

SHORT COMMUNICATION

Sticking to it: testing passive pull-off forces in waterfall-climbing fishes across challenging substrates

Amanda M. Palecek^{1,*}, Heiko L. Schoenfuss² and Richard W. Blob¹

ABSTRACT

The pelvic sucker of Hawaiian waterfall climbing gobies allows these fishes to attach to substrates while climbing waterfalls tens to hundreds of meters tall. Climbing ability varies by species and may be further modulated by the physical characteristics of the waterfall substrate. In this study, we investigated the influence of surface wettability (hydrophobic versus hydrophilic surface charges) and substrate roughness on the passive adhesive system of four species of gobies with different climbing abilities. Overall, passive adhesive performance varied by species and substrate, with the strongest climbers showing the highest shear pull-off forces, particularly on rough surfaces. Thus, differences in passive adhesive performance may help to explain the ability of some species to migrate further upstream than others and contribute to their ability to invade new habitats.

KEY WORDS: Biomechanics, Locomotion, Roughness, Wettability, Goby, Adhesion

INTRODUCTION

Attachment mechanisms are commonly utilized by plants and animals, including invertebrates (Gorb et al., 2019; Kier and Smith, 2006; Smith, 1991; Zhou et al., 2014), mammals (Riskin and Fenton, 2001; Thewissen and Etnier, 1995), reptiles (Autumn et al., 2000; Russell, 2017), amphibians (Endlein et al., 2013; Kappl et al., 2016) and fishes (Chuang et al., 2017; Ditsche and Summers, 2019; Ditsche et al., 2014). These mechanisms are diverse and may incorporate intermolecular forces including van der Waals forces (Autumn et al., 2002), wet adhesion through capillarity or Stefan adhesion (Federle et al., 2006; Wicaksono et al., 2016), friction or interlocking structures (Naylor and Higham, 2019), and/or suction (Ditsche et al., 2014; Maie et al., 2012). Achieving adequate attachment performance can allow an organism to remain stationary despite exposure to external forces (Smith, 1991), or may allow an organism to defy gravity and adhere to substrates only accessible by sticking or climbing (Maie et al., 2012). The mechanism type and its performance are highly dependent on the external conditions to which it is exposed to during adhesion (Ditsche and Summers, 2014; Ditsche et al., 2017; England et al., 2016; Huber et al., 2007; Peng et al., 2014; Persson and Gorb, 2003; Stark et al., 2015). Moreover, the evolution of novel functional capacities such as

adhesion can facilitate the ability of species to occupy new or expanded niches (Blob et al., 2019; Lister, 1976; Maie et al., 2012; Price et al., 2010).

A well-established example of attachment mechanisms in an evolutionary radiation can be found among amphidromous gobiid fishes (Blob et al., 2019; Schoenfuss and Blob, 2007). In species that exhibit this life cycle, adults breed in freshwater streams, but fry are swept downstream to the ocean upon hatching, where they develop for several months before returning as juveniles to adult habitats (Schoenfuss and Blob, 2003). Juveniles face multiple challenges in their return journey upstream, including, for some species, tall waterfalls that stand as gateways to breeding habitats (Blob et al., 2008; Moody et al., 2017; Schoenfuss et al., 2013). All gobies possess an adhesive disc formed through developmental fusion of the pelvic fins (Budney and Hall, 2010; Maie et al., 2007; Taft et al., 2017), for which suction is a primary mechanism of attachment to underwater structures (Christy and Maie, 2019; Maie et al., 2012). In some amphidromous species, enhanced performance of the sucker enables scaling of waterfalls (Blob et al., 2007; Maie et al., 2012, 2013; Schoenfuss and Blob, 2003).

In the Hawaiian archipelago, gobies can be found at different stream elevations that may correlate with differences in their climbing abilities and attachment performance. The species *Stenogobius hawaiiensis* cannot climb and remains in estuaries upon returning from the ocean (Schoenfuss and Blob, 2007). Although it has a larger suction disc relative to body size than most climbing species, its disc exerts lower passive pressure differentials than those of climbing species at most body sizes, particularly as sucker size increases (Maie et al., 2012). *Awaous stamineus* climbs as a juvenile, but is typically found above only short waterfalls (~10 m high) and rarely climbs as an adult (Blob et al., 2007). Based on recordings of pressure differentials during climbing trials on Plexiglas, *A. stamineus* was calculated to exert lower suction forces per unit body mass than the two remaining Hawaiian species, *Sicyopterus stimpsoni* and *Lentipes concolor* (Maie et al., 2012). Both of these last species can climb waterfalls >100 m high, with *L. concolor* showing the greatest penetration upstream (Schoenfuss and Blob, 2003, 2007; Schoenfuss et al., 2013) and the greatest estimated capacity for suction to support its body weight (Maie et al., 2012).

