Evidence for self-cleaning in fluid-based smooth and hairy adhesive systems of insects

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SUMMARY

Insects possess adhesive organs that allow attachment to diverse surfaces. Efficient adhesion must be retained throughout their lifetime even when pads are exposed to contamination. Many insects groom their adhesive structures, but it is possible that self-cleaning properties also play an important role. We measured attachment forces of insect pads on glass after contamination with microspheres and found that both smooth pads (stick insects: *Carausius morosus*) and hairy pads (dock beetles: *Gastrophysa viridula*) exhibit self-cleaning. Contaminated pads recovered high levels of adhesion after only eight simulated steps; this was accompanied by the deposition of spheres. Self-cleaning was strongly enhanced by shear movements, and only beetle pads showed the ability to self-clean during purely perpendicular pull-offs. Hairy pads also self-cleaned more efficiently than smooth pads for both large (45 μm) and small (1 μm) particle sizes. However, the beetles' self-cleaning was not superior to smooth pads when contaminated with 10-μm beads. This limitation of self-cleaning is explained by the coincidence of bead diameter and inter-seta distance, which caused beads to remain trapped in between setae.

Key words: self-cleaning, contamination, adhesion, locomotion, biomechanics.

INTRODUCTION

Many insects are capable of climbing and walking upside down on diverse substrates using adhesive organs on their legs (Scherge and Gorb, 2001). Despite the enormous diversity of insects, tarsal adhesive organs have only two alternative designs. 'Hairy' pads are densely covered with flexible, micron-sized setae and occur in several insect orders, including flies, beetles and earwigs (Beutel and Gorb, 2001) (Fig. 1A). 'Smooth' adhesive pads have a relatively even surface profile and a specialised, soft cuticle; they are present in many insects including ants, bees, cockroaches and stick insects (Beutel and Gorb, 2001; Scholz et al., 2008) (Fig. 1B). In both systems, adhesion is mediated by a fluid that is secreted into the contact zone (Gorb, 2001).

Hairy adhesive systems have evolved independently multiple times in arthropods and invertebrates (Federle, 2006). The frequent origin of hairy adhesive systems suggests that this design is optimised for surface attachment. Several theoretical studies have suggested that the hairy pad design allows not only close contact to rough surfaces (Persson, 2003; Persson and Gorb, 2003) but also increased adhesion due to contact splitting (Arzt et al., 2003) and a more effortless detachment (Autumn and Hansen, 2006; Autumn et al., 2006; Federle, 2006; Gravish et al., 2008). The mentioned benefits of fibrillar adhesive systems raise the question of whether they are superior to smooth pads. However, insects with smooth pads have to fulfil largely the same biological requirements, i.e. they also need to be able to conform well to rough substrates and to detach efficiently. Comparing hairy pads of beetles and smooth pads of stick insects directly, Bullock and coworkers found little difference in friction or adhesive stresses (Bullock et al., 2008). Moreover, both smooth and hairy systems showed a strong direction-dependence.

A further possible advantage that hairy systems might have over smooth systems is an ability to self-clean as they walk. Insects are continuously exposed to various contaminating particles such as dust, microorganisms, spores and pollen grains. Some plants have evolved leaf or stem surfaces covered by epicuticular wax crystals that easily exfoliate and thus contaminate insect adhesive structures. Contamination by wax crystals has been shown to disrupt attachment for insects both with smooth and hairy adhesive systems (Stork, 1980; Edwards, 1982; Federle et al., 1997; Gaume et al., 2004). Although adhesive pads can degenerate with age due to a loss of flexibility (Ridgel et al., 2003), insects usually retain the ability to adhere to substrates throughout their life. Clearly, insects must be able to remove contamination from their adhesive pads.

Many insects are known to groom their body, including the legs (Farish, 1972), and it is likely that grooming removes particles from adhesive structures. However, many insects with adhesive pads do not, or only rarely, perform cleaning behaviours (e.g. stick insects; C.J.C and W.F., personal observation) and even insects that groom more frequently take numerous steps between cleaning movements. Thus, it is likely that many insects would accumulate contamination and lose their adhesive ability if they only relied on active grooming to clean their pads.

A possible alternative mechanism for removing contaminating particles from adhesive pads is self-cleaning by contact. It was recently reported that gecko adhesive pads are able to self-clean within just a few steps after being contaminated by particles (Hansen and Autumn, 2005). Not only live geckos but also isolated setal arrays lost particles and recovered adhesion in simulated steps following contamination. Hansen and Autumn explained the geckos' ability to self-clean by the contact geometry of the hairy system (Hansen and Autumn, 2005). They argued that dirt particles adhere more strongly to the substrate than to the small number of fine seta endings on the foot. This balance of forces would remove the dirt and clean the pad with every step taken. A similar model was used
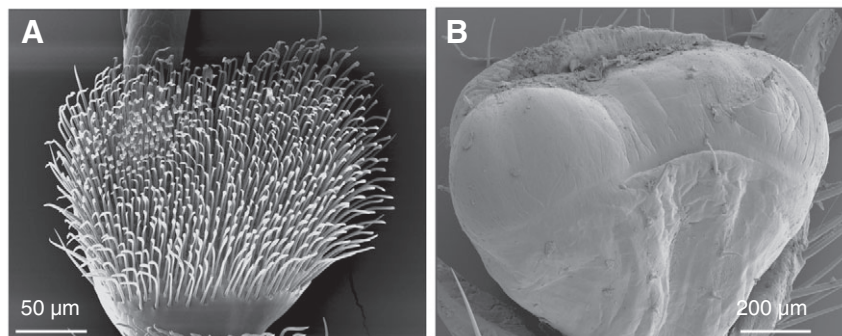
Fig. 1. Scanning electron microscopy images of (A) the distal, fibrillar adhesive pad of the dock beetle (*G. viridula*) and (B) the smooth pad (arolium) of the Indian stick insect (*C. morosus*).

to explain an observed force recovery in synthetically produced adhesive arrays of polypropylene microfibres, an important advance in the development of biomimetic self-cleaning adhesives (Lee and Fearing, 2008).

