

ATTACHMENT FORCES OF ANTS MEASURED WITH A CENTRIFUGE: BETTER 'WAX-RUNNERS' HAVE A POORER ATTACHMENT TO A SMOOTH SURFACE

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Summary

The symbiotic ant partners of glaucous *Macaranga* ant-plants show an exceptional capacity to run on the slippery epicuticular wax crystals covering the plant stem without any difficulty. We test the hypothesis that these specialised 'wax-runners' have a general, superior attachment capacity. We compared attachment on a smooth surface for 11 ant species with different wax-running capacities. The maximum force that could be withstood before an ant became detached was quantified using a centrifuge recorded by a high-speed video camera. This technique has the advantage of causing minimum disruption and allows measurements in very small animals. When strong centrifugal forces were applied, the ants showed a conspicuous 'freezing reflex' advantageous to attachment.

Attachment forces differed strongly among the ant species investigated. This variation could not be explained by different surface area/weight ratios of smaller and

larger ants. Within species, however, detachment force per body weight (F/W) scaled with the predicted value of $W^{-0.33}$, where W is body weight in newtons.

Surprisingly, our results not only disprove the hypothesis that 'wax-runners' generally attach better but also provide evidence for the reverse effect. Superior 'wax-runners' (genera *Technomyrmex* and *Crematogaster*) did not cling better to smooth Perspex, but performed significantly worse than closely related congeners that are unable to climb up waxy stems. This suggests an inverse relationship between adaptations to run on wax and to attach to a smooth surface.

Key words: epicuticular wax, ant-plant, arolium, attachment, adhesion, ant, *Macaranga*, *Crematogaster*, *Technomyrmex*, *Oecophylla*.

Introduction

The surfaces of many plant species are glaucous ('waxy'), i.e. they are covered by a bluish layer of epicuticular wax crystals. Such wax blooms are known to have anti-adhesive properties and to be highly slippery for insects (e.g. Knoll, 1914; Stork, 1980b; Eigenbrode, 1996). We recently discovered some species of ant that are specialised 'wax-runners'. These ants (members of the genera *Crematogaster*, *Technomyrmex* and *Camponotus*) live in association with *Macaranga* (Euphorbiaceae) host plants that have glaucous stems (Federle et al., 1997). In contrast to most other ant species, the mutualistic ant partners of these trees are capable of moving around on the slippery, glaucous twig surfaces with no difficulty (Fig. 1).

Thus far, nothing is known about the mechanism of this striking 'wax-running' capacity. Federle et al. (1997) found a tendency for smaller ants to have a better wax-running performance, an effect easily explained by scaling laws (lower weight/surface area ratio in smaller animals). In other words, a high ratio of adhesive area to body weight (e.g. smaller ants with relatively larger attachment organs) could provide a

simple explanation for the observed 'wax-running' capacity. If this explanation were true, however, good 'wax-runners' should also attach well to a smooth surface. Here, we test this hypothesis by comparing the attachment forces to a smooth Perspex surface of wax-runners and closely related ants that are unable to climb up waxy twigs.

The capacity of many insects to hold on to smooth surfaces has fascinated biologists for centuries (e.g. Hooke, 1665; Rombouts, 1883; Dahl, 1884; Dewitz, 1884; Simmermacher, 1884; Knoll, 1914; Nachtigall, 1974; Stork, 1983a,b; Walker et al., 1985; Wigglesworth, 1987; Lees and Hardie, 1988; Dixon et al., 1990; Gorb, 1998). When surfaces are rough, insects can hook their claws onto small projections. Attachment to smooth surfaces, however, is accomplished by a variety of specialised adhesive organs on the tarsus or pretarsus, which differ considerably among insect orders. The structures involved are either pads of numerous spatulate hairs (e.g. in the Diptera and Coleoptera) or smooth appressoria, which can often be inflated by haemolymph pressure (e.g. in many Thysanoptera, Orthoptera and Hymenoptera).



Fig. 1. The protective barrier effect of slippery epicuticular wax crystal layers in *Macaranga*. The wax bloom on the lower part of the twig had been wiped off so that workers of the aggressive generalist *Crematogaster* cf. *artifex* could gain access. The specialist *Crematogaster* (*Decacrema*) ant (above) is obviously well protected by the wax barrier.

