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ORIGINAL ARTICLE

Physiological Entomology: How Insects Work - Linking Genotype to Phenotype

Surface wettability affects attachment of male bed bugs *Cimex lectularius* to rough Perspex substrates

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Abstract

Insects attach to various surfaces that differ, among others, in roughness and wettability. Identifying surface characteristics that allow or prevent insects from attaching are an important research avenue of pest control. Here we take an experimental approach to analyse the attachment of common bed bugs, *Cimex lectularius* Linnaeus (1758), to Perspex (PMMA) substrates. We construct a reliable centrifuge device that allows the measurement of attachment forces at substrate roughnesses, Ra, between 0.02 and 1.3 μm and at two wettabilities. Our results suggest that bed bug attachment to surfaces is minimal at a substrate roughness of 0.2 and 0.4 μm on normal PMMA, where the lowest attachment force was 0.8 mN and the safety factor 15. At lower and higher roughness, attachment forces were higher and the safety factor increased to a maximum of 133. On PMMA that was made superhydrophobic by spray-coating, attachment was lowest (0.2 mN) at the lowest roughness and continuously increased with increasing roughness, reaching 2.5 mN and a safety factor of 46. For every roughness, attachment forces were lower on superhydrophobic than on normal PMMA. This knowledge may inspire the development of repelling substrates for bed bug control.

KEYWORDS
attachment, centrifugal force test, *Cimex lectularius*, PMMA, roughness, wettability

INTRODUCTION

Bed bugs are important, blood-sucking human parasites. One promising research avenue for their control is to explore surfaces to which bed bugs cannot adhere. However, bed bugs attach to a wide range of surfaces. For a bloodmeal, they temporarily attach to, and pierce through, the skin. Between the blood meals, they live in refugia that can be several metres away from the host on surfaces that can include wood, concrete walls, textiles or wallpaper. In general, attachment is a non-specific term that comprises friction, adhesion and behavioural–physiological effects. Previous research on the ability of bed bugs to adhere to various substrates (Baker & Goddard, 2018; Hinson et al., 2017; Hottel et al., 2015; Kim et al., 2017; Reinhardt et al., 2019; Walpole, 1987; Wigglesworth, 1938) was mainly related to specific attachment organs, the so-called fossula spongiosa. In adult bed bugs, the fossula spongiosa consist of spatulate tenent setae on the basal tibiae that serve as hairy adhesive pads (Gorb, 2001). The attachment organs and the resulting attachment forces on various surfaces of different hydrophobicity differed between males, females and nymphs (Reinhardt et al., 2019). Male bed bugs, despite being smaller than females, attach stronger to surfaces, holding up to 303-fold their own body weight. This sexual difference in attachment forces and the larger dimension and number of setal spatulae per unit area in males suggested the attachment system functions in the context of mating. For example, when males attach to females, strong adherence might prevent them being dislodged by the female or by rival males (Reinhardt et al., 2019). Specifically, the tendency of males to attach slightly better to hydrophobic than hydrophilic smooth surfaces was used to suggest the attachment may be related to the smooth, hydrophobic female integument surface, rather than more rough substrates (Reinhardt et al., 2019).

However, the attachment system does function in circumstances other than reproduction. For example, bed bugs also possess paired curved claws at the distal tarsi (Figure 1). These prominent chitinous structures at the end of the tarsi serve to attach to bare skin, to skin folds and to hairs when bed bugs walk on human skin, or attach during feeding (Reinhardt et al., 2019). However, both mating (taking less than 5 min around five times a week—Reinhardt et al., 2011) and feeding (lasting 20 min less than twice a week (Reinhardt et al., 2010) are relatively short periods in a bed bug's lifetime). Bed bugs spend most of their lifetime in the refugia where surfaces include wood, cloth, brick or wall paper. Exploring control options by designing surfaces to which bed bugs cannot adhere, therefore, need to include surfaces of a large range of roughness and wettability.