However, the assumptions of this model may only be plausible on smooth but not rough surfaces, where the real contact area between the particles and the substrate can be very small. This should cause the particles to adhere more strongly to the setae, making self-cleaning unlikely. As an alternative, it was suggested that self-cleaning could occur by small shear movements of the adhesive setae (Persson, 2007), which scratch away particles. In fact, Hansen and Autumn's demonstration of self-cleaning in geckos (Hansen and Autumn, 2005) involved shear movements, and it is unclear whether gecko pads would also self-clean without shear. From their model, Hansen and Autumn predicted that self cleaning in geckos should occur for contaminating particles of all sizes (Hansen and Autumn, 2005). However, it is still unclear whether and how the self-cleaning ability of insect pads, if present, is influenced by particle size; this question will be addressed experimentally in the present study.

So far, self-cleaning has only been studied and modelled for fibrillar adhesive systems. It is unknown whether animals with smooth adhesive systems possess a similar self-cleaning ability. Insects also differ from geckos in that they secrete an adhesive fluid into the contact zone. Does this fluid impede or facilitate self-cleaning? It was recently shown that the fluid secretion does not act to increase adhesion on smooth surfaces but does so only on rough substrates, where it fills in crevices and thus maximises contact area (Drechsler and Federle, 2006). However, the fluid may have additional functions, and it is possible that it is involved in the deposition of contaminating particles by continuously 'washing' the pad.

Here, we investigate the self-cleaning ability of fluid-based adhesive pads of insects by addressing the following questions. (1) Can smooth and hairy pads of insects remove contaminating particles by self-cleaning? (2) Is the self-cleaning ability of smooth and hairy pads different? (3) Does self-cleaning require a shear movement? (4) What is the effect of particle size on self-cleaning?

MATERIALS AND METHODS
Study animals
We tested adult stick insects (Phasmatodea: *Carausius morosus* Brunner; *N*=16) and adult male beetles (Coleoptera: *Gastrophysa viridula* De Geer; *N*=12). Both insects were taken from laboratory colonies kept at 24°C. We measured adhesive and frictional forces for the distal adhesive pads (i.e. the pretarsal arolium of *C. morosus* and the pad on the third tarsal segment in *G. viridula*). For performing force measurements, the insects were restrained and their adhesive pads immobilised. Stick insects were enclosed

in a hollow glass tube, taking advantage of their typical stick-like camouflage position, with their front legs protruding from the open end. The dorsal side of the pre-tarsus of the front leg was attached to a piece of solder wire using dental cement (ESPE Protemp II; 3M, St Paul, MN, USA). Beetles were fastened to a mount using parafilm tape, and their front leg immobilised in Blu-Tack (Bostik, Leicester, UK).

Contamination
To contaminate the pads, polystyrene spheres of nominal diameters 1 μm, 10 μm and 45 μm (Polybead microspheres, Polysciences Inc., Warrington, PA, USA) were used. The actual diameters given by the manufacturer are 0.992±0.026 μm, 9.606±0.763 μm and 43.33±2.23 μm, respectively. A single drop (~5 μl) with 2.6% of solid beads was placed near the corner of a glass coverslip (18 mm × 18 mm × 0.1 mm); the droplet was then freeze-dried for 2 h at –20°C over Silica Gel. This resulted in a circular patch on the glass cover slip (5 mm diameter) densely covered by spheres. Freeze-drying minimised the aggregation of spheres into colloidal crystals along the contact line of the evaporating fluid; the treatment was performed to achieve a dispersed distribution of the particles.