Although the differences in calculated suction force across Hawaiian goby species appear to correspond well with their patterns of in-stream distribution, previous analyses were not able to address two potential complications. The first is that suction force estimates were calculated from measurements of pressure differential and sucker dimensions (Maie et al., 2012). Although this allowed estimation of forces exerted during climbing, these measurements may not reflect the forces required to actually dislodge attached fish, and do not account for additional components contributing to adhesion, such as friction or mucus (Denny and Gosline, 1980; Federle et al., 2006; Langowski et al., 2019; Smith, 2002). Second,

¹Department of Biological Sciences, Clemson University, Clemson, SC 29634, USA. ²Aquatic Toxicology Laboratory, Saint Cloud State University, Saint Cloud, MN 56301, USA.

*Author for correspondence (apalece@g.clemson.edu)

 A.M.P., 0000-0002-9908-3103; H.L.S., 0000-0001-5464-992X; R.W.B., 0000-0001-5026-343X

Table 1. Tenacity for each species of Hawaiian stream goby on each respective substrate, with bodyweight-normalized averages of the forces

	<i>Stenogobius hawaiiensis</i> (n=6)	<i>Awaous stamineus</i> (n=5)	<i>Sicyopterus stimpsoni</i> (n=5)	<i>Lentipes concolor</i> (n=5)
Body mass (g)	3.623	2.195	2.718	2.155
SL (mm)	55–70	60–75	50–65	60–70
PTFE				
Tenacity (Pa)	0±0	0.1028±0.0476	0.3109±0.1504	0.3129±0.1149
Normalized force	0×BW	2.102×BW	6.153×BW	8.194×BW
Glass				
Tenacity (Pa)	0±0	0.0859±0.04345	0.4440±0.1197	0.4264±0.1685
Normalized force	0×BW	2.612×BW	9.316×BW	9.449×BW
P600				
Tenacity (Pa)	0.2214±0.0311	0.6339±0.0383	0.9318±0.1784	1.2849±0.3606
Normalized force	5.571×BW	15.143×BW	21.714×BW	40.276×BW
P400				
Tenacity (Pa)	0.1917±0.0490	0.5802±0.0526	1.0795±0.3434	1.5893±0.0004
Normalized force	6.989×BW	16.204×BW	18.633×BW	30.010×BW

Tenacity is given as mean±1 s.e.m. and bodyweight (BW)-normalized forces are averages. Average body mass and standard length (SL) ranges are also listed.

whereas previous measurements were collected on a consistent substrate, substrate conditions encountered by climbing fishes may vary. Substrate roughness has been shown to impact climbing performance, with some roughness potentially improving attachment via friction, but rougher surfaces potentially preventing the disc from forming an effective seal (Blob et al., 2006). As fishes climb waterfalls, the presence of water may also affect suction or seal formation. Substrates with different wettability, or the ability of a substrate to maintain contact with water, may affect the ability of the pelvic sucker to form a seal if mucus contains hydrophobic components such as phospholipids. On hydrophobic substrates, water will bead as a result of high surface tension, whereas on hydrophilic substrates, water will spread across the substrate. Fish may encounter hydrophobic substrates such as rocks fouled with algae (Ozkan and Berberoglu, 2013), or hydrophilic silica rock (Chang et al., 2018). Fouling and differences in wettability might also cause slippage across a substrate and prevent adequate adhesion, thus decreasing the force required to detach fish (Ditsche et al., 2014).

In the current study, we measured shear pull-off forces required to detach the four species of Hawaiian gobies across a range of substrates with different characteristics. These comparisons address

two questions. First, does the ability of species to remain attached to surfaces differ in a pattern consistent with their measured climbing ability? Second, is the attachment performance of goby suckers affected by substrate characteristics such as roughness or wettability?