In insects, surface roughness and wettability have previously been shown to affect the attachment in defined test substrates and model species, such as chrysomelid leaf beetles (e.g., Bullock & Federle, 2011; Eimüller et al., 2008; Gorb & Gorb, 2002, 2009; Grohmann et al., 2014; Hosoda & Gorb, 2011; Peressadko & Gorb, 2004; Stork, 1980; Voigt et al., 2008, 2012; Voigt, de Souza, et al., 2019; Zhou et al., 2014; Zurek et al., 2017), staphylinid rove beetles (Betz et al. 2002), tortricid codling moths (Al Bitar et al., 2010) and pentatomid bugs (Voigt, Perez Goodwyn, et al., 2019). These

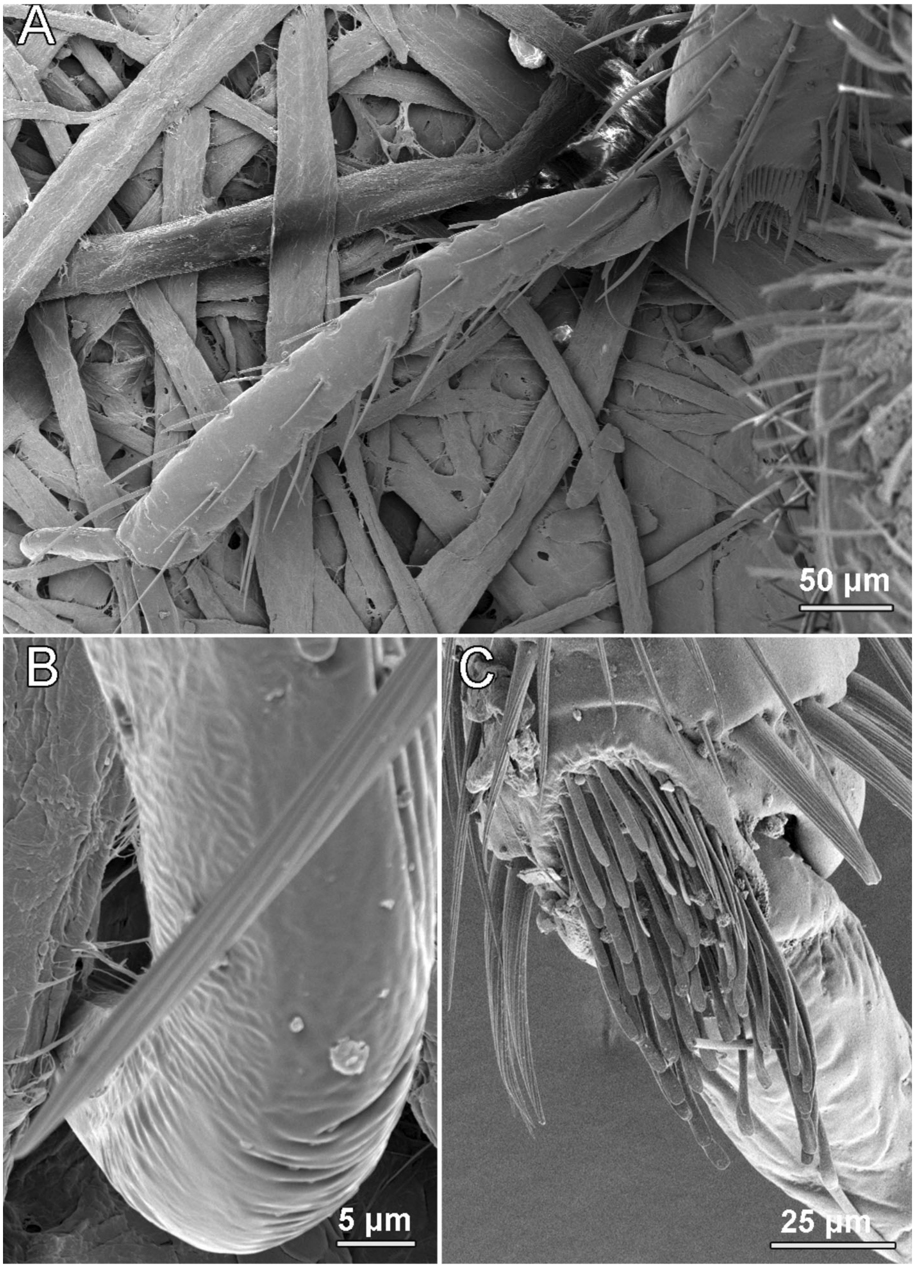

FIGURE 1 Cryo-SEM images of the attachment devices on the leg of adult male *Cimex lectularius*. (a). Basal tibia and tarsus in contact with a rough substrate (filter paper fibres). (b). Detail of the curved claw, where the tip is interlocked with a filter paper fibre. (c). Detail of tenent setae at the ventral tibio-tarsal joint. See Reinhardt et al. (2019) for further details.