Single-pad force measurements
A schematic diagram of the experimental setup is shown in Fig. 2. Friction and adhesion forces were measured using a two-dimensional bending beam (spring constant 33 Nm^{-1}) equipped for each direction with two 350 Ω foil strain gauges in a half-bridge configuration (1-LY13-3/350; Vishay, Malvern, PA, USA). Adhesion forces alone were measured with a one-dimensional full-bridge bending beam (spring constant 150 Nm^{-1}) equipped with 540 Ω semiconductor strain gauges, affording higher sensitivity (SS-060-033-500PU; Micron Instruments, Simi Valley, CA, USA). The glass cover slip containing the patch with spheres was attached to the distal end of the bending beam and brought into contact with the insect foot. The adhesive contact area was recorded under reflected light using an externally triggered (10 Hz) Redlake PCI 1000 B/W camera (Redlake, Tallahassee, FL, USA) mounted on a Leica MZ16 stereo microscope with coaxial illuminator (Federle and Endlein, 2004). Video analysis was performed with custom-made software using MATLAB (The Mathworks, Natick, MA, USA). Force input signals were amplified (GSV1T8; ME-Systeme, Henningsdorf, Germany) and recorded to a data acquisition board (PCI-6035E; National Instruments, Austin, TX, USA) with a sampling frequency of 1000 Hz. The bending beam was mounted on a computer-controlled three-dimensional positioning stage (M-126PD, C-843; Physik Instrumente, Karlsruhe, Germany). Motor movements, video trigger and force recording were synchronised using a custom-made LABVIEW (National Instruments) program that allowed a 50 Hz feedback control of the normal force.
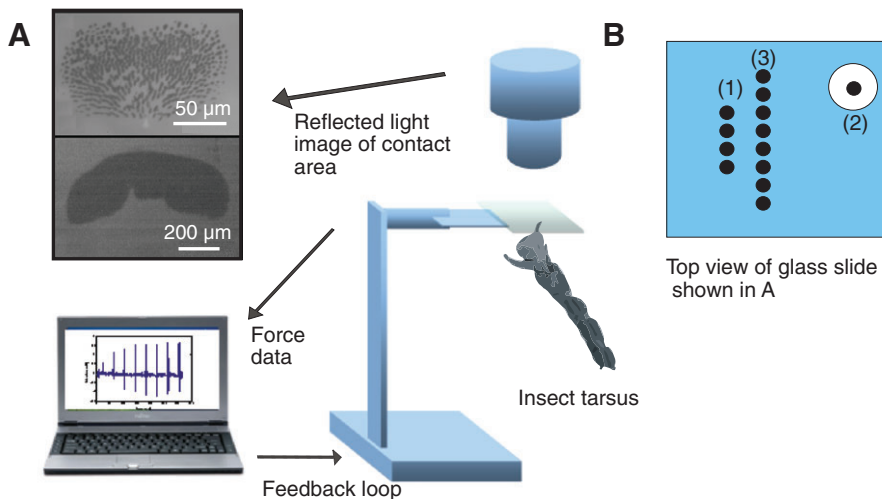
Fig. 2. (A) Experimental setup for recording friction, adhesion and contact area of insect adhesive pads. Contact area images show hairy pad (above) and smooth pad (below). (B) Order and pattern of 'steps' performed on the glass plate to test the effect of contamination and self-cleaning. Four initial steps were followed by a 'contamination step' and eight steps on clean areas of the glass plate.

To measure the attachment forces of pads before and after a contamination event, we performed series of consecutive press-downs and pull-offs ('steps'). Each step was made at a new position on the glass plate. Steps lasted 5s with a feedback-controlled load of 1 mN for the stick insects and 0.3 mN for the beetles (see Bullock et al., 2008); the duration between steps was 20 s. To quantify forces without contamination, we initially performed four pull-offs from the clean glass plate. The pad was then brought in contact with the patch of spheres in the same way as for the other steps. After this contamination event, eight consecutive pull-offs were performed to assess the effect of the contamination and the extent of recovery in adhesion and friction forces. The order and location of 'steps' on the glass plate are shown schematically in Fig. 2B.

To examine whether self-cleaning requires a shear movement of the pad, we performed experiments with two different types of consecutive steps: (1) without shear – the movement consisted only of a perpendicular approach and pull-off (velocity $0.5\,\mathrm{mm\,s^{-1}}$); (2) with shear – approach and pull-off were performed as before but, after the initial approach phase and before the pull-off, the pad was dragged horizontally over a distance of 0.5 mm (velocity $0.5\,\mathrm{mm\,s^{-1}}$). The shear movement was performed in the proximal direction, corresponding to a pull of the pad towards the insect's body. A pull in this direction is observed during the attachment and stance phase in freely running insects; it brings the adhesive pad structures in contact and maximises their adhesive contact area (for *C. morosus* and *G. viridula*) (see Bullock et al., 2008).

Count of deposited spheres

After each series of consecutive force measurements, we took images of the footprints on the glass plate using a 12-bit monochrome digital camera (QIC-FM12; QImaging) mounted on a Leica DMR-HC (Leica Microsystems, Wetzlar, Germany) upright microscope. For the smaller 1 μm and 10 μm spheres, we automated the counting using a custom-made MATLAB script. Spheres were visible as black objects on a bright background, and a greyscale threshold was applied to obtain the total area of the image occupied by beads. After quantifying the area equivalent to a single bead, the total number of spheres in a footprint image was calculated. If beads were deposited on top of each other in layers, each stacked layer was captured at a different focal plane, and the spheres in them were counted manually.

Statistics

To test the effect of contamination, adhesion and friction forces were converted to a percentage of the force before contamination in order to reduce size-related variation between insects. For other analyses comparing the efficiency of self-cleaning between bead sizes and between insects, the measured force, F_n (adhesion or friction), of the n-th step was converted into a recovery index, $R_n=(F_n-F_{\mathrm{contaminated}})/(F_{\mathrm{clean}}-F_{\mathrm{contaminated}})$, which is identical to the recovery index used by Hansen and Autumn (Hansen and Autumn, 2005). Page's L tests (Page, 1963) were performed to test the hypothesis that R_n increases over consecutive steps. Pearson's correlation was used to test whether adhesion force was correlated with the number of deposited spheres.

RESULTS
Effect of contamination

Contamination strongly reduced adhesive and frictional forces in both insects. Forces for the first step after contamination were always smaller (t-tests for both insects and all three bead sizes, $P<0.001$) and decreased by 50–90%. The effect of contamination on adhesion and friction is a result of the variation in adhesive contact area. Contamination strongly reduced both force and adhesive contact area (Fig. 3), such that adhesive stress (force per unit contact area) did not change over the course of each trial (10 μm beads, repeated-measures ANOVA comparing 1st step before, as well as 1st and 8th step after contamination: stick insects, $F_{2,6}=3.65$, $P=0.069$; beetles, $F_{2,10}=1.53$, $P=0.248$). Similarly, shear stresses also showed no significant changes during each trial (stick insects, $F_{2,6}=1.83$, $P=0.214$; beetles, $F_{2,10}=1.74$, $P=0.208$). Thus, the loss of attachment forces after contamination is not based on a decrease of adhesive or shear stress but on the loss of contact area.