Materials and methods

We selected 11 tropical arboreal ant species for the measurements (see Table 1). Ant genera were identified according to Bolton (1994). *Crematogaster* (*Decacrema*) mssp. 1, 3, 4 and 6 (Myrmicinae) are obligate ant partners of *Macaranga* trees (morphospecies numbers follow Fiala et al., 1999). Colonies of *Technomyrmex* sp.A (Dolichoderinae) regularly inhabit the stipule domatia of the glaucous *Macaranga pruinosa*; *Technomyrmex* spp.B and C are similar morphospecies. Despite thorough examination, we could detect no morphological difference between *Technomyrmex* sp.A and sp.C. However, the different nest location (sp.C nests under tree bark or leaf undersides) and the strikingly different wax-running capacity (see Results) suggest that they are indeed different taxa. We use morphospecies names corresponding to Federle et al. (1997). Reference ant specimens are in the collection of W. Federle.

Determination of 'wax-running' capacity

A simple field experiment was conducted in Peninsular Malaysia to determine the 'wax-running' capacity of the 11 selected ant species (Federle et al., 1997). We used vertical, glaucous stems (diameter 15 mm) of the ant-plant *Macaranga pruinosa* (Euphorbiaceae). With the aid of a paint-brush, we placed ants individually on the small wax-free scars left by the abscission of the leaves. Of each species, we tested 20 workers of similar size. We determined the proportion of ants that managed to walk past one of two markers located 5 cm above and below the release point within 10 min (for details, see Federle et al., 1997).

Force measurement

We used a centrifuge technique that allows measurements with no prior treatment of the insects and which is applicable to very small animals. The experimental arrangement is shown in Fig. 2. Centrifuge methods have previously been used by Dixon et al. (1990) and Brainerd (1994).

With a paint-brush or a paper strip, ants were carefully placed onto the outside of a Perspex (polymethylmethacrylate, PMMA) cylinder (diameter 80 mm) in the rotor of a centrifuge. The centrifuge could be gradually accelerated from 0 to 6000 revs min^{-1} . The Perspex cylinder was manufactured to be as smooth as possible so that its surface was glossy and free of visible scratches. We quantified its roughness using a surface roughness detector (Mitutuyo SurfTest 211). The roughness index R_a (ISO, DIN) was determined to be $0.054 \pm 0.010 \mu\text{m}$ (mean \pm s.d., $N=20$ vertical lines along the cylinder measured). PMMA has a critical surface tension (γ_c) of 39 mN m^{-1} at 20°C (Baier et al., 1968). Before each experiment, the cylinder was carefully cleaned with a lens cloth and 25% ethanol. When we pulled ants resting on such a smooth Perspex surface in the horizontal direction, we could make them slide in a perfectly even movement (W. Federle, unpublished results), suggesting that the microscopic irregularities on the Perspex surface were not large enough for their claws to interlock with.

The centrifuge was accelerated and the run recorded from above using a high-speed video camera (NAC HSV 400) at 200 frames s^{-1} . Because of the stroboscopic illumination at 200 Hz, the ants could be observed during the centrifuge runs. At lower speeds (and lower centrifugal forces), the ants were still able to move on the outside of the drum. When we increased the speed of rotation, however, the movements of the ants became slower and finally stopped completely (see Results). Once this 'freezing' stage had been reached, we continued accelerating the centrifuge very slowly until the insect lost its foothold and fell off. A complete run lasted 1–2 min. The centrifuge runs had no visible effect on the behaviour of the ants, and individuals could be tested several times. For each ant worker, we conducted three consecutive measurements and calculated its maximal attachment force. The ants were allowed to recover for at least 15 min between these three measurements.

The video recordings were analysed using the computer program Unimark 3.6 (Rüdiger Voss Services, Tübingen). We determined the angular velocity (ω , rad s^{-1}) of the rotor at the

moment of the detachment by measuring the turning angle (α , rad) over 0.05 s (=10 frames):

$$\omega = \alpha/0.05 = 20\alpha. \quad (1)$$

We also determined the distance (d) between the ant's body (the underside of the metathorax) and the surface of the cylinder. This approximation of the ant's centre of centrifugal force was used for calculating its radial position (R), which is equal to the sum of the radius (r) of the drum and d . As a consequence of the perspective of the video camera, values of d were slightly underestimated for ants sitting in the lower part of the centrifuge drum, at the most by $rh/(D+h) \approx 2.3$ mm (where D is the distance from the camera to the drum and h is the height of the cylinder; see Fig. 2). The acceleration (a , m s^{-2}) required to detach the ant is:

$$a = R\omega^2. \quad (2)$$

To calculate the resulting forces, the ants were weighed using a micro-balance.

For each of the 11 ant species, two colonies were collected in Peninsular Malaysia between March and April 1997; they were then maintained in the laboratory in Germany. We took similar numbers of workers from the two different colonies for all the ant species tested.