studies generally conclude that spatula-shaped thin tips of setae provide an optimum substrate adaptability due to the low bending stiffness of the plate-like extension of the setae (terminal plate) (Eimüller et al., 2008; Gorb et al., 2012; Gorb & Varenberg, 2007; Kim & Varenberg, 2017; Persson & Gorb, 2003; Varenberg et al., 2010). Such setae are present in *Cimex lectularius* Linnaeus (1758) (Reinhardt et al., 2019). In addition, smaller gaps between the spatula-shaped tips of the setae and substrate irregularities are filled with tarsal fluid in insects, increasing the effective contact surface (Dirks et al., 2010; Dirks & Federle, 2011; Gorb, 1998), including in *C. lectularius* (Reinhardt et al., 2019).

Here we use an experimental approach to examine the attachment ability of bed bugs. This includes the construction of a reliable centrifuge device that is particularly suitable for testing small arthropod species on various substrates, such as differently roughened and spray-coated, superhydrophobic poly(methyl methacrylate) (PMMA, i.e., Perspex; $(C_5H_8O_2)_n$; Ma et al., 2007, Jaffer et al., 2021). Our results suggest that bed bug attachment to surfaces is minimal at substrate roughness of 0.2 and 0.4 μm.

MATERIALS AND METHODS

Study insects

Cimex lectularius L. (Heteroptera, Cimicidae) individuals have been originally collected in London (UK) and been kept in the Animal and Plant Sciences Laboratory at the University of Sheffield for more than 5 years at the time of the study, and before that for ca. 40 years in a laboratory in London. Bed bugs were mass-reared in vials in incubators at 25°C and 70% rH (for details see Reinhardt et al., 2003). From the large, outbred laboratory population of more than 1000 individuals, we obtained adult males. Males were isolated for a week to ensure their blood reserves in the gut have been used up. We used males as they showed larger attachment force, and lower variability, than females and nymphs (Reinhardt et al., 2019).

Substrates

We used Perspex, that is, (poly)methyl methacrylate (PMMA) discs (ME303121/2; Goodfellow Cambridge Ltd., Huntingdon, UK) as test substrates, allowing us to compare our results with previous studies using this substrate (Federle & Holldobler, 2000; Stork, 1980). Perspex surfaces are smooth and glossy and have a roughness of Ra = 0.023 ± 0.009 μm (Goodfellow Cambridge Ltd. 2024, personal communication), a critical surface tension at 20°C of 39 m Nm^{-1} (Federle et al., 2002; Federle & Holldobler, 2000) and a water contact angle of 68° (Ma et al., 2007). Such a surface roughness is ideal to evaluate the attachment exclusive provided by adhesive setae because the roughness is too small for insects to use their claws to interlock with the surface (Federle et al., 2002; Federle & Holldobler, 2000). The setal attachment is essential for conclusions in the present study.

By sanding PMMA discs with abrasive paper (CXS Tools, Colchester Essex, UK) of five different grades, we generated a roughness gradient (Table 1). The actual roughness for every paper grade was measured using a Talysurf instrument (Taylor Hobson Ltd., Leicester, Leicestershire, UK) (Table 1). To analyse the effect of wettability, we created a superhydrophobic surface, that is, a surface with a contact angle of water >150° by treating the surface of every roughness with a superhydrophobic spray coating (Rain Repel goggles & visors; Storm Care Solutions Ltd., Alfreton, Derbyshire, UK). This spray is commonly used for motorcyclist's visors and causes the water to quickly run off to prevent impairing their vision. It was applied to the surface of the rough Perspex disc using a soft lens cloth saturated in the substance.