Pads of both insects exhibited a clear recovery of forces by self-cleaning in subsequent steps, but this recovery was influenced by the presence or absence of a shear movement before the pull-off.

Can insect adhesive pads self-clean?
Pull-offs without shear

Pull-offs without a preceding shear movement were performed only with the 10 μm-diameter beads. For the smooth pads of stick insects, we did not find any evidence of a recovery of adhesion forces over consecutive pull-offs (Page's L test, $L_{8,6}=910$, $P=0.946$). However,
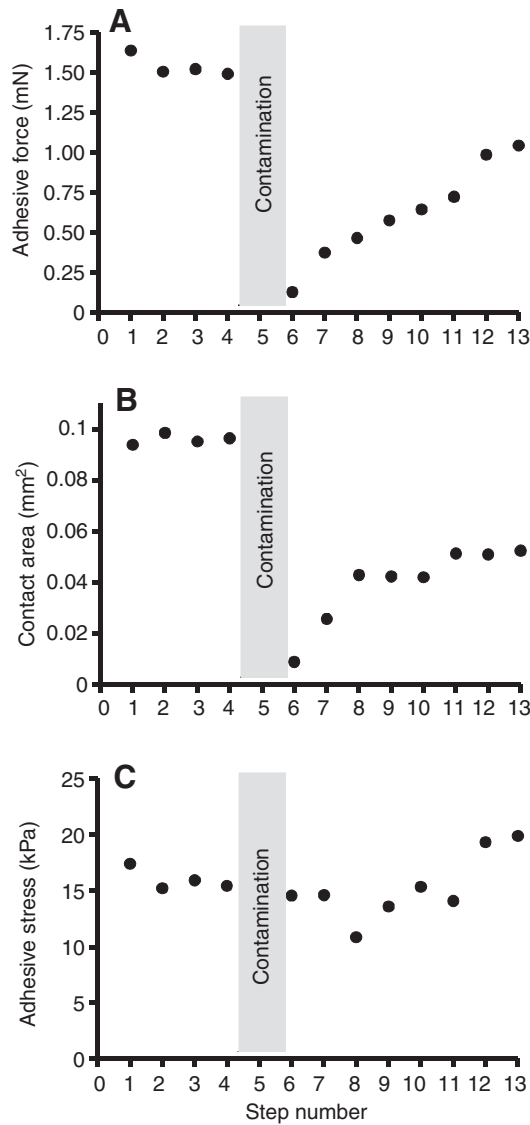
Fig. 3. (A) Adhesive force, (B) contact area and (C) adhesive stress (adhesive force per unit contact area) for a stick insect pad contaminated with 10 μm beads. The initial four steps represent values for a clean uncontaminated pad. The fifth step is used to contaminate the pad with beads. Steps 6–13 show eight steps after contamination, increase in adhesive force relates to increase in contact area, and adhesive stress remains unchanged.

significant recovery of adhesion, friction and contact area over eight steps. Forces recovered by self-cleaning in both stick insects and beetles for all three tested bead sizes (Page's *L* test, *P*<0.05 for all insects and bead sizes).

In beetles, the shear movement did not appear to increase the efficiency of self-cleaning; there was no significant difference between the corresponding recovery slopes of adhesion, with or without a shear movement (10 μm beads; $F_{1,12}=0.737$, $P=0.407$).

Deposition of particles

Examination of the footprints left on the glass plate revealed that many spheres were deposited with every step, together with liquid and solid footprint material. Figs 4 and 5 show that spheres were deposited throughout the entire slide so that the effect of the shear movement was to 'wipe' spheres off the pad. This pattern was observed both in beetles and stick insects. The number of spheres per footprint was highest in the first step and decreased in consecutive slides, correlating to the increase in friction and adhesion (10 μm beads; stick insects, adhesion $r=-0.82$, $P=0.012$, friction $r=-0.89$, $P=0.003$; beetles, adhesion $r=-0.88$, $P=0.003$, friction $r=-0.95$, $P<0.001$).

Effect of sphere size on self-cleaning ability

To test the effect of bead size on self-cleaning ability, we performed linear regressions of the recovery index for the steps after contamination in each insect and compared the slope (rate of recovery). Steps were included until the recovery index was no longer significantly different from 1, as judged by a one-tailed *t*-test. Later steps were not included in the regression, as the forces had almost completely recovered.

For stick insects, the rate of recovery did not significantly depend on bead size (Table 1). By contrast, bead size had a striking effect on the rate of recovery in beetles (Table 1). While forces recovered quickly for the 1 μm and the 45 μm spheres, recovery was much weaker and slower for pads contaminated with 10 μm-diameter spheres, which was significantly different from the other bead sizes (SNK *post-hoc* tests, *P*<0.05 for both comparisons).

To further characterise the beetle pads' poor ability to self-clean for the 10 μm beads, we performed a longer series of 30 consecutive steps in both *C. morosus* and *G. viridula*. Fig. 6 shows that while adhesion and friction for the stick insect pad completely recovered within ~15 steps, the forces of the beetle pads did not return to their

the hairy pads of beetles tested under the same conditions exhibited a 50% recovery of adhesion, by the 8th step after contamination, providing evidence for self-cleaning (Page's *L* test, $L_{8,6}=1109$, *P*<0.001).

