations of locust attachment system morphology

The attachment system which is situated at the end of the locust's fore-, mid- and hindlegs, mainly consists of two segments, the tarsus and the pretarsus (Figure 4(a)). The pretarsus bears two rigid, cured ventrally claws and a compliant pad called the arolium (Figure 4(b)), which can adjust the angle formed by the two claws. The tarsus possesses four smooth adhesive pads, which are integrated as complete structure at the bottom of the tarsus (Figure 4(c)). This structure of smooth pads is propitious for closely replicating the microstructure of substrates and results in significant increase of real contact area. Several setae are sparsely distributed on the surface of both the laws and the pads (Figure 4(b), (c)). There is no obvious difference in the width of the pads, between the fore-, mid- or hindlegs or between maleand female locusts. However, the length of pads appears to differ among legs and genders (Table 2).

The section area of fractured claws from the fore-, mid- and hindlegs, which are used to calculate the shear strength of the claw tip, were obtained from the SEM images. The section areas show obvious discrimination (Table 3), which presumably results from the fracture positions. The inner structure of the claws in the fore-, mid- and hindlegs consists of two main parts: (1) the exocuticle, which a thickness of 28.59±6.10 μm (N=2, n=8), and (2) the endocuticle, 32.47± 4.57 μm thick (N=2, n=10) (Figure 4(d)). The exocuticle is a relatively thick layer consisting of significantly
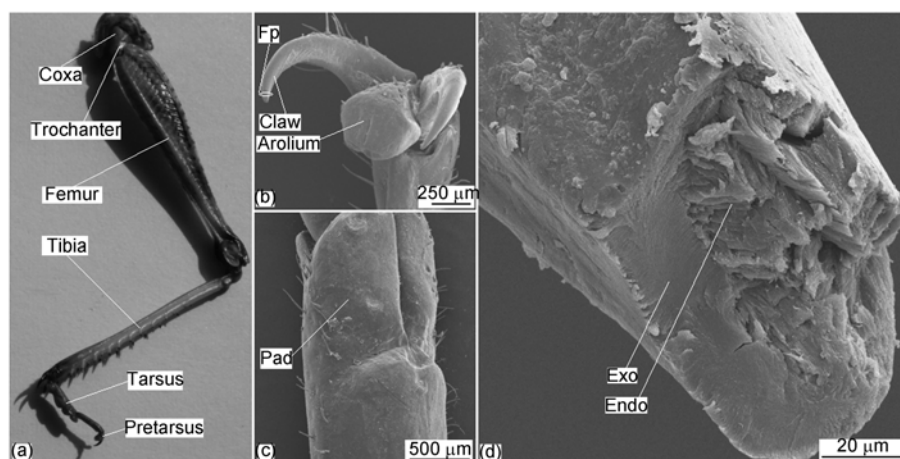

Figure 4 Attachment organs (from male, hindleg) of *Locusta migratoria manilensis*. (a) General structure of a hindleg. The fore- and midlegs possess similar structures, but differ significantly in geometrical dimensions; (b) SEM image of pretarsus. Fp stands for the fracture position on the claw tips in the fracture experiment; (c) SEM image of pad from tarsus; (d) SEM image of the fractured claw in the cross plane.

dense material, whereas the endocuticle is composed of thicker lamellae and is not densely packed. Unlike the claw structures of the beetle *Pachnoda marginata*, no central lumen was seen in the inner structure of locust claws [7].

2.4 Calculating the shear strength of claw tips

The shear strength of claw tip from the fore-, mid- and hindlegs can be calculated from the fracture force (Table 1) and the section area of fractured claws (Table 3) with the following formula:

$$\tau_{max} = F/A, \qquad (1)$$

where τ_{max} is the maximal shear strength of claw tip, and F stands for the fracture force, and A is the section area of fractured claw. Results of these calculations showed that claws in the forelegs possessed the greatest shear strength (45.2 N mm^{-2}), whereas claws in the midlegs exhibited similar value (39.8 N mm^{-2}) to those in the hindlegs (40.2 N mm^{-2}).