Centrifugal force tests

Centrifugal setups are established tests to determine attachment forces of insects (Brainerd, 1994; Dixon et al., 1990; Federle & Holldobler, 2000; Gorb et al., 2001a, 2001b). To carry out our experiment, we designed a custom-made device incorporating a laser, phototransistor and reed switch centrifugal method for measuring the attachment force (Figure 2; Supplementary Methods, Figures S1–S5). The device was operated via the software Labview (National Instruments (U.K.) Corp., Theale, Reading, UK) and we generated a setup that allowed quick and easy testing of bed bugs, and the automated recording of results (McKeever, 2010; Supplementary Methods, Figures S1–S5).

Every bed bug was weighed (analytical balance; Scales World, Kettering, Northants, UK) immediately prior to testing. It was then placed onto the disc, more than 10 mm from the centre of the circle (Figure 2), to ensure the radius, *R* at which the insect was positioned was calculated as this is the distance the laser and phototransistor are positioned from the centre. We had to ignore the direction the bed bug was facing. Some insects responded by 'freezing' once on the disc (see Results), but they could generally move, even at higher rpm

TABLE 1 Grades of abrasive papers applied to the Perspex (PMMA) surfaces to generate a range of surface roughness in the study of the attachment of bed bugs *Cimex lectularius*.

Abrasive paper	Ra [μm]	Rq [μm]	Rz [μm]
-	0.02 ± 0.009[a]		
P1000	0.16 ± 0.048	0.19 ± 0.214	0.58 ± 0.186
P800	0.21 ± 0.044	0.26 ± 0.580	1.37 ± 0.165
P600	0.40 ± 0.071	0.52 ± 1.161	2.77 ± 0.210
P400	0.60 ± 0.118	0.75 ± 1.571	3.78 ± 0.358
P180	1.29 ± 0.332	1.59 ± 2.973	7.15 ± 1.168

Note: Three roughness parameters were measured. Ra, the arithmetic average of profile height deviations from the mean line, Rq, the root mean square average of profile height deviations from the mean line, and Rz, the maximum peak-to-valley height of the profile, within a single sampling length. Substrate roughness was measured after roughening treatment. Values are means ± sd, $n = 10$.
[a]Manufacturer's data.

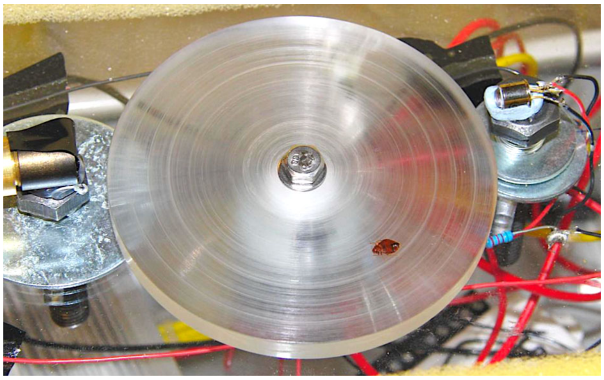

FIGURE 2 The centrifuge experimental apparatus. A bed bug male (♂) is visible on the top of the rotating Perspex (PMMA) disc (arrow: Rotation direction). See Supplementary Methods and Figures S1–S5 for a detailed description.

and so would change the initial position. Each of the 10 males examined were tested on all PMMA surfaces at 22–23°C and 45% relative humidity. Each bed bug was tested five times consecutively on each surface, but there were at least 24 h between each surface testing. Any dust or residue from previous testing or from the environment on the PMMA discs was removed by saturating a lens cloth in methanol (99.85%; Chemiphase International Ltd., Burscough, Lancashire, UK) and wiping the disc clean. Methanol cleans the disc well but also rapidly evaporates, avoiding any adverse effects on the bed bugs. To reduce the impact of trials where the insects did not attach, and the impact of their position on the disc, we used the maximum force of five attachment trials, rather than the mean. In total, 500 individual tests were carried out and statistically evaluated using the SigmaPlot 12.0 software (Systat Software, Inc.).