MATERIALS AND METHODS

Specimen collection

Mixed-sex adult specimens from each species ($N=5-6$ per species; body sizes reported in Table 1) were collected from their native streams in March 2020 on the Island of Hawai'i, using o'pae (prawn) nets (Fig. 1A–D). *Stenogobius hawaiiensis* Watson 1991 and *Awaous stamineus* (Eydoux and Souleyet 1850) were collected from Waiakea Pond using nets attached to long-handled poles. *Sicyopterus stimpsoni* (T. N. Gill 1860) and *Lentipes concolor* (T. N. Gill 1860) were collected from Hakalau and Nanue streams while snorkeling. Specimens from these species, therefore, were individuals that had successfully scaled a barrier to reach adult breeding habitats. Consistent with prior studies, fish were maintained in aerated stream water with feeding rocks and housed at the Fisheries Research Station of the Hawai'i Division of Aquatic Resources in Hilo, Hawai'i, until trials were conducted (within

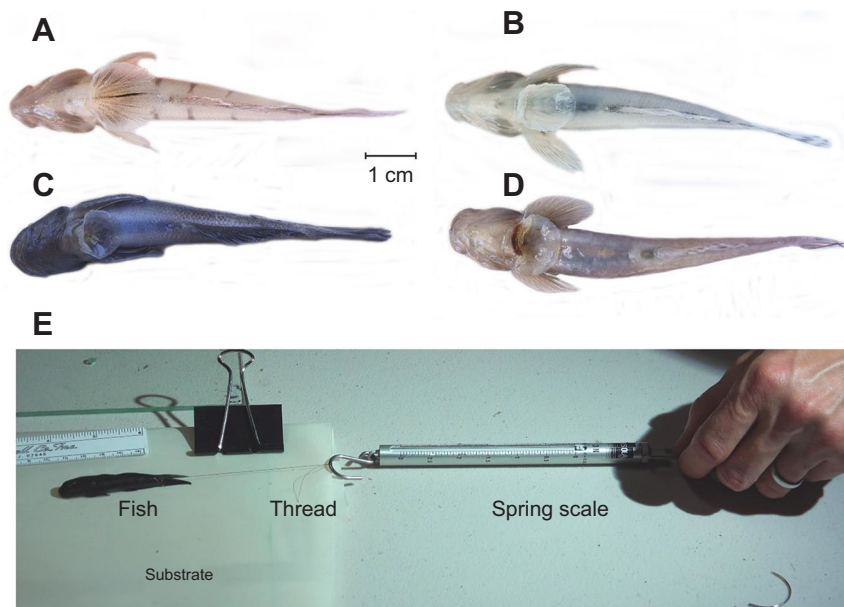


Fig. 1. Photographs of Hawaiian stream goby species, illustrating the pelvic sucker (in ventral view), and the experimental set up. (A) *Stenogobius hawaiiensis*. (B) *Awaous stamineus*. (C) *Sicyopterus stimpsoni*. (D) *Lentipes concolor*. (E) Experimental set up to measure the shear adhesive pull-off forces of the pelvic suckers in waterfall-climbing gobies. The photograph shows a fish threaded through the caudal peduncle and connected to a manual spring-scale. Trials were filmed as the scale was pulled backward, capturing the force at failure.

2–6 days of collection, depending on the species). Collections were conducted under Hawai'i Special Activity Permit 2021-07, and all animal collection and care procedures were approved by the Institutional Animal Care and Use Committee (IACUC) at Clemson University (IACUC 2017-085).