Strain gauge force measurement

To compare the results of the centrifuge method with a conventional force-measuring technique, we used a strain gauge force transducer (see, for example, Walker et al., 1985). *Oecophylla smaragdina* ants were anaesthetised by cooling on ice for 2 min. A fine thread was tied to the thorax between the front and middle legs, so that the loop did not touch either the legs or coxae. The ants were allowed to recover for more than 1 h. The other end of the thread was attached to the strain gauge. The voltage output was recorded on a DAT recorder (Biologic DTR-1801). Before each measurement, the transducer was calibrated by loading it with weights (in steps of 100 mg). Ants were placed onto a horizontal smooth Perspex plate (with material and surface properties identical to those of the cylinder used in the centrifuge) and pulled away very slowly using the hand-held strain gauge until they fell off. For each ant, we recorded five detachment events within a period of 1–3 min. The recordings were digitised using a 1401 A/D converter (CED) and then analysed using the Program Spike2 (V2.24, CED; sampling frequency 10 Hz). To exclude short force peaks caused by vibrations of the hand-held strain gauge, we calculated mean forces and averaged them over 1 s. From these mean forces, we determined the maximum force that could be applied before the ant became detached.

Table 1. Survey of known insect attachment forces measured vertically on a smooth glass or Perspex surface

Insect species	<i>N</i>	Body mass (mg)	Vertical attachment force (mN)	Force/weight	Reference
<i>Periplaneta americana</i> (Blattodea, Blattidae)		900	13	1.5	Pell, unpublished, cited in Walker (1992)
<i>Chrysolina polita</i> , ♀ (Coleoptera, Chrysomelidae)	29	57.6	(22.7*)	(40.2*)	Stork (1980a)
<i>Epilachna vigintioctomaculata</i> , ♀ (Coleoptera, Coccinellidae)	6	56.6	2.9	5.3	Ishii (1987)
<i>Calliphora vomitoria</i> (Diptera, Calliphoridae)	1	72	2.4 (19.9*)	3.4 (28.1*)	Walker et al. (1985)
<i>Megoura viciae</i> (Homoptera, Aphididae, Aphidinae)	11	3.3	0.594	18.3	Lees and Hardie (1988)
<i>Aphis fabae</i> (Homoptera, Aphididae, Aphidinae)	12	0.383	0.064	17.4	Dixon et al. (1990)
<i>Drepanosiphum platanoidis</i> (Homoptera, Aphididae, Drepanosiphinae)	15	1.52	0.0956	6.4	Dixon et al. (1990)
Ants (Hymenoptera, Formicidae)					
<i>Crematogaster</i> (<i>Dc.</i>) msp.1	11	0.324±0.11	0.264	86.1	This study
<i>Crematogaster</i> (<i>Dc.</i>) msp.3	13	0.315±0.09	0.447	146.4	This study
<i>Crematogaster</i> (<i>Dc.</i>) msp.4	11	0.339±0.08	0.462	142.1	This study
<i>Crematogaster</i> (<i>Dc.</i>) msp.6	13	0.355±0.10	0.161	49.9	This study
<i>Crematogaster</i> cf. <i>artifex</i>	11	1.072±0.16	0.558	53.9	This study
<i>Oecophylla smaragdina</i>	13	6.488±2.30	7.468	118.4	This study
Strain gauge	11		3.882	63.9	This study
<i>Technomyrmex</i> sp.A	13	0.445±0.12	0.182	41.8	This study
<i>Technomyrmex</i> sp.B	12	0.641±0.10	0.402	63.4	This study
<i>Technomyrmex</i> sp.C	12	0.341±0.08	0.203	63.1	This study
<i>Tapinoma</i> sp.A	11	0.141±0.03	0.066	48.0	This study
<i>Tetraponera</i> cf. <i>attenuata</i>	9	1.320±0.20	0.789	62.5	This study

Values are means ± S.D. for this study; other values are means.

*Horizontal pulling forces are given in parentheses.

Dc., *Decacrema*.

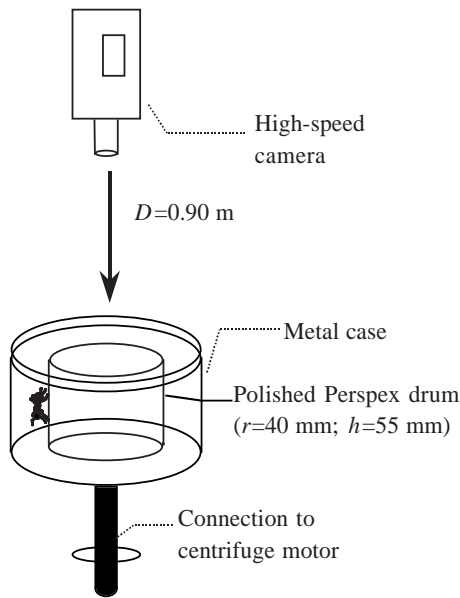


Fig. 2. Centrifuge method used for measuring surface attachment forces of insects. The ant was placed on the Perspex drum, which was accelerated until the ant became detached. A high-speed video camera recorded the run from above and was used to determine the maximum force of detachment. D , distance from the camera to the centre of the drum; h , height of the drum; r , radius of cylinder.