With the start of the programme, the disc started to rotate. There was an initial jump in speed that sometimes caused the bed bugs to adopt a 'freezing' position. The disc then constantly accelerated until the bed bug was no longer able to adhere. The maximum speed achieved was approximately 1600 rpm. The radius, *r*, of the position of the insect was recorded at the point of release. The radius, together with the rotational speed (number of rotations per unit time), and the mass, *m*, of the bed bug allowed the calculation of the force that is required for it to be displaced from the disc (attachment force *F*). *F* was determined from the angular velocity, ω (the rate of change of angular displacement per unit of time), at which the bug was detached from the disc, its mass, *m* and the radius ($F = m\,r\,\omega^2$). On the centrifuge, the bed bug is also subject to aerodynamic drag that opposes its attachment force. The drag force was calculated as 0.0179 mN (Supplementary Methods), that is, 0.31% of the maximum attachment force generated by an individual bed bug (5.74 mN). We, therefore, did not consider drag in our calculations.

RESULTS

Roughness, Ra, averaged between 0.1554 and 1.286 µm (Table 1). The body mass of unfed males averaged 5.2 ± 1.04 mg ($n = 10$). The mean claw tip diameter was 1.7 ± 0.57 µm ($n = 6$) (Figure 1). Overall, attachment forces varied between 0.0254 and 5.739 mN (Figure 3; Table S1). The relationship between roughness and attachment force on PMMA was non-linear. For non-spray-coated surfaces, the attachment force showed a clear local minimum (Figure 2, Table 2) around an average roughness (Ra) of 0.2–0.4 µm. When roughness increased from there, maximum attachment forces also increased: normal PMMA = 0.9 + (2.6 * surface roughness, $R^2 = 0.6$, $p = 0.116$). The lowest mean attachment force of 0.8 mN was found on non-spray-coated PMMA at Ra = 0.21 µm. By contrast, on spray-coated surfaces, there was a minimum at the smallest roughness value we measured, and a continuous increase thereafter: linear regression; spray-coated PMMA = −0.02 + (1.9 * surface roughness, $R^2 = 1.0$, $p < 0.001$). The lowest roughness value (Ra = 0.16 µm) caused the lowest attachment force, of 0.2 mN (Figure 3). On every roughness, the maximum forces were lower on the spray-coated than on non-spray-coated PMMA (Figure 3). On spray-coated surface, bed bugs appeared reluctant to attach at all. Nevertheless, they still withstood a force of 3.6 times their own body weight (safety factor) (Table 2).

The attachment force was significantly influenced by roughness and wettability individually but also showed a significant interactive effect (Table 3; Figure 3). We also noticed an unusual behaviour: during testing, bed bugs were observed to rub their legs on the surface appearing to evaluate the best position to place their feet.

DISCUSSION

We found that surface roughness and wettability affect the attachment of male bed bugs to the substrate. Attachment was stronger on regular than on a superhydrophobic PMMA of the same roughness. Notably, on regular PMMA, a local minimum of attachment forces occurred at 0.2 and 0.4 µm roughness, whereas attachment was continuous with roughness on superhydrophobic PMMA, with lowest attachment values at lowest roughness values. Below we discuss how four components of the attachment system may be related to these differences.

Significance of tenent setae

We confirmed a local minimum of attachment to normal PMMA in bed bugs. Attachment was poorest at roughness Ra values = 0.2 and 0.4 µm (Figure 3). Modelling suggests that such reduction is caused by a greater overall distance between the terminal plate and the substrate (Peressadko & Gorb, 2004). Similar local minima of attachment forces at asperity sizes between 0.3 and 1.0 µm (root-mean-squared roughness 90.0 and 238.4 nm) have previously been reported for hairy attachment devices of flies (*Musca domestica* L.) (Peressadko & Gorb, 2004; Persson & Gorb, 2003), beetles (*Gastrophysa viridula*, *Leptinotarsa decemlineata*, *Nicrophorus* sp.) (Gorb, 2001; Hosoda & Gorb, 2011; Peressadko & Gorb, 2004; Schnee et al., 2019; Voigt