Pull-offs with a shear movement

When the experimental 'steps' included a proximal shear movement (corresponding to a pull of the foot towards the insect's body), not only the hairy pads of beetles but also the smooth pads showed a

Table 1. Rate of recovery (regression slopes from Fig. 8) after contamination with different-sized beads in smooth pads of stick insects

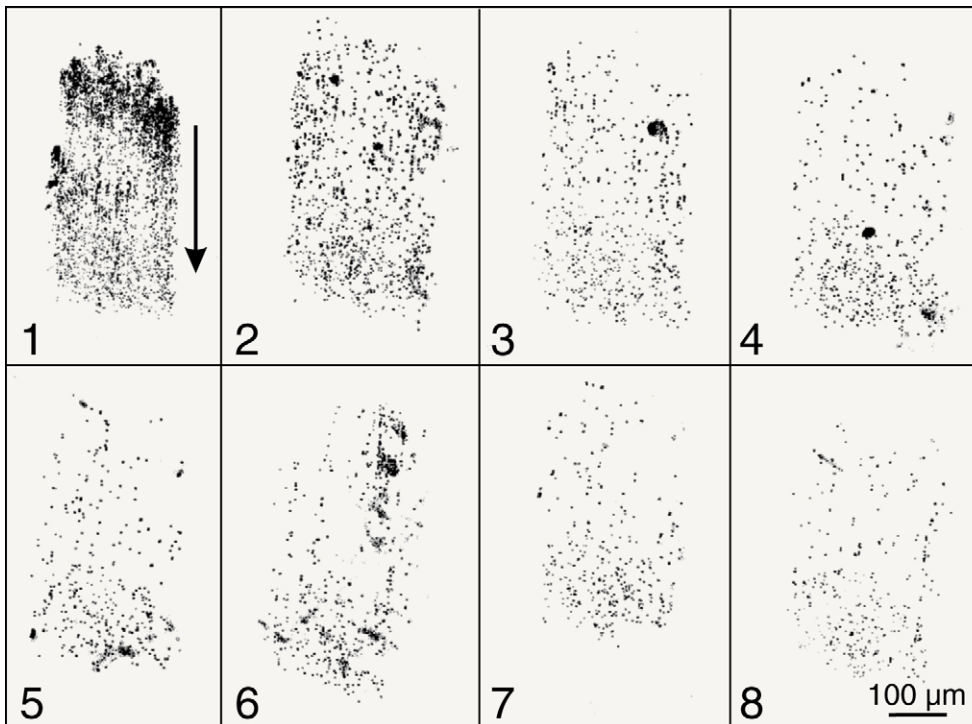|		Friction slope comparison			Adhesion slope comparison
C. morosus					
	Regression	d.f.=2, MS=0.001		Regression	d.f.=2, MS=0.011
	Error	d.f.=18, MS=0.008		Error	d.f.=18, MS=0.004
		$F_{2,18}=0.123$, $P=0.885$			$F_{2,18}=2.736$, $P=0.092$
G. viridula					
	Regression	d.f.=2, MS=0.264		Regression	d.f.=2, MS=0.092
	Error	d.f.=10, MS=0.017		Error	d.f.=13, MS=0.008
		$F_{2,10}=15.6$, $P<0.001$			$F_{2,13}=11.1$, $P=0.002$

Fig. 4. 1 μm spheres deposited by *G. viridula* in eight consecutive footprints after contamination. The steps include a 0.5 mm proximal sliding movement. Arrow shows direction of pad movement.

initial values even over 30 steps. The forces exponentially approached an asymptote of ~50% force, indicating that little or no further recovery would occur even for larger numbers of consecutive steps.

To understand the underlying mechanism of this effect, we imaged pads after eight consecutive steps using SEM (Fig. 7). It can be seen that the 45 μm spheres are too large to fit between setae, and they are therefore rapidly removed by self-cleaning. By contrast, many 1 μm and 10 μm beads are still adhering to the setae after eight steps. While the 1 μm beads adhere loosely to the seta stalks and leave the setae free to move, the 10 μm spheres make contact with several setae simultaneously and thus likely immobilise them. The 10 μm spheres become trapped in between setae, because their diameter approximately corresponds to the inter-seta distance, which for dock beetles is 10.19±1.16 μm (Fig. 1A).

Comparison of self-cleaning between smooth and hairy pads

The initial reduction of adhesion and friction forces due to contamination was not significantly different between smooth and hairy pads for any bead size (*t*-tests, *P*>0.05 for all bead sizes). However, the rate of force recovery after contamination differed significantly between beetles and stick insects (Table 2). The beetles' pads recovered more than two times faster when contaminated with 45 μm and 1 μm beads, but no difference and even a trend towards slower recovery in the beetles was found for the 10 μm beads (Fig. 8, Table 2).