Pull-off trials

Fish were killed with neutral buffered 0.1% MS-222. The shear pull-off force of each fish was tested on four different dry substrates that were secured to a testing table: polytetrafluoroethylene (PTFE), glass, P600 fine-grained waterproof sandpaper and P400 coarse-grained waterproof sandpaper (Ali Industries, Inc., Fairborn, OH, USA; see Fig. S1 for SEM images of PTFE and sandpaper substrates, Table S1 for contact angle values). These different substrates were chosen to test differences in wettability (hydrophobic PTFE versus hydrophilic glass) and roughness (glass, 600-grit P600 sandpaper and 400-grit P400 sandpaper). Contact angle (wettability) was measured with Fiji using the *Contact Angle* plugin (Schindelin et al., 2012). A needle was used to pass 4-0 silk suture thread through the dorso-ventral midpoint of the caudal peduncle, immediately anterior to the caudal fin rays. This suture harness was then tied to a 3 N spring scale sensitive to 0.025 N (Pesola Medio-Line 40003). The scale was laid horizontally on the testing table and aligned with the long axis of the fish (Fig. 1E). Testing was conducted parallel to the long axis of each fish to best mimic the shear forces incurred from laminar flow during station holding or climbing. Specimens were lightly pressed onto the test substrate to engage the sucker, similar to previous studies (Ditsche et al., 2014; Wainwright et al., 2013). Trials were conducted by slowly pulling the spring scale caudally until the sucker failed. Engagement of the specimens with the surface, and pulling during trials, were performed by the same researcher (R.W.B.) to help ensure comparability across trials. Failure was classified as slippage of the specimen on the substrate or complete detachment of the specimen from the substrate. Trials were filmed at 30 frames s^{-1} with a Cyber-shot DSC RX10 4 camera (Sony Corporation, Tokyo, Japan) with both the fish and the spring-scale in the field of view, capturing the maximum shear force before slippage of the fish or failure of the sucker. Substrate order was randomized across each individual fish, and each fish was tested twice on each substrate. Between trials, glass and PTFE substrates were cleaned using a Kimwipe™ (Kimberly-Clark Corp., Irving, TX, USA) to remove water and residual mucus. Sandpaper was replaced between trials as it could not be effectively cleaned.

Statistical analysis

Each specimen was pulled twice on each substrate. The trial with the maximum shear pull-off force from each specimen on each substrate was used to conduct comparisons of the highest possible, biologically relevant pull-off forces. Prior to comparisons, shear pull-off forces for individuals were normalized by specimen body weight (in N) and divided by sucker area to produce calculations of tenacity, thus accounting for potential differences in performance related to body size. All statistical analyses were completed in R (<http://www.R-project.org/>). To compare measured tenacities, we used a fixed effect model with species, substrate and the interaction between species and substrate as variables. From this model, we ran a two-way ANOVA to test the effects of species, substrate type and their interaction on tenacity. Additional *post hoc* planned comparisons of the estimated marginal means were used to compare significance among the interactions between substrates and species using the *emmeans* and *car* packages in R (Russell, 2017).

RESULTS AND DISCUSSION

We measured shear pull-off forces and calculated tenacity for 21 gobies ($n=6$ *S. hawaiiensis*, $n=5$ each for *A. stamineus*, *S. stimpsoni* and *L. concolor*; Table 1; Table S2). Both species ($P<0.01$, d.f.=3, $F=18.9958$) and substrate ($P<0.01$, d.f.=3, $F=16.8778$) significantly affected maximum tenacity. However, the interaction between species and substrate did not have a significant effect on the maximum tenacity ($P=0.08582$, d.f.=9, $F=1.7915$).

To further explore interactions between individual species and substrates, *post hoc* planned comparisons were performed to compare tenacity between substrates in an individual species, and between species for each individual substrate (Fig. 2; Tables S3 and S4). There were no significant effects of substrate for the non-climbing species, *S. hawaiiensis*. For the lowest-climbing species, *A. stamineus*, there was a significant effect of glass versus both rough sandpapers, and between PTFE and the fine (P600) sandpaper. In each of these cases, tenacity was higher on the rough substrates than on smooth glass or PTFE. *Sicyopterus stimpsoni* and *L. concolor* had no significant difference in tenacity between the smooth substrates or between the rough substrates but did show a significant difference in tenacity between smooth substrates and rough substrates, where resistance to dislodgement was highest on rough substrates.

Species also showed some significant differences in performance within each substrate type (Table 1; Table S4). For example, on glass and PTFE, there were no significant differences in tenacity between any species. However, on fine (P600) sandpaper, the non-climber, *S. hawaiiensis*, had significantly lower tenacity than the two species found at the highest elevations, *S. stimpsoni* and *L. concolor*, but did not differ significantly from the lowest-climbing species, *A. stamineus*. On rough (P400) sandpaper, there were no significant differences between the non-climber *S. hawaiiensis* and lowest climber *A. stamineus*, but there were significant differences between these species and the two highest-climbing species, where species found in higher elevation streams had significantly higher tenacity.