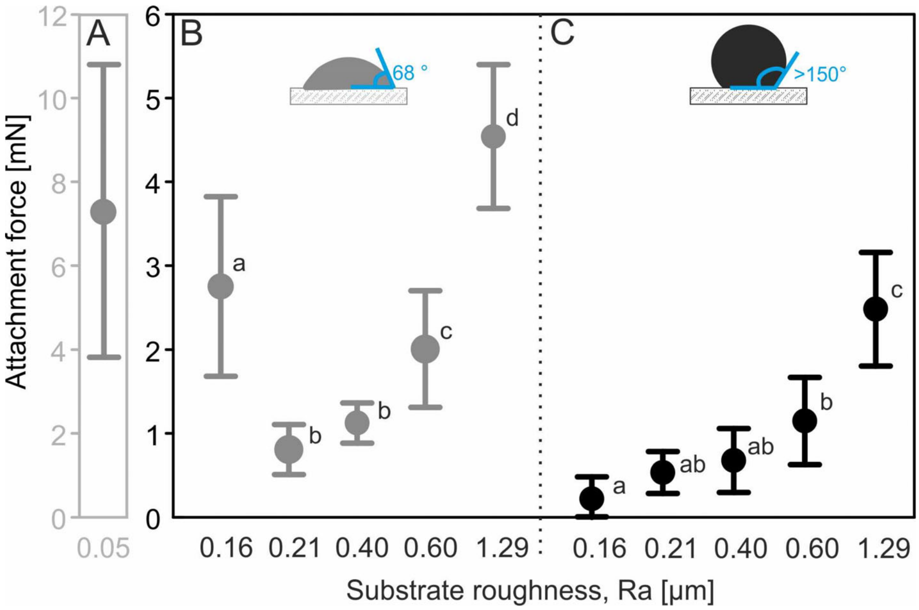

FIGURE 3 Attachment forces generated by male bed bugs *Cimex lectularius* during tangential centrifuging on Perspex (PMMA) substrates differing in roughness. (a), "native" PMMA control surface obtained from the provider (from Christie, 2009), (b), PMMA roughened with abrasive paper, (c), spray-coated roughened PMMA (superhydrophobic). Values are means ± sd, $N = 10$ males. The insets show the corresponding contact angle of water with the test substrates. Different letters indicate statistically significant force differences between different substrate roughness values within the same spray-coating treatment (all pairwise multiple comparison procedures Holm-Sidak method, $p < 0.05$). See Table 3 for details of the statistical analysis and Table 2 for corresponding safety factors.

TABLE 2 Maximum attachment forces and safety factors (force corresponding the times body weight) generated on differently rough Perspex (PMMA) surfaces during rotating on the centrifuge drum; mean ± sd, $N = 5$, $n = 10$ per substrate. 'n.a.'—not analysed.

	Maximum forces (mN)		Maximum safety factors	
Surface roughness, Ra (μm)	Roughened	Spray-coated	Roughened	Spray-coated
0.02	7.3 ± 3.55[a]	n. a.	133.1 ± 68.42[a]	n. a.
0.16	2.8 ± 0.30	0.2 ± 0.28	52.1 ± 22.56	3.6 ± 5.36
0.21	0.8 ± 0.30	0.5 ± 0.25	15.3 ± 7.08	8.7 ± 5.68
0.40	1.1 ± 0.24	0.7 ± 0.38	20.9 ± 5.88	12.7 ± 7.35
0.60	2.0 ± 0.69	1.1 ± 0.52	36.0 ± 10.63	21.4 ± 11.84
1.29	4.5 ± 0.86	2.5 ± 0.68	83.2 ± 19.07	46.1 ± 15.12

[a]Untreated (Christie, 2009).