Results

Walking capacity on slippery plant wax crystals

Ant species differ strikingly in their running performance on slippery wax crystal surfaces (Fig. 1; Federle et al., 1997). In a previous study, we quantified ‘wax-running’ capacity by placing ants on vertical, glaucous *Macaranga* twigs of 15 mm diameter and determining the proportion of ants that succeeded in walking 5 cm upwards or downwards (for details, see Federle et al., 1997). Using the same method, we quantified the running performance on glaucous stems of the 11 ant species selected for the present study. The results are shown in Fig. 3 (some of the data are taken from Federle et al., 1997).

Within the *Crematogaster* (*Decacrema*) and the *Technomyrmex* group, the running performance on waxy *Macaranga* stems differed considerably. The ant species that are regularly associated with glaucous host-plants, *Crematogaster* (*Decacrema*) mssp. 1 and 6 and *Technomyrmex* sp.A, performed much better than their congeners.

Attachment to a smooth surface

Freezing reflex

In all the 11 ant species investigated, we observed a characteristic behaviour when centrifugal accelerations were applied. We could easily watch the ants during the centrifuge runs because of the 200 Hz stroboscopic flash illumination (at circulation periods near multiples of 0.005 s, images of subsequent turns become superimposed by the human eye). At low accelerations most of the ants were still running around on the Perspex surface. When we gradually speeded up the

centrifuge, however, the ants at first walked much more slowly and finally stood motionless. In this stereotyped ‘freezing’ position, the ants kept all their legs spread out and in contact with the surface. We could elicit the same freezing behaviour when we directed strong puffs of air at running ants. Most of these ants also ‘froze’ immediately and spread out their legs.

These observations indicate that the detachments in the centrifuge were not caused by spontaneous, erratic movements of the ants. On the contrary, we assume that, by ‘freezing’, the ants bring themselves into a body position in which attachment is particularly strong. In the relatively large workers of *Oecophylla smaragdina*, we observed that the freezing reflex on a smooth glass surface was accompanied by a conspicuous inflation of the attachment organs (‘arolia’; Snodgrass, 1956). It is likely that a similar reaction also occurs in other ants.

Attachment forces

Fig. 4 shows the results of the centrifuge measurements. For each individual, we counted only the maximum attachment force from three measurements. As a rule, forces decreased slightly over the course of the three trials (mean of second measurement, 84.5% of first; mean of third, 75.1% of first; Friedman rank analysis of variance, ANOVA: d.f.=2, $\chi^2=28.3$, $P<0.001$).

The ant species tested differed strongly with regard to the measured forces (F in newtons) (data with heterogeneous variances; Kruskal–Wallis test: $H=99.64$; d.f.=10; $P<0.001$) and attachment force per body weight (F/W , where W is body weight in newtons) ($H=69.19$; d.f.=10; $P<0.001$). When ants fall off a slippery waxy plant stem, their own body weight causes them to detach. Therefore, we compared F/W values for ‘wax-runners’ and related ants. The ant species tested included two groups of morphologically similar, congeneric ants,

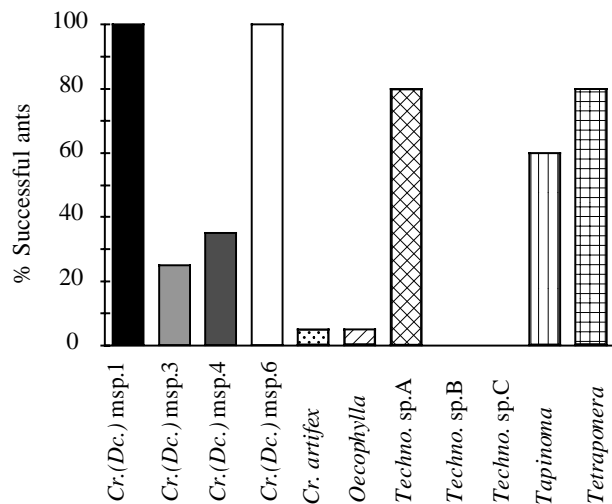


Fig. 3. The ability of the 11 ant species investigated to walk on vertical, glaucous twigs of *Macaranga pruinosa* of 15 mm diameter ($N=20$ ant workers per species). Ants that walked for 5 cm, upwards or downwards, along a twig were classified as ‘successful’ (some of these data are taken from Federle et al., 1997). *Cr.*, *Crematogaster*; *Dc.*, *Decacrema*; *Techno.*, *Technomyrmex*.

