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?

2. p.12: The authors hypothesise that the absence of adhesion in some measurements 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.

3. 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.)?

4. 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.

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

6. 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.