et al., 2008; Zurek et al., 2017) but also spiders (*Philodromus dispar*) (Wolff & Gorb, 2012) and geckos (Huber et al., 2007). Because the terminal parts of setae form intimate contact with the surface and generate friction and adhesion, the attachment force is, in part, related to the width of the setal tip (Wolff & Gorb, 2012), as found in dock beetles (3.8 μm—Voigt et al., 2020), pentatomid bugs (3.8 μm—Voigt, Perez Goodwyn, et al., 2019), Colorado potato beetles (9.8 μm—Voigt et al., 2020), flies (1.8 μm—Peressadko & Gorb, 2004), philodromid spiders (0.8 μm—Wolff & Gorb, 2012) and geckos (0.2 μm—Ruibal & Ernst, 1965). The tenent spatulate seta terminals of male bed bugs are 3 μm wide (Reinhardt et al., 2019) and, using the graph of Wolff and Gorb (2012), would predict to generate only 0.2 mN, much lower attachment forces than we found. This difference suggests that in bed bugs, setae size is a much less powerful predictor of attachment, and surface material properties and different kinematics are also important. A possibly important and large difference to the animals selected by Wolff and Gorb (2012) may be the location of the setae, which in bed bugs, unlike in the other animals, are located on the tibia, not the tarsus. Furthermore, the movement resulting from the specific body posture of bed bugs is likely to alter the forces and setae–substrate interactions. Finally, the work by von Varenberg et al. (2010) and Voigt et al. (2020) shows that not just the width of individual setae is important but also the sum of all setae widths, called the 'peeling line'.

TABLE 3 Statistical comparison of attachment force values obtained for non-fed male *Cimex lectularius* in the centrifugal force experiment (two-way repeated-measures analysis of variance, two-factor repetition, general linear model).

Source of variation	DF	SS	MS	F	p
Individuum	9	0.7	0.1	0.4	0.9
Roughness	4	97.8	24.5	56.5	< 0.001
Wettability	1	37.1	37.1	241.6	< 0.001
Interaction					
Roughness × Wettability	4	20.1	5.0	12.6	< 0.001
Residual	35	14.0	0.4		
Total	98	189.7	1.95		

Note: The effect of the two independent factors PMMA substrate roughness (0.05 vs. 0.16 vs. 0.21 μm, 0.40 vs. 0.60 vs. 1.29 μm) and wettability (normal vs. hydrophobic), as well as their interaction are shown. $N_{♂♂} = 10$, $n = 5$ runs per male individual per substrate; the maximum value of these five runs was considered for further evaluation. Abbreviations: DF, degrees of freedom; SS, sum of squares; MS, mean sum of squares; F, F statistics; p, probability value.

Significance of adhesion-mediating fluid

Smooth and hairy insect attachment pads often have adhesion-mediating fluids, including, for example, pulvilli (Ghazi-Bayat & Hasenfuss, 1980) and adhesive setae of true bugs (Voigt, Perez Goodwyn, et al., 2019). The fluids facilitate attachment on flat, smooth surfaces when the fluid layer is thin (de Gennes et al., 2004). Thicker fluid layers were suggested to reduce adhesion to substrates and/or to fill substrate irregularities to enhance attachment on rough substrates (Dirks & Federle, 2011; Drechsler & Federle, 2006). Bed bugs also secrete fluids onto surfaces via their attachment pads (Reinhardt et al., 2019) and so are also likely to mediate the attachment forces. Tarsal adhesion-mediating fluids in insects are considered to consist of polar and non-polar compounds. Therefore, they behave in a biphasic way and should assist in attaching to both hydrophilic and hydrophobic surfaces and wet a broad range of surfaces of different chemistry and roughness (Dirks et al., 2010; Federle et al., 2002; Gorb, 2001; Vötsch et al., 2002). In bed bugs, we found lower force values on superhydrophobic than on normal PMMA, suggesting that the tarsal fluid may not be fully biphasic and be more effective on less superhydrophobic PMMA substrates. On superhydrophobic rough PMMA substrates, polar and non-polar compounds are less effective. Their high contact angles with water and low free surface energy may repel watery and lipid compounds in tarsal fluid (Grohmann et al. 2014). On such surfaces, ladybird beetles *Coccinella septempunctata* (Coleoptera, Coccinellidae) and water lily leaf beetles *Gallerucella nymphaea* (Coleoptera, Chrysomelidae) also generated lower attachment forces (Gorb et al., 2010; Grohmann et al., 2014). By contrast, England et al. (2016) found no significant effect of chemical and wetting surface properties on attachment ability but a strong effect by surface roughness.