Attachment performance, measured through shear pull-off trials, correlated with climbing ability and upstream penetration in Hawaiian gobies. Regardless of substrate, the non-climbing species, *S. hawaiiensis*, exhibited minimal tenacity, with the lowest-elevation climber, *A. stamineus*, showing slightly stronger attachment (Table 1). The two highest-elevation climbers, *S. stimpsoni* and *L. concolor*, exhibited greater tenacity in shear. Moreover, although the two high-elevation species overlapped in shear resistance on smooth surfaces, on more natural rough surfaces the performance of these species followed expectations based on in-stream species distributions, with *L. concolor* (the species found at the highest elevations) showing greater tenacity than *S. stimpsoni*. This gradient of passive attachment performance, measuring actual dislodgement forces and accounting for characteristics such as sucker mucus and friction forces, concurs with patterns identified from *in vivo* estimates of suction pressure, where non-climbing species exhibited lower body weight-standardized suction forces compared with climbing species found at increasing stream elevations (Maie et al., 2012). Such differences in attachment performance may, in part, be due to the pelvic lever system, wherein better climbers have larger input levers than poor climbers and non-climbers (Maie et al., 2013). The correspondence across these studies suggests largely complimentary contributions of the different components of the sucker system (e.g. sucker size, pressure production, mucus, friction) to adhesive performance, which might reflect evolution in a highly integrated, rather than

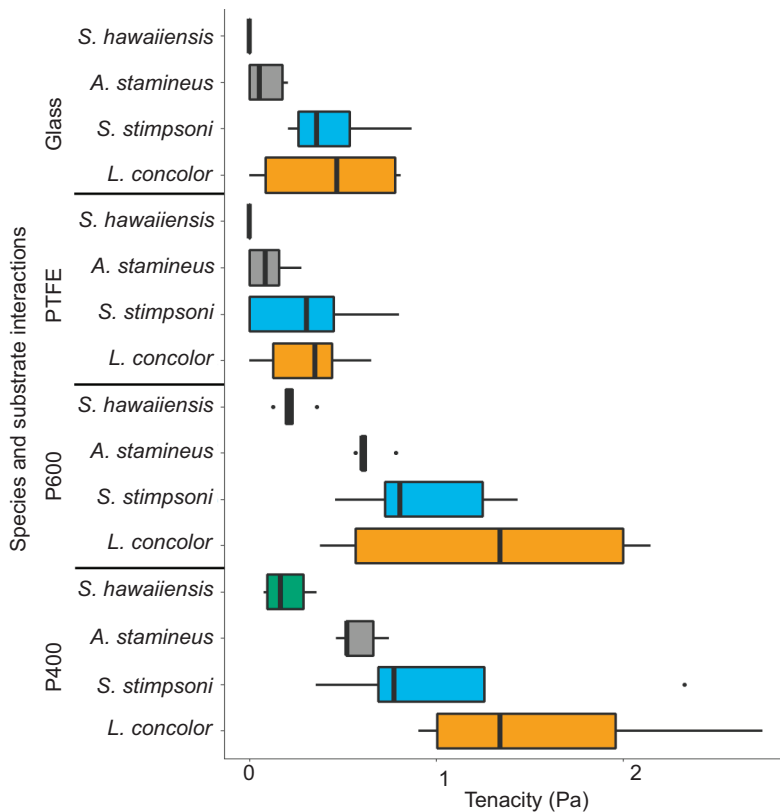


Fig. 2. Box and whisker plot of tenacity for each species and substrate interaction. Tenacity (Pa) was measured for the non-climber *S. hawaiiensis*, and for climbing *A. stamineus*, *S. stimpsoni* and *L. concolor*. Dark vertical bars are medians, light vertical bars (from left to right) on the boxes are 1st and 3rd quartiles, whiskers show minimum and maximum values outside of outliers, and dots represent outliers. The roughness of substrates (with grit size, if applicable) increases from top to bottom.

mosaic fashion. Such synergistic adhesive mechanisms have been previously suggested in invertebrates (Smith, 1991; Thomas and Hermans, 1985), lizards (Crandell et al., 2014; Irschick et al., 2006; Naylor and Higham, 2019) and fishes (Wicaksono et al., 2016).