Table 2. Comparison of the rate of recovery (regression slopes from Fig. 8) between smooth and hairy pads (of *C. morosus* and *G. viridula*) for three different bead sizes

|		Friction				Adhesion			
1 μm	Rate of recovery	*C. morosus*: 0.067 *G. viridula*: 0.193				*C. morosus*: 0.051 *G. viridula*: 0.113			
		d.f.	MS	*F*	*P*	d.f.	MS	*F*	*P*
	Regression	1	0.129	48.51	0.001	1	0.081	19.7	0.001
	Residual	9	0.003			12	0.004		
10 μm	Rate of recovery	*C. morosus*: 0.069 *G. viridula*: 0.047				*C. morosus*: 0.072 *G. viridula*: 0.052			
		d.f.	MS	*F*	*P*	d.f.	MS	*F*	*P*
	Regression	1	0.010	0.896	0.363	1	0.009	1.55	0.236
	Residual	12	0.011			12	0.006		
45 μm	Rate of recovery	*C. morosus*: 0.076 *G. viridula*: 0.504				*C. morosus*: 0.083 *G. viridula*: 0.314			
		d.f.	MS	*F*	*P*	d.f.	MS	*F*	*P*
	Regression	1	0.349	15.93	0.005	1	0.102	11.7	0.011
	Residual	7	0.022			7	0.009		
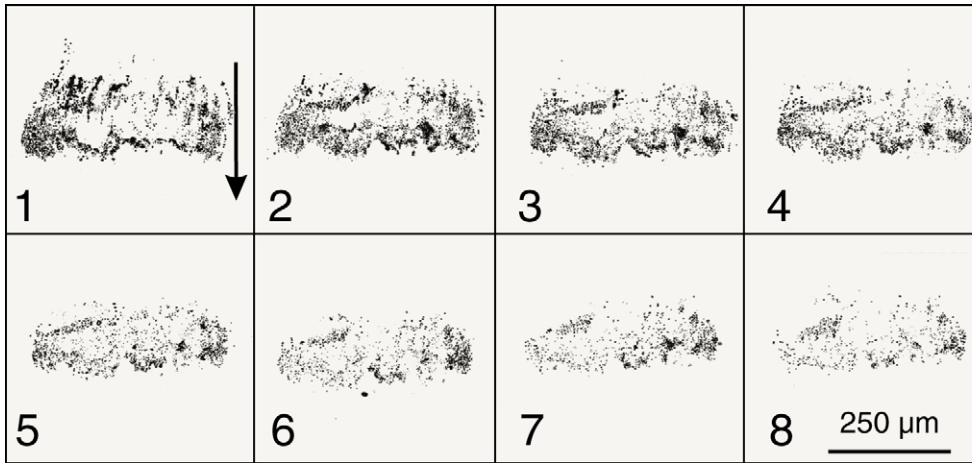
Fig. 5. 1 μm spheres deposited by *C. morosus*, conditions as for Fig. 4.

DISCUSSION
Self-cleaning in insect adhesive systems

This study has confirmed that insect adhesive pads are able to self-clean with repeated steps. The ability is present both in insects with smooth and hairy adhesive organs. Adhesion and friction forces often returned to 100% of the force before contamination within only a few steps. The insects' self-cleaning ability is comparable to that previously observed for dry gecko adhesives (Hansen and Autumn, 2005) and may even exceed it in terms of efficiency. Under similar experimental conditions, whole digits of geckos recovered 35.7% of the lost shear force (5 μm diameter particles) (Hansen and Autumn, 2005) over eight steps, whereas smooth stick insect pads recovered 53.4% and hairy beetle pads 98.4% (1 μm particles).

Mechanisms for self-cleaning

Our results show that the effects of both contamination and recovery are based on changes of adhesive contact area. Neither shear nor adhesive stress increased for recovering pads (nor did they decrease following contamination). Instead, the increase in forces seen with each step after contamination was matched by an increase in contact area.

Effect of shear

Smooth and hairy adhesive pads of insects were able to self-clean over consecutive steps when these included a shear movement. It is likely that sliding movements help to dislodge spheres from the useful contact zone. Previous studies (Hui et al., 2006; Persson, 2007) have suggested that shear movements of fibrillar pads are important, in particular the cyclical pulling and pushing movements that control attachment and detachment. Spheres may be transported to the edge of the contact zone by scratching, sliding or rolling and may be removed by further sliding or when the seta or pad detaches from the surface (Persson, 2007).
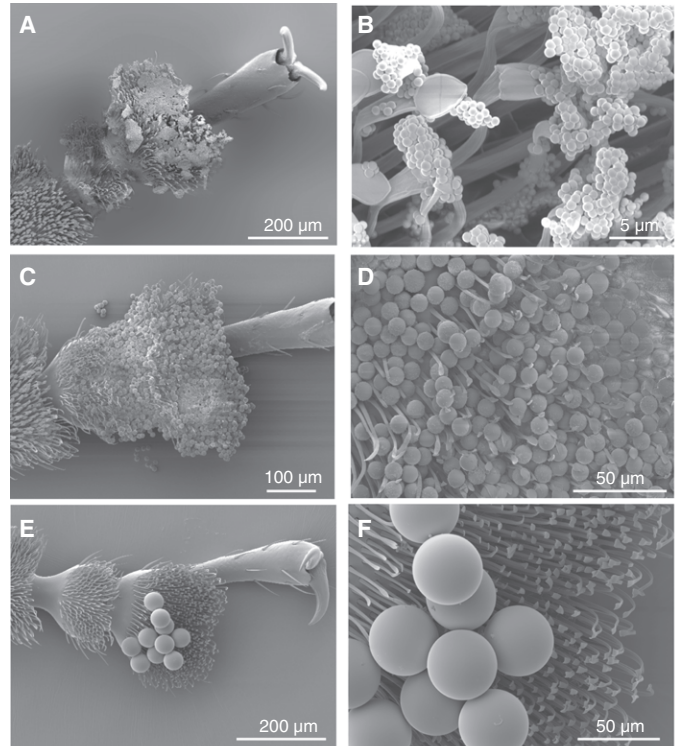
Fig. 7. Scanning electron microscopy images of adhesive pads of *G. viridula* after contamination with beads of different sizes, followed by eight consecutive steps to allow self-cleaning. (A,B) 1 μm-diameter beads; (C,D) 10 μm-diameter beads; (E,F) 45 μm-diameter beads. As pads contaminated with 45 μm beads did not contain any beads after self-cleaning, E and F show a freshly contaminated pad.
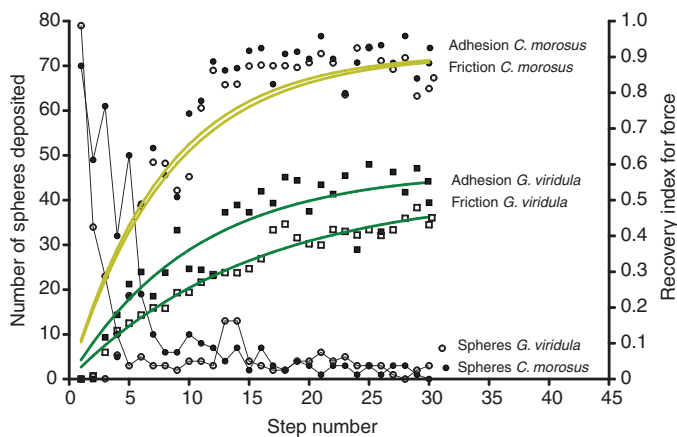

