This manuscript presents the results of a combined experimental and theoretical study of the underwater capillary adhesion of beetle pads. In the experiments, the beetles are restricted in their freedom to move. Then they are brought towards various substrates that can be hydrophilic or hydrophobic, in air or immersed in water. In the latter case, the water may be degassed beforehand to prevent the formation of an air bubble wrapping the adhesive setae. The kinematics of approach is controlled and similar to some extent to the terrestrial locomotion of beetles. The normal force between the animal and the substrate is measured. Results indicate that the adhesion on immersed substrates is as strong as on non-immersed substrates, provided that the former are hydrophobic. By contrast, adhesion is strongly diminished on immersed hydrophilic substrates. The possible presence of a bubble has much less influence on the adhesion than thought in recent literature. The authors then propose a simple but effective model of the capillary bridges between the setal tips and the substrate. The model captures well the variations of the bridge shape and resulting force with the contact angle. The total adhesive force of the pad can finally be obtained by summing the force generated by each bridge, considering that contact angle would differ if the seta is immersed or in the bubble. With a minimal amount of ingredients, the model predicts the correct order of magnitude of the measured total adhesive force, and it rationalises the observed variations with the substrate.

I recommend the publication of this manuscript in the Journal of Experimental Biology. The following minor suggestions may be considered:

1. p. 7: In the description of the experiments, I could not find the approximate time during which the animal is immersed. Would there be any chance that the adhesive properties evolve over time?

The ladybug was immersed for not more than 15 mins underwater, during which 5 adhesion tests were performed. We did not observe any significant change in the adhesion during this time period.

1. p.12: The authors hypothesise that the absence of adhesion in somemeasurements could be due to the bundling of the setae. Owing to the measured stiffness of the hairs (e.g. Peisker et al., Nat. Comm. 4, 1661,2013) and corresponding model (Gorb and Filippov, Beilstein J. Nanotechnol. 5,837-845, 2014), this scenario seems very unlikely.

We believe that in this case, the bundling of the setae might be promoted by the presence of an air meniscus within the lower part of the hairs, resulting in an elasto-capillary bundling effect. Although the degassed water should dissolve most of the trapped air bubble, it is still possible that a small bubble remains underneath the array, which doesn’t contact with the surface but rather causes the hair to bundle by surface tension forces. An advanced imaging technique is however needed to verify this hypothesis, and could be interesting to look at in a future study.

1. p.16 - table 1: Why does the model use arbitrary (though realistic) values of contact angles and not the receding contact angle measurements reported in the supplementary material ? Also, is there any rationale for the other geometrical parameters (contact area fraction, hair aspect ratio, etc.)?

TODO

1. Similar models for the capillary force of a liquid bridge were developed in previous work (e.g. Arutinov et al., IEEE transactions on robotics,31(4), 1033-1043, 2015). Although the boundary conditions might not be the same as in this work, a quick review (in a few lines and citations) of previous capillary force models would be appreciated.

TODO

1. The model assumes that the contact line remains pinned at the edgeof the setal tip. Is this hypothesis justified for discoidal tips? And for other tips?

The relatively sharp rim of the discoidal shaped hair tip should in principle provide a mechanical pinning site for the secreted fluid. However, we don’t expect this assumption to be valid for other hair geometries such as the spatula or pointed shaped hairs. This is the reason why the experiments were done only on male ladybugs, which possess mostly discoidal hairs.

1. In section 4, the authors make a list of several ingredients that were omitted in the model and that could justify the discrepancy between the subsequent predictions and the force measurements. I wonder if the deformation of the setal tips in response to the capillary forces would be a significant additional ingredient to consider. Indeed, Gernay et al. (J. R. Soc. Interface 13, 20160371) have shown that even discoidal tips experience significant capillary-induced deformations upon contact.

We agree that the elastic property of the hairs will indeed influence adhesion as illustrated by the nice 2016 study by Gernay et. al.. However, when comparing the adhesion on smooth surfaces in air and underwater conditions, we expect that the elastic contribution should remain similar for each contact mode. Since the goal of the model was to understand how underwater adhesion would be different from that in air, neglecting any elastic effects is an assumption that we made to simplify our analysis.

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