3 Discussion

Based on our results concerning the attachment force of locusts with an intact attachment system, and with pads or claws being destroyed, as well as the shear strength of the claw tip, we contend that the claws in the locust attachment system play a more important role during standing or walking on substrates than do the pads. From our observations of locust walking behavior on substrates, we proposed a mechanical model for analyzing the conduction of attachment force to further the more important role of claws.

3.1 Role of pad and claw in the attachment force of locust

In insects, attachment pads are responsible for contact formation on diverse natural substrates. These possess a remarkable degree of deformability, having an extremely

Table 2 Geometrical dimensions of locust pads[a]

	Forelegs	Midlegs	Hindlegs
Male			
Length	2.293±0.201	3.204±0.121	4.657±0.154
Width	1.203±0.092	1.225±0.061	1.307±0.064
Female			
Length	2.932±0.097	3.326±0.156	4.725±0.214
Width	1.209±0.042	1.230±0.038	1.309±0.036

a) Values are means±S.D., unit: mm, N=6, n=20.

Table 3 Sectional area of fractured claws in the fore-, mid- and hindlegs of locusts[a]

	Foreleg	Midleg	Hindleg
Sectional area (μm^2)	4398.1±477.1	4432.7±438.4	4730.1±462.0

a) Values are means±S.D., N=6, n=12.

flexible cuticle or long deformable setae and the pressure derived from the insect weight contributes to the contact formation [19,20]. Claws with rigid tips can grasp surface irregularities of substrata to form mechanical interlock, so sufficient force is required for standing or walking on the surface. In this case, claws are usually controlled by the retractor action of a single muscle situated in the inner structure of insect legs. Muscle contraction leads to the formation of the mechanical interlock between claw and substrate [21]. Generally, adhesive pads and rigid claws are the two crucial structures by which insects acquire sufficient attachment force for effective locomotion on a diverse range of plant surfaces. Because plant surfaces exhibit a wide range of architectures, such as hairy, smooth or covered with wax crystals and moist secretions, the claws and pads may have different roles during the attachment process. It has been previously reported that insects depend on their claws to obtain enough attachment force only on very rough surface [7,22], while on very smooth surfaces, pads with flexible cuticle provided the adhesive force by closely duplicating the substrate texture [23,24]. The attachment force measurement results of the treated locusts suggest that claws contribute much more to the attachment, even on rather smooth substrates.

On sandpaper bearing great surface roughness (R_a=8.50 μm), locust claws can grasp the surface irregularities steadily and the mechanical interlock generated provides adequate attachment force. The attachment force values generated by locusts with pads being completely destroyed are similar to those generated by locusts with intact attachment organs (Figure 3). This presumably demonstrates that the pads only slightly influence the attachment force. When the claws were entirely cut, the attachment forces are smaller (Figure 3), indicating that the claw is a significant factor contributing to the attachment force. On the silicate glass plate (R_a=0.01 μm), compared with the attachment force supplied by locusts bearing intact attachment system, similar and clearly lower values were also shown when pads or claws were destroyed, respectively (Figure 3). In this situation, the four claws situated at the bottom of the hindleg's tibia (Figure 4(a)) interacted with the smooth surface to form a steady plane (mostly consisting of four anchorage points), which provided sufficient holding force to allow the whole body of locust to suspend from the surface. Therefore, a small lateral force can result in effective propulsive movement. The lateral force is presumably provided by pads in the forelegs, because the low surface roughness cannot supply effective anchorage points for the claws to generate mechanical interlock. Notably, attachment force of the treated locusts on sandpaper is significantly greater (about 2–3 times) than on the silicate glass plate, which may indicate that a surface with macroscopic roughness allow the locust claws obtain greater attachment force via the mechanical interlock. It can be concluded in the locust attachment system that the claws have a more important role

when standing and walking on rough and smooth substrates, and the pads perform a supplementary function. This supplementary function of pads may become more significant when the locust attaches to rather smooth surfaces.