Despite the low attachment forces, we found that even on superhydrophobic surfaces, bed bugs attached with a force of three times their body weight (safety factor), compared with 83 on 1.29 μm rough PMMA, 133.1 on smooth, non-treated PMMA (Christie, 2009), or 183 on smooth epoxy resin (Reinhardt et al., 2019).

Significance of claws

Claws enable insects to cling to substrates with a large roughness (over 12 μm) and to filamentous structures (Betz, 2002; Dai et al., 2002; Gorb et al., 2004; Gorb & Gorb, 2006; Voigt, 2019; Voigt et al., 2007). Across insect species, Dai et al. (2002) have reported a relationship between the dimension of the claw tip and the substrate texture the species commonly attach to. This relationship suggests that insect claws only attach to substrates whose roughness is at least as large as the diameter of the claw tips. If claws are involved, attachment will increase continuously with roughness, and the increase will be similar on normal and superhydrophobic surfaces. We found such an increase on both surfaces, suggesting that bed bugs used their claws for mechanical interlocking in addition to adhesion by pads. When both mechanisms work in tandem, very strong attachment forces can potentially be generated. However, on nm-rough superhydrophobic surfaces, the attachment force is generally low because neither adhesion (tenent setae, tarsal fluid) nor interlocking (claws) are able to be fully applied.

Significance of behaviour

When bed bugs are gently blown upon, they briefly respond by 'freezing', that is, standing still and holding the body tight to the substrate. This posture helps to increase the attachment force they are able to generate. We found that this freezing also occurred in some bed bugs in response to a sudden increase in acceleration—a response previously recorded in ants (Federle & Holldobler, 2000).

A second behaviour we observed was that bed bugs rubbed their legs on the surface during the experiments. A similar behaviour was observed in dock beetles. They used the friction force between tarsal attachment pads and the substrate to gain information about the degree of contamination of their own attachment structure (Hosoda & Gorb, 2011). In dock beetles, foot grooming did not correlate with contamination, but rather with the decrease in friction force (Hosoda & Gorb, 2011), indicating dynamically foothold tuning and presumably the use of mechanoreceptors for sensing either tensile/compressive forces in the cuticle or tensile forces between leg segments. It will be interesting to study if the behaviour in bed bugs served similar functions.

CONCLUSIONS

Using a combination of hairy adhesive pads and claws, male bed bugs generated reliable foothold on rough Perspex substrates when rotated in tangential direction in centrifugal force tests. Similar to previous studies with beetles, flies, moths and spiders, surface roughness of 0.16 μm on superhydrophobic, 0.21 and 0.4 μm on both normal and superhydrophobic Perspex led to decreased attachment forces. This relationship and the increasing attachment with increasing roughness on >4 μm rough surfaces were more pronounced on the less wettable superhydrophobic substrates. Unlike in insect-inspired dry polyurethane shear-activated adhesives (Kim & Varenberg, 2020), the effect of substrate chemistry matters for the tarsal fluid-mediated bed bug attachment on smooth and rough substrates. An interactive impact of surface roughness and wettability as observed in bed bugs (Table 3) has been previously reported for dock beetles (*Gastrophysa viridula*, Coleoptera, Chrysomelidae), where hydrophobicity caused a decrease in attachment (Gorb & Gorb, 2009). When combined with roughness, the decrease in beetle force was four times greater, similar to results on bed bugs in the present study. This knowledge may inspire the development of repelling substrates for bed bug control.

AUTHOR CONTRIBUTIONS

Rob Dwyer-Joyce: Conceptualization; funding acquisition; methodology; writing – review and editing; software; supervision. **Dagmar Voigt:** Investigation; writing – original draft; validation; visualization; writing – review and editing; formal analysis; data curation. **Klaus Reinhardt:** Conceptualization; writing – original draft; writing – review and editing; project administration; supervision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in https://datadryad.org, at doi:10.5061/dryad.cjsxksng8

ETHICS STATEMENT

This study did not contain any research with human subjects or vertebrate animals and studies were in concordance with institutional policies.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Supporting information.

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