While our results support a trend of increasing performance with increasing climbing ability, it is important to acknowledge the potential for differences in performance between live, active fish and freshly euthanized fish (Christy and Maie, 2019; Maie et al., 2012). Active climbing in *Sicyopterus* spp. on a 'fine sand' substrate exhibited suction pressures capable of supporting on average 3.055 times body mass (Christy and Maie, 2019), whereas our results suggest that average dislodgement force of *S. stimpsoni* on the roughest sandpaper (P400) is 18.635 ± 2.596 times body mass. A variety of factors might contribute to the different numeric values of results across these studies, including variation in substrate roughness, differences in substrate orientation (60 deg incline versus flat), and the differences between the natural preload of the fishes versus manual preloading from our experiment. Nonetheless, patterns of performance across species are largely consistent among comparative studies of attachment performance.

In our dislodgement tests, some substrates proved strikingly difficult for gobies to attach to. Glass is a relatively smooth, hydrophilic substrate (Birdi and Vu, 1993). In our personal observations, glass aquaria must be fitted with lids to prevent fish from climbing out; however, the species we tested all performed poorly on glass. This may suggest a strong role for active factors in adhesion to clean glass surfaces by gobies, where movements of the body and fins, or muscles surrounding the pelvic sucker, work to allow suction to glass. Alternatively, this could suggest that gobies adhere better to glass if it is fouled in some way. In contrast, PTFE substrates are hydrophobic, resisting water and preventing adhesion in some conditions (Crisp et al., 1985; Stark et al., 2013; Watson et al., 2010). Wettability may play a role in adhesive forces,

especially when an active adhesive mechanism is in place. However, our tested species not only performed poorly on the hydrophobic substrates but also overall showed little difference in adhesion between hydrophilic glass and hydrophobic PTFE (with the non-climber, *S. hawaiiensis*, showing no adhesion to either). It is possible that differences in adhesion across smooth substrates with different levels of wettability could be revealed by removing the epidermal mucus present on the pelvic sucker. Further testing of climbing kinematics and adhesive forces on substrates of varying wettability could improve understanding of how substrate wettability affects adhesion and movements during climbing.

Differences in surface roughness may also impact adhesive performance. For both species that penetrate further upstream (*S. stimpsoni* and *L. concolor*), adhesive performance was better on sandpaper than on smooth glass but decreased on the rougher P400 surface (though this difference was only significant for *L. concolor*). These results parallel those of climbing trials from juvenile gobies of the same species, in which climbing performance typically improved on surfaces coated with sand, compared with smooth surfaces (Blob et al., 2006). Other species of adhesive fishes, such as river loaches and clingfishes, also attach to rough substrates as well as (or better than) they do to smooth substrates (Chuang et al., 2017; Ditsche et al., 2014). This may suggest that among fishes using suction adhesion, attachment is enhanced on complex substrates which possess some element of roughness. However, among gobies on rough substrates, we observed a decrease in attachment performance with only a slight increase in roughness (P600 to P400), suggesting a potentially small window of surface roughness that facilitates optimal passive attachment. Active control may be necessary to allow adjustments that could promote performance across a wider range of surfaces in nature. Further studies should expand the variety of rough substrates that are tested to find the limits of passive adhesion and determine which

substrates gobies prefer to climb (Chuang et al., 2017; Wainwright et al., 2013).

Attachment to challenging substrates has been an emerging focus in many research groups, as manufactured adhesives often perform poorly when placed on substrates that are rough, wet or fouled (Ditsche and Summers, 2019; Ditsche et al., 2014; Endlein et al., 2013; Stark et al., 2013). Animal models have been a popular source for inspiration of such designs, as many animals possess mechanisms that regularly overcome these physical challenges. Differences in adhesive capacity across different goby species could provide an additional avenue to explore design factors that contribute to adhesive success under challenging conditions. A limited range of differences appear able to transform a weakly adherent structure into one able to climb roughly 300 m in rushing water. Further studies can seek to isolate the factors on which such outstanding performance depends, particularly with detailed comparisons of sucker morphology and material properties.