3.2 Shear strength of claw tips

Previous studies have measured the bending strength of claws in the beetle *Pachnoda marginata* [7], as well as that of arthropod arthrodial membranes and the solid cuticle of sclerites [25]. The bending stress of the beetle claws was evaluated at 143.4 N mm^{-2} when taking into account both exocuticle and endocuticle layers of the claw's inner structures, and the breaking stress was calculated to be 684.2 N mm^{-2} if only considering the endocuticle layer. The bending stress of the solid cuticle of sclerites from arthropods was about 78.5± 11.7 N mm^{-2}, which is approximately five times greater than in arthrodial membranes (15.6 N mm^{-2}). In our experiment, the greatest, intermediate and relatively smallest shear strength of claw tips was calculated to be 45.2 N mm^{-2} in the foreleg, 40.2 N mm^{-2} in the hindleg, and 39.8 N mm^{-2} in the midleg, respectively. These values of shear strength seem lower than the material stress of claws in the beetle *Pachnoda marginata*, but much higher than those of a diverse range of plant surfaces. The rather high mechanical stress of the claws presumably permits the tips to effectively interact with the vast majority of plant surfaces, when locusts are feeding or escaping from predators. The slightly greater claw shear stress in the forelegs may indicate that the forelegs have a more important role in the locust's propulsive movement.

3.3 Mechanical model of locust climbing on slanting substrate surface

When climbing on a slanting surface, the locust attaches to the surface with its rigid claws generating mechanical interlock and its smooth pads engendering adhesive attachment to obtain sufficient force for standing or propulsive movement. Anchorage and lateral force caused by the hindlegs interacting with the substrate pushes forward the whole body of the locust away from the surface. The midlegs provide sustenance force to suspend the centre of gravity steadily, and the forelegs interlock with the surface, generating lateral force to pull the suspended body.

A mechanics model (Figure 5) was proposed to analyze the conduction and final result of the forces generated by the locust attachment organs. Three assumptions were made for the mechanical model: (1) all the forces generated by locust attachment organs are finally transmitted to the locust's centre of gravity, (2) when the forces are transmitted through the joints formed by the tibia-femur, femur-trochanter and trochanter-coxa (Figure 4(a)), no transmission loss is generated, and (3) sustenance force provided by the forelegs and lateral force generated by the midlegs were ignored.

Based on the above assumptions, in the direction along the substrate, composition of these forces F is

$$F = F_f - N_h \cos(\pi - \beta) - W \sin \alpha, \qquad (2)$$

$$F = F_f + N_h \cos \beta - W \sin \alpha, \qquad (3)$$

when the locust starts walking from a resting state (force equilibrium), $\cos\beta$ is below zero, so sufficient lateral force F_f must first be generated by the locust forelegs to make the F larger than zero. During our experiment, we observed that a locust walking on the substrate enacted its forelegs first. This interesting phenomenon probably confirms the above analysis. N_h serves two functions: supporting the weight of the locust and increasing or decreasing the lateral force provided by the forelegs. Furthermore, when the angle β changes from obtuse (about 150°) to 90°, N_h serves the function of reducing the resultant lateral force. When β changes from 90° to acute (about 30°), N_h has the role of increasing the resultant lateral force. When locust rests on the substrate, $N_h=0$, and $F_f=0$, therefore the locust must depend on the friction force generated between the locust body and the substrate to balance its weight.

In the direction perpendicular to the substrate, composition of these forces N is

$$N = N_m + N_h \sin(\pi - \beta) - W \cos \alpha, \qquad (4)$$

$$N = N_m + N_h \sin \beta - W \cos \alpha. \qquad (5)$$

Whatever the β changes (generally from obtuse to acute), the $\sin\beta$ is larger than zero, so part of the resultant sustenance force N is always provided by the N_h which supplements the N_m provided by the locust's midlegs. Relatively lower shear strength of claw tips in the midlegs probably indicate that the midlegs alone can not supply enough sus-
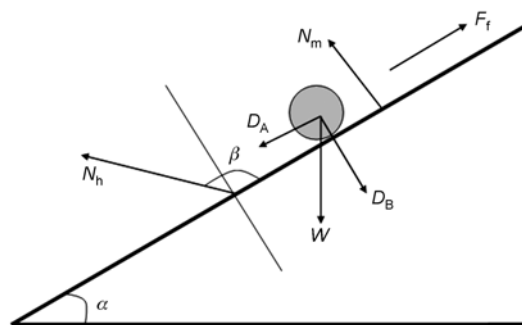