Fig. 6. Recovery of adhesion and friction over 30 steps in stick insects (*C. morosus*) and beetles (*G. viridula*) when contaminated with 10 μm-diameter beads. The lines are exponential data fits of the form $R_n=R_\infty(1-e^{-kn})$, where n is the step number after contamination and R_∞ is the value to which the recovery index may converge over an infinite number of steps, and k is the exponential decay constant.

The smooth pads of stick insects exhibited self-cleaning only in the presence of a shear movement. By contrast, forces for the hairy pads of beetles were able to recover even when steps consisted only of pull-offs. This suggests that beetles might self-clean by a mechanism similar to the one proposed for dry gecko setae by Hansen and Autumn (Hansen and Autumn, 2005). Hansen and Autumn suggested that self-cleaning results from the greater attraction of particles to the surface than to the tips of the setae, resulting from the contact geometry, stiffness and low surface energy of fibrillar adhesive systems. Self-cleaning in the beetles' adhesive pads may be further enhanced by microscale shear movements of the setae. In a hairy adhesive system, contaminating particles need to be moved by only a very small distance to reach the edge of a seta's adhesive contact zone. When pressed onto the substrate, the tip of a seta may simply push particles aside, thereby moving them to a place where they adhere more strongly to the substrate and less to the seta. By contrast, a soft, smooth pad pressed onto the substrate will deform and enclose a contaminating particle, leaving the particle within the contact zone and with a stronger adhesion to the pad than to the surface.

Role of adhesive fluid

The presence of adhesive fluid differentiates the insects' 'wet' adhesive systems from that of the gecko. The greater efficiency of self-cleaning found in this study suggests that the fluid secretion facilitates the deposition of contaminating particles. In fact, many particles are found in fluid droplets left behind by insect pads after contamination. As footprint secretion is produced and deposited continuously with every adhesive pad surface contact, the fluid may effectively 'wash' particles off the pad.

Effect of particle size

Our findings demonstrate a significant effect of particle size on the self-cleaning ability of the hairy system of the beetle but not on the smooth system of the stick insect. While smooth pads appeared to work equally well for all sphere sizes, hairy pads showed a significantly slower recovery for 10 μm size beads when compared with smaller or larger bead sizes. Even in longer trials of 30 repeated steps, beetle pads were unable to fully recover when contaminated by particles of this size. One probable reason for this may be that the 10 μm particles become trapped in between setae, because their diameter approximately corresponds to the inter-seta distance. This condition not only makes the removal of particles very difficult but it also immobilises setae and restricts their lateral movements. As discussed above, such microscale shear movements may be important for the recovery of fibrillar adhesives in that they allow setae to push particles aside.