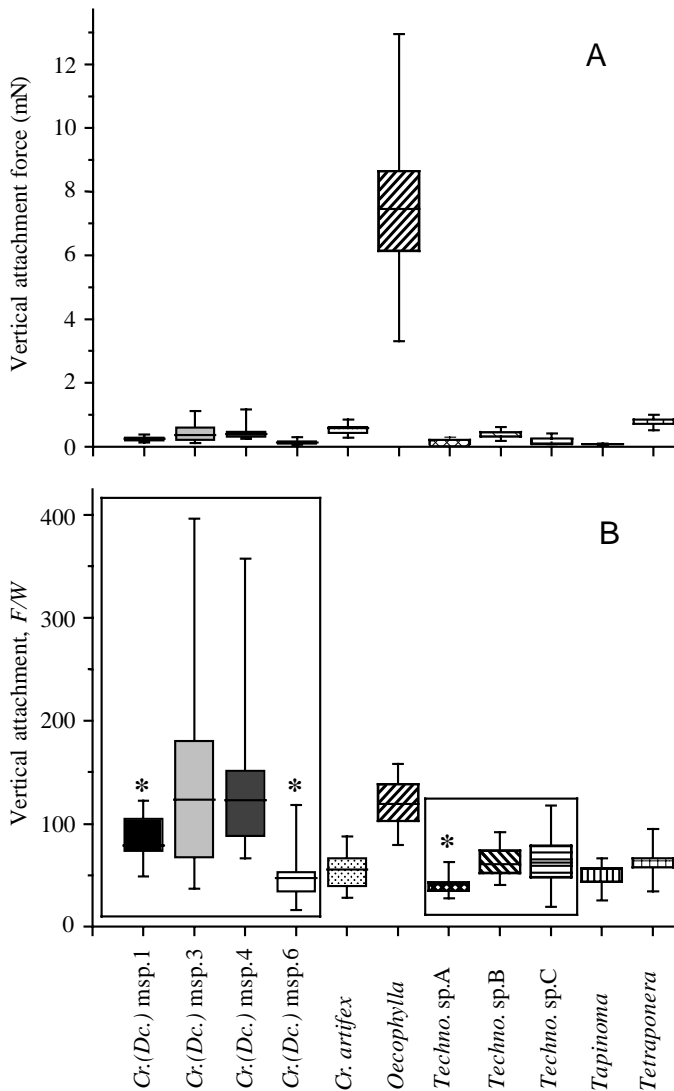


Fig. 4. Attachment of 11 selected ant species to smooth Perspex. Box plots of (A) detachment forces (mN) and (B) attachment force per body weight (F/W , where F is the detachment force and W is body weight) perpendicular to the surface that caused the animals to fall off the Perspex cylinder. Central lines denote medians, boxes denote the inner two quartiles, and error bars mark the upper and lower 5%. For each individual ant ($N=9-13$ per species), only the maximum of three consecutive measurements was considered. The two rectangular frames highlight groups of closely related ant species containing wax-runners (marked with an asterisk) and non-wax-runners, *Crematogaster (Decacrema)* and *Technomyrmex* spp. *Cr.*, *Crematogaster*; *Dc.*, *Decacrema*; *Techno.*, *Technomyrmex*.

Technomyrmex and *Crematogaster (Decacrema)*, comprising both wax-runners and non-wax-runners. Within each of these groups, F/W varied significantly between species [analysis of covariance, ANCOVA, log-transformed data, body mass as the covariate, *Crematogaster (Decacrema)* spp., d.f.=3, $F=9.557$, $P<0.001$; *Technomyrmex* spp., d.f.=2, $F=4.692$, $P=0.016$]. However, the wax-runners did not show higher attachment forces as predicted by our hypothesis. Instead, our data provide

significant evidence for the opposite effect (Fig. 4). *Crematogaster (Decacrema)* msp. 3 and 4 are associated with glossy *Macaranga* host plants and have a strikingly poorer attachment to crystalline epicuticular wax surfaces than the wax-runners *Crematogaster (Decacrema)* msp. 1 and 6 (Fig. 3; see also Federle et al., 1997). However, they attached best to the smooth surface (F/W means of msp.3 and 4: 146.4 and 142.1, respectively). The difference between *Crematogaster (Decacrema)* wax-runners and non-wax-runners was highly significant [ANCOVA, nested design, log-transformed data, mass as the covariate, *Crematogaster (Decacrema)*, d.f.=1, $F=19.649$, $P<0.001$].

We obtained an analogous result in the three morphologically similar *Technomyrmex* species investigated. *Technomyrmex* sp.A, which is much better at running on a crystalline wax surface than her congeners *Technomyrmex* spp.B and C (Fig. 3), attached significantly less well to the smooth surface (ANCOVA, nested design, log-transformed data, mass as the covariate, *Technomyrmex*, d.f.=1, $F=8.869$, $P=0.0054$).