Figure 5 Mechanical model of locust climbing on slanting substrate. α, slanting angle of the surface; β, contact angle between the hindleg and the surface (β changed from obtuse (about 150°) at the start of a walking step to acute (about 30°) at the end of a walking step); F_f, lateral force of the locust foreleg received from the surface; N_m, sustenance force of the locust midleg provided by the surface; N_h, the force generated by the locust hindleg on the surface, the direction of N_h is determined by observing the behavior of the hindlegs when the locust is standing or walking on substrate; W, weight of locust; D_A, the direction along the slanting substrate; D_B, the direction perpendicular to the slanting substrate.

tenance force, and in this case, is supplemented by the sustenance force provided by the hindlegs. The resultant sustenance force serves the function of suspending the centre of locust gravity away from the substrate, so a small lateral force can effectively result in propulsive movement.

In fact, during our experiments, observations of the actions of pads and claws in the fore-, mid- and hindlegs when locust climbing on substrates showed that the four claws at the bottom of the tibia on the hindlegs attached to the substrate steadily, rather than the claws on the pretarsus or pads in the tarsus. For the forelegs, it was mainly the two claws on the pretarsus that interacted with the surface, and for the midlegs, the claws on the pretarsus and most parts of the pads on the tarsus attached to the substrate. These behaviors presumably indicate that the hindlegs depend on the claws of the tibia to generate N_h, and the midlegs use claws and pads to provide N_m. In the forelegs, F_f is mainly caused by the mechanical interlock of the claws on the pretarsus. Therefore, locusts mainly depend on the claws in different legs to obtain sufficient force for attachment to or locomotion on various substrates.

4   Conclusions

In conclusion, the discrimination in the attachment force between locusts with intact attachment system, and those with entire pads on the tarsus or claws on the pretarsus destroyed, strongly demonstrated that claws have a more important role in the walking and standing of locust, while pads serve a supplementary function. The rather high shear strength of locust claws allows the tips to interact with the vast majority of plant surfaces, and sufficient lateral force can be generated by the mechanical interlock of the claws. Mechanical analyses of locusts walking on a slanting surface showed that the force generated by the hindlegs can suspend the whole body of the locust upward and push the body forward, while the force provided by the midlegs keeps the body away from surface. In this situation, even a small pulling force, mainly supplied by claws on the forelegs, can effectively result in propulsive movement.

1   Betz O. Performance and adaptive value of tarsal morphology in rove beetles of the genus *Stenus* (Coleoptera, Staphylinidae). J Exp Biol, 2002, 205: 1097–1113

2   Frantsevich L, Gorb S. Structure and mechanics of the tarsal chain in the hornet, *Vespa Crabro* (Hymenoptera: Vespidae): Implications on the attachment mechanism. Arthropod Struct Dev, 2004, 33: 77–89

3   Voigt D, Schuppert J M, Dattinger S, et al. Sexual dimorphism in the attachment ability of the Colorado potato beetle *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) to rough substrates. J Inst Physiol, 2008, 54: 765–776

4   Bullock J, Drechsler P, Federle W. Comparison of smooth and hairy attachment pads in insects: Friction, adhesion and mechanisms for direction-dependence. J Exp Biol, 2008, 211: 3333–3343

5   Voigt D, Gorb E, Gorb S. Plant surface-bug interactions: *Dicyphus errans* stalking along trichomes. APIS, 2007, 1: 221–243