Particles with diameters larger than the inter-seta distance, such as the 45 μm spheres in our study, cannot or only partly penetrate the setal arrays. Such particles may therefore have a relatively smaller contact area with the setae, resulting in faster removal by self-cleaning. This is the situation investigated by Hansen and Autumn (Hansen and Autumn, 2005); the spatula density of 3.79 μm^{-2} reported for the tokay gecko corresponds to an inter-spatula distance of ~0.55 μm, which is considerably less than the 5-μm diameter of the tested particles.
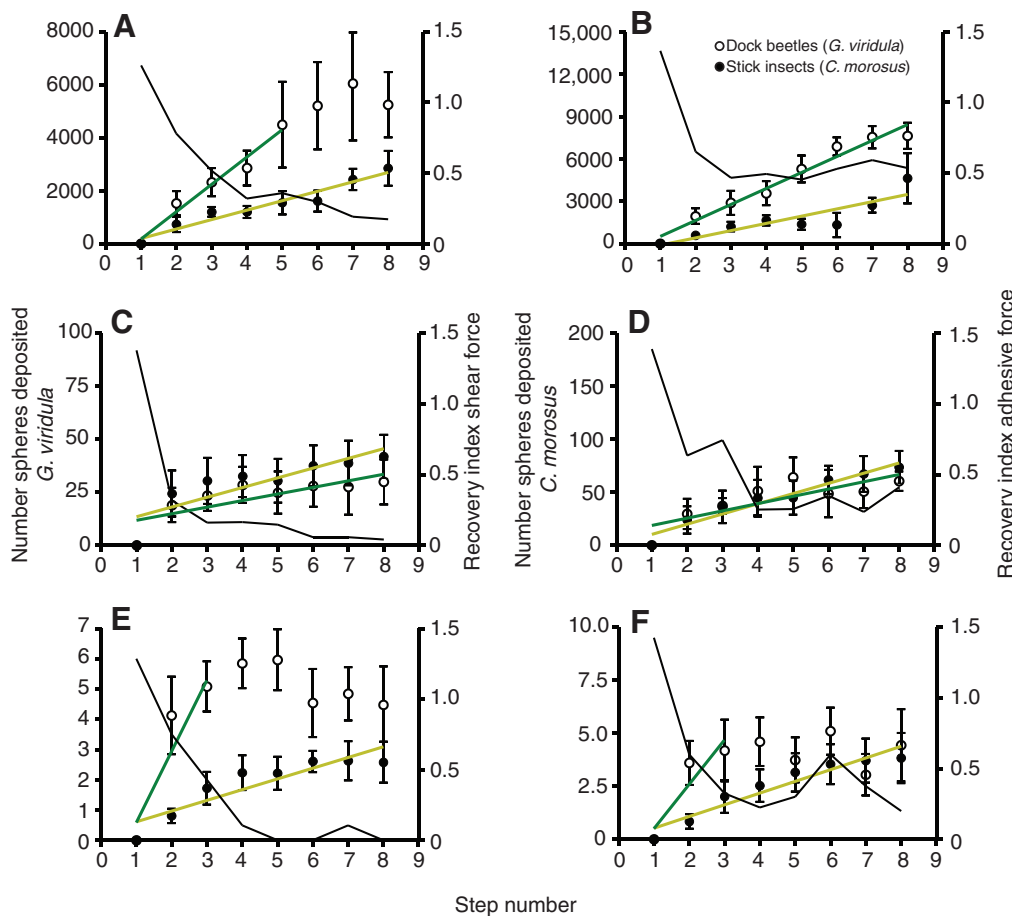

Fig. 8. Comparison of the rate of adhesion and friction force recovery after contamination of smooth pads (filled circles) and hairy pads (open circles) for different particle sizes. (A,B) 1 μm beads; (C,D) 10 μm beads; (E,F) 45 μm beads. Lines show least-square regression fits for all steps where the forces were significantly different from 1 using a one-tailed t-test. Error bars represent s.e.m., N=6 for all points.

The dependence of self-cleaning ability on particle size is unlikely to be a phenomenon restricted to beetles but may also occur in hairy pads of other animals. However, self-cleaning ability in diverse animals may be influenced by the very different seta dimensions (Peattie and Full, 2007). Specifically, we predict that self-cleaning may be slowest for particles matching the inter-seta distance and fastest for particles larger than it.

It is additionally important to note that all contaminating particles used in this study were smooth and of a perfect spherical shape. While standardised spheres allow for a test of the effect of particle size, 'natural' particles (such as stone or dust fragments) are rarely smooth and spherical, leading to a reduced area of contact between the particles and the substrate. In general, surface roughness and surface chemistry (of both substrate and particles) are likely to have important implications on self-cleaning performance and need to be investigated in future work.

Self-cleaning performance of smooth *vs* hairy systems

Hairy adhesive pads have arisen frequently throughout the animal kingdom. Several predictions have been proposed as to their possible benefits, including a superior self-cleaning ability (Federle, 2006; Hansen and Autumn, 2005). In a previous study comparing smooth and hairy pads, we found similar adhesion and friction stresses in both pads (Bullock et al., 2008). The results presented here thus provide the first direct evidence for a superior performance of hairy systems. Hairy pads of beetles not only outperformed the smooth pads of stick insects in their ability to self-clean without a shear movement but they also recovered more rapidly from contamination. For 1 and 45 μm particles, beetle pads recovered 2–10 times faster than the smooth pads of stick insects. In fact, despite the reduced rate of recovery for forces of beetle pads when contaminated with 10 μm beads, recovery rate was still not significantly lower than that of the stick insects. This suggests that even the slowest rates of recovery for hairy pads are not much worse than rates seen for smooth pads. The excellent ability of hairy pads to recover from contamination may be an important factor explaining the widespread appearance of hairy pad morphology across different taxa.

We have discussed above possible reasons why the fibrillar design might allow a more efficient self-cleaning. However, the detailed mechanisms of self-cleaning in animal adhesive pads are still not fully understood, and further experimental and theoretical work is needed to clarify them.

Self-cleaning ability is an important property of biological adhesive systems and will be an important criterion for the design of bio-inspired adhesives. Scotch tape is a prime example of an adhesive that is not self-cleaning and consequently it is of no use after several applications. Efforts are underway to manufacture a fibrillar adhesive that is effective after more than one use (Gorb et al., 2007; Lee and Fearing, 2008; Sethi et al., 2008). The hard polymer adhesive developed by Lee and Fearing (Lee and Fearing, 2008) demonstrated the first example of self-cleaning in an artificial fibrillar adhesive. However, despite these advances, the currently existing technology still falls vastly short of the impressive self-cleaning ability of insects.

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