Scaling analysis

The weight (W) of an animal is proportional to the cube of its body length, but the body surface area (A) only to the square. If animals had identical body shapes and densities, A would scale with $W^{0.66}$ (see, for example, Pedley, 1977; McMahon and Bonner, 1983).

Assuming that the surface area of the unfolded arolia (H) is a constant proportion of the body surface area (A) and that the attachment force (F) is a linear function of H (Stork, 1980a; Walker et al., 1985; but see Lees and Hardie, 1988), the expected scaling of force per body weight (F/W) would be:

$$F \propto H \propto A \propto W^{0.66}$$

or

$$F/W \propto m^{-0.33}. \quad (3)$$

Fig. 5A shows our data as a logarithmic plot of F/W against m , where m is body mass. Pooled across all the species investigated, we found a positive scaling coefficient (slope of the regression line, $b=0.101$; $r^2=0.032$; $P<0.05$). Within species, however, most correlations with body mass were negative ($r_s<0$ in nine out of the 11 species investigated, where r_s is the Spearman rank correlation coefficient; see legend to Fig. 5A). Because body shapes probably vary more strongly among species than within species, the positive interspecific scaling coefficient (Fig. 5A) may be explained by different body shapes. To correct for the apparent large interspecific differences (see, for example, *Oecophylla smaragdina* in Fig. 5A), we standardised our data by calculating 'relative' F/W and m values (=relative proportion of the species means). Fig. 5B gives a plot of the corrected values ($b=-0.331$; $r^2=0.038$; $P<0.05$). The intraspecific, negative scaling coefficient is therefore consistent with the predicted value of -0.333 , although there is considerable scatter in the data.

Comparison with a strain gauge force transducer

In the large ant *Oecophylla smaragdina*, we compared the

forces measured using the centrifuge method with those measurements using a strain gauge. In contrast to the ‘freezing behaviour’ observed in the centrifuge (see above), the ants tied to the thread generally continued to move during the measurements and only rarely were all six legs simultaneously in contact with the surface. Fig. 6 shows that the vertical attachment forces measured in the centrifuge were of the same order of magnitude, but significantly higher (ANCOVA, body mass as the covariate, d.f.=1, $F=28.8$, $P<0.001$). We conclude that this difference may be because the ants are more strongly manipulated in the strain gauge method than in the centrifuge method (anaesthetization, uneven pull of the thread, etc.).

Discussion

Our findings clearly reject the hypothesis that the ‘wax-running’ behaviour of some *Macaranga*-associated ants is caused by a general, superior attachment capacity. There was no positive correlation between running performance on slippery plant wax crystals and clinging capacity to a smooth surface. On the contrary, the attachment force to smooth Perspex was found to be inversely related to the capacity to walk on waxy stems. This suggests that an unknown trade-off is involved in the specialisation of ants for wax-running. We assume that the effect is not caused by an alternative use of either claws or arolia depending on surface roughness. *Crematogaster* (*Decacrema*) msp.1 ‘wax-runners’ deprived of their arolia were unable to