6   Gladun D, Gorb S N. Insect walking techniques on thin stems. APIS, 2007, 1: 77–91

7   Dai Z D, Gorb S N, Schwarz U. Roughness-dependent friction force of the tarsal claw system in the beetle *Pachnoda marginata* (Coleoptera, Scarabaeidae). J Exp Biol, 2002, 205: 2479–2488

8   Varenberg M, Gorb S N. Hexagonal surface micropattern for dry and wet friction. Adv Mater, 2009, 21: 483–486

9   Niederegger S, Gorb S N, Jiao Y. Contact behaviors of tenant setae in attachment pads of the blowfly *Calliphora vicina* (Diptera, Calliphoridae). J Comp Physiol A, 2002, 187: 961–970

10   Gorb S N, Beutel R. Evolution of locomotory attachment pads of hexapods. Naturwissenschaften. 2001, 88: 530–534

11   Federle W, Rohrseitz K, Holldobler B. Attachment forces of ants measured with centrifuge: Better "wax-runners" have a poorer attachment to a smooth surface. J Exp Biol, 2000, 203: 505–512

12   Gorb S, Jiao Y, Scherge M. Ultrastructural architecture and mechanical properties of attachment pads in *Tettigonia viridissima* (Orthoptera, Tettigoniidae). J Exp Biol, 2000, 204: 1421–1431

13   Scholz I, Buckins M, Dolge L, et al. Slippery surfaces of pitcher plants: Nepenthes wax crystals minimize insect attachment via microscopic surface roughness. J Exp Biol, 2010, 213: 1115–1125

14   Dai Z D, Gorb N S. Study on the micro-structure of locust's pad and FEM analysis of its contact (in Chinese). J Shanghai Jiao Tong Univer, 2003, 37: 66–69

15   Jiao Y, Gorb S N, Scherge M. Adhesion measured on the attachment pads of *Tettigonia viridissima* (Orthoptera, Insecta). J Exp Biol, 2000, 203: 1887–1895

16   Goodwyn P P, Peressadko A, Schwarz H, et al. Material structure, stiffness, and adhesion: Why attachment pads of the grasshopper (*Tettigonia viridissima*) adhere more strongly than those of the locust (*Locusta migratoria*) (Insecta: Orthoptera). J Comp Physiol A, 2006, 192: 1233–1243

17   Votsch W, Nicholoson G, Muller R, et al. Chemical composition of the attachment pad secretion of locust *Locusta migratoria*. Insect Biochem Mol Biol, 2002, 32: 1605–1613

18   Gorb E, Kastner V, Peressadko A, et al. Structure and properties of the glandular surface in the digestive zone of the pitcher in the carnivorous plant *Nepenthes ventrata* and its role in insect trapping and retention. J Exp Biol, 2004, 207: 2947–2963

19   Gorb S N, Jiao Y, Scherge M. Ultrastructural and mechanical properties of attachment pads in *Tettigonia viridissima* (Orthoptera, Tettigoniidae). J Comp Physiol A, 2000, 186: 821–831

20   Federle W, Endlein T. Locomotion and adhesion: Dynamic control of adhesive surface contact in ants. Arthropod Struct Dev, 2004, 33: 67–75

21   Frazier S F, Larsen G S, Neff D, et al. Elasticity and movements of the cockroach tarsus in walking. J Comp Physiol A, 1999, 185: 157–172

22   Wang L X, Zhou Q, Xu S Y, et al. Investigation of the sliding friction behaviors of locust on slippery plates. Chinese Sci Bull, 2009, 54: 4549–4554

23   Beutel R, Gorb S N. Ultrastructure of attachment specialization of hexapods (Arthropoda): Evolutionary patterns inferred from a revised ordinal phylogeny. J Zool Syst Evol Res, 2001, 39: 177–207

24   Dixon A F G, Croghan P C, Gowing R P. The mechanism by which aphid adhere to smooth surface. J Exp Biol, 1990, 152: 243–253

25   Hepburn H R, Chandler H D. Material properties of arthropod cuticles: The arthrodial membranes. J Comp Physiol A, 1976, 109: 177–198