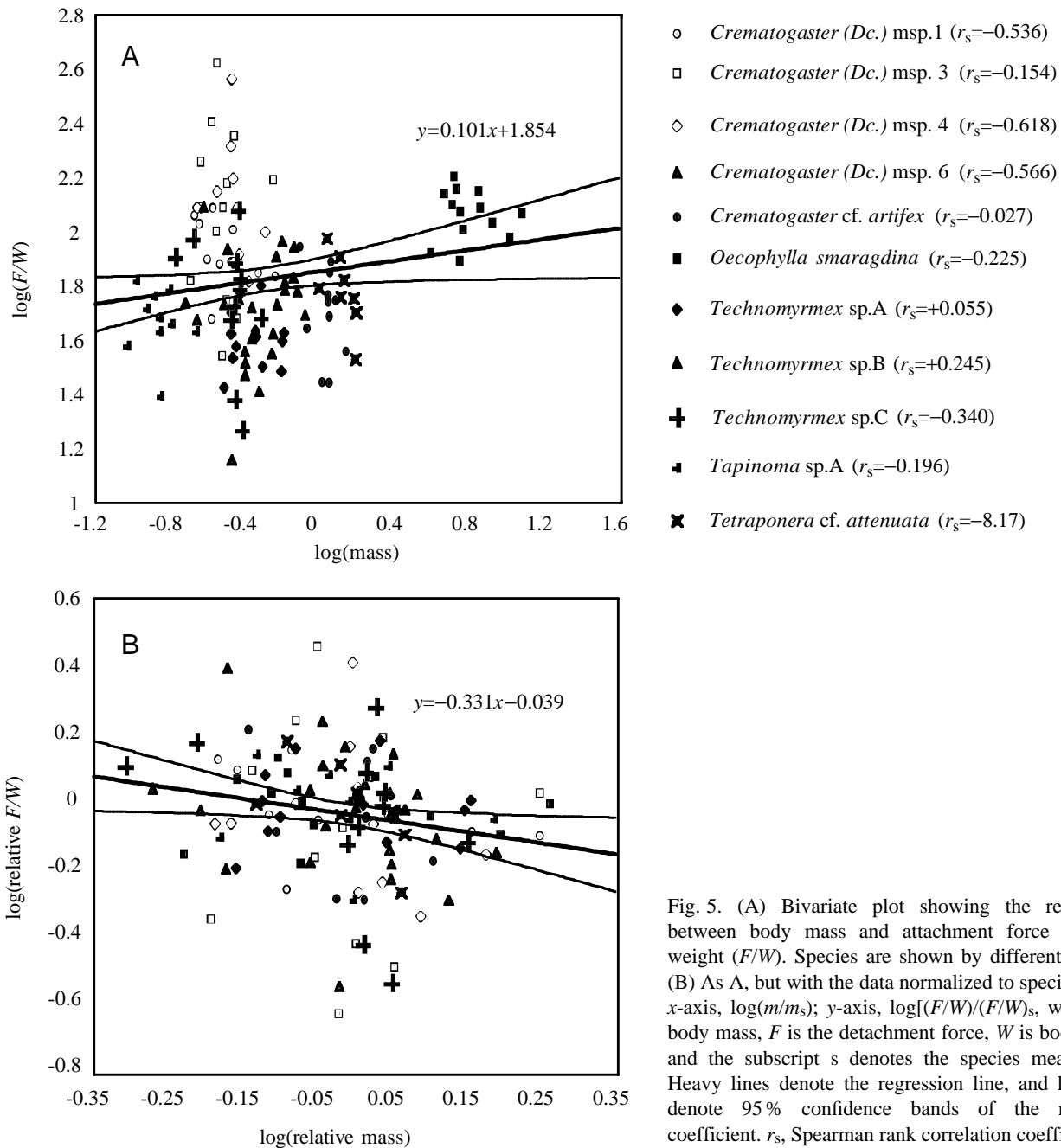


Fig. 5. (A) Bivariate plot showing the relationship between body mass and attachment force per body weight (F/W). Species are shown by different symbols. (B) As A, but with the data normalized to species means: x -axis, $\log(m/m_s)$; y -axis, $\log[(F/W)/(F/W)_s]$, where m is body mass, F is the detachment force, W is body weight and the subscript s denotes the species mean value]. Heavy lines denote the regression line, and light lines denote 95% confidence bands of the regression coefficient. r_s , Spearman rank correlation coefficient.

climb up waxy *Macaranga* stems (W. Federle, unpublished results). Thus, the micro-roughness of plant wax crystals is probably not sufficient for claws to hook onto (see also Knoll, 1914). Moreover, scanning electron microscope examination of the pretarsi of *Crematogaster (Decacrema)* mssp.1, 3, 4 and 6 and of *Technomyrmex* spp.A, B and C failed to detect any clear morphological differences in the claws or the arolium between 'wax-runners' and closely related ants incapable of climbing up glaucous stems W. Federle, unpublished results). We are currently investigating whether the properties of an adhesive secretion and/or behavioural mechanisms could provide an explanation for the wax-running capacity and the paradoxical results found in this study.

The freezing behaviour described in this study appears to be a reflex advantageous to attachment that has not been described previously. When insects walk (typically using a tripod gait), the legs have to be lifted and their attachment potential is lost. Walker et al. (1985) have shown that there is an approximately linear relationship between leg number and attachment force. Freezing behaviour may be identical to the reaction to vibrations reported for ants and honeybees (Fuchs, 1976; Little, 1962; Michelsen et al., 1986). Freezing as a response to puffs of air or to accelerations appears to be a general phenomenon widespread among insects. We have observed similar behaviour in members of the Diptera (*Musca domestica*, Muscidae), Coleoptera (*Clytra quadripunctata*, Chrysomelidae) and Heteroptera (*Graphosoma italicum*, Pentatomidae), even though these taxa have completely different attachment organs (see Bauchhenß, 1979; Ghazi-Bayat and Hasenfuss, 1980; Stork, 1980c). However, we were unable to provoke a visible freezing reflex in some ground-living ant species (e.g. *Pheidologeton* sp., *Lasius flavus*), even though these ants possess arolia. When exposed to strong air puffs, they continued to run and were easily detached from smooth surfaces (as a consequence, centrifuge force measurement cannot be applied in these species). We assume that freezing is adaptive to arboreal ants, but more data are needed to test this hypothesis.

The intraspecific scaling coefficient of attachment found in

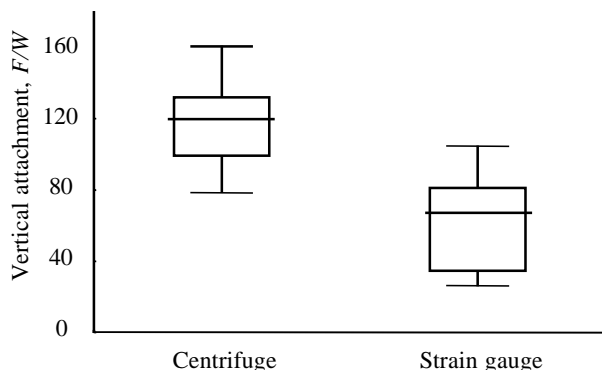


Fig. 6. Box plot comparing attachment forces measured using the centrifuge method ($N=13$) and data obtained using a strain gauge force transducer ($N=11$ workers). Only workers of *Oecophylla smaragdina* were tested. Central lines denote medians, boxes denote the inner two quartiles, and error bars mark the upper and lower 5%.

this study ($F \propto W^{0.66}$) is consistent with the hypothesis that attachment force is a linear function of the adhesive area. In their study of four aphid species, Dixon et al. (1990) found similar scaling coefficients (interspecific relationship $F \propto W^{0.62}$). Proportionality of force to contact area is in agreement with the widely accepted view that most insects attach to smooth surfaces using wet adhesion (for a review, see Walker, 1992). However, it is beyond the scope of the present study to investigate the physical mechanism of adhesion in ants.

Our results show that attachment capacity differs considerably among ant species. Table 1 compares our results with other known records of insect attachment to smooth surfaces. The clinging capacities of the 11 species of arboreal ants selected for the present study are outstanding. With respect to detachment force per body weight, they far exceed the values known for other insects.

For wingless insects such as ants, survival in arboreal habitats requires the capacity to get there 'on foot'. Moreover, when subordinate arboreal ants with restricted territories fall off a tree where they nest or forage, they will almost certainly die, since no odour trails lead them back to their nest and they may be confronted with superior numbers of other aggressive ant species. This is especially true for host-specific plant-ants, e.g. the *Crematogaster (Decacrema)* partner ants of *Macaranga* trees investigated in this study, but also for generalist colonisers of extreme habitats such as mangrove forests. The exceptional clinging capacities of the *Crematogaster (Decacrema)* plant-ants and of some other arboreal ant species measured in the present study thus appear to be adaptive to their particular habitat. In accordance with this, some ground-living ponerine and leptanilline ant species lack an adhesive arolium (Freeland et al., 1982).

As mentioned by Stork (1980a), wind and vibrations of a twig can strongly increase detachment forces, so that an insect must resist forces higher than those caused by gravity alone. However, the capacity of some ants to sustain attachment forces of more than 100 times their own body weight may be more than sufficient to prevent them from falling off their 'home' trees. Other ecological factors may be important in this respect. Many ant species transport prey items that are much heavier than their own body or tear their prey to pieces during group hunting (Hölldobler and Wilson, 1990). An extreme example is the Asian weaver ant *Oecophylla smaragdina*, which is known to transport very large vertebrate prey (Wojtusiak et al., 1995). In this ant, exceptional attachment forces are also needed during the construction of their leaf tent nests. Before leaves can be connected using larval silk, many workers (and often chains of workers) have to pull the leaves together. On the back of these living 'clamps', the last one or two workers are attached to the smooth upper side of a leaf and must sustain the entire force.

Our data show that the considerable forces measured in this study may be traced back in part to the centrifuge method, which probably yields higher values than other force-measuring techniques. Thus far, measurements of adhesive forces have been conducted by connecting insects with thread

to a force transducer (Stork, 1980a; Walker et al., 1985; Dixon et al., 1990) or by loading them with weights (Ishii, 1987; Lees and Hardie, 1988). These experimental approaches required a hook or a thread to be fixed to the insect body. For these treatments, insects had to be anaesthetised and, glue or wax droplets were usually applied to the insect cuticle. Obviously, very small insects were difficult to measure using this method. Even in larger insects, the attachment forces may have been weakened by the manipulations. Moreover, when ants are pulled by a thread, the freezing reflex is much less pronounced, and all six legs do not generally touch the surface. We therefore think that the centrifuge technique is a more appropriate method. It requires less manipulation, can be applied to very small insects and allows rapid measurements under a variety of experimental conditions.

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