Acknowledgements

We would like to thank the staff of the Hilo Division of Aquatic Resources Research Station (N. Ahu, L. Nishiura, T. Sakihara, T. Shimoda and T. Shindo) for facility access, assistance and hospitality. We thank T. Maie for assistance in catching fishes for the experiment, K. Diamond and C. Mayerl for suggestions on R code and statistical analysis methods, A. Summers for helpful discussion on standardizing tenacity forces, G. Korneva for assistance in collecting contact angle measurements, and two anonymous reviewers for their time and effort in improving the manuscript.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: A.M.P., H.L.S., R.W.B.; Methodology: A.M.P., H.L.S., R.W.B.; Software: A.M.P.; Validation: A.M.P.; Formal analysis: A.M.P.; Investigation: A.M.P., R.W.B.; Resources: A.M.P., R.W.B.; Data curation: A.M.P.; Writing - original draft: A.M.P.; Writing - review & editing: A.M.P., H.L.S., R.W.B.; Visualization: A.M.P.; Supervision: H.L.S., R.W.B.; Project administration: H.L.S., R.W.B.; Funding acquisition: A.M.P., R.W.B.

Funding

This work was supported by Clemson University Creative Inquiry grant no. 479 and the Clemson Biological Sciences Professional Development Grant-in-Aid of Research.

Supplementary information

Supplementary information available online at <https://jeb.biologists.org/lookup/doi/10.1242/jeb.228718.supplemental>

References

- Autumn, K., Liang, Y. A., Hsieh, S. T., Zesch, W., Chan, W. P., Kenny, T., Fearing, R. and Full, R. J.** (2000). Adhesive force of a single gecko foot-hair. *Nature* **405**, 671-702. doi:10.1038/35015073
- Autumn, K., Sitti, M., Liang, Y. A., Peattie, A. M., Hansen, W. R., Sponberg, S., Kenny, T. W., Fearing, R., Israelachvili, J. N. and Full, R. J.** (2002). Evidence for van der Waals adhesion in gecko setae. *Proc. Natl. Acad. Sci. USA* **99**, 12252-12256. doi:10.1073/pnas.192252799
- Birdi, K. S. and Vu, D. T.** (1993). Wettability and the evaporation rates of fluids from solid surfaces. *J. Adhes. Sci. Technol.* **7**, 485-493. doi:10.1163/156856193X00808
- Blob, R. W., Rai, R., Julius, M. L. and Schoenfuss, H. L.** (2006). Functional diversity in extreme environments: Effects of locomotor style and substrate texture on the waterfall-climbing performance of Hawaiian gobiid fishes. *J. Zool.* **268**, 315-324. doi:10.1111/j.1469-7998.2005.00034.x
- Blob, R. W., Wright, K. M., Becker, M., Maie, T., Iverson, T. J., Julius, M. L. and Schoenfuss, H. L.** (2007). Ontogenetic change in novel functions: Waterfall climbing in adult Hawaiian gobiid fishes. *J. Zool.* **273**, 200-209. doi:10.1111/j.1469-7998.2007.00315.x
- Blob, R. W., Bridges, W. C., Ptacek, M. B., Maie, T., Cediell, R. A., Bertolas, M. M., Julius, M. L. and Schoenfuss, H. L.** (2008). Morphological selection in an extreme flow environment: Body shape and waterfall-climbing success in the Hawaiian stream fish *Sicyopterus stimpsoni*. *Integr. Comp. Biol.* **48**, 734-749. doi:10.1093/icb/icn086
- Blob, R. W., Lagarde, R., Diamond, K. M., Keeffe, R. M., Bertram, R. S., Ponton, D. and Schoenfuss, H. L.** (2019). Functional diversity of evolutionary novelties: insights from waterfall-climbing kinematics and performance of juvenile gobiid fishes. *Integr. Org. Biol.* **1**, obz029. doi:10.1093/iob/obz029
- Budney, L. A. and Hall, B. K.** (2010). Comparative morphology and osteology of pelvic fin-derived midline suckers in lumpfishes, snailfishes and gobies. *J. Appl. Ichthyol.* **26**, 167-175. doi:10.1111/j.1439-0426.2010.01398.x
- Chang, X., Xue, Q., Li, X., Zhang, J., Zhu, L., He, D., Zheng, H., Lu, S. and Liu, Z.** (2018). Inherent wettability of different rock surfaces at nanoscale: a theoretical study. *Appl. Surf. Sci.* **434**, 73-81. doi:10.1016/j.apsusc.2017.10.173
- Christy, R. M. and Maie, T.** (2019). Adhesive force and endurance during waterfall climbing in an amphidromous gobiid, *Sicyopterus japonicus* (Teleostei: Gobiidae): Ontogenetic scaling of novel locomotor performance. *Zoology* **133**, 10-16. doi:10.1016/j.zool.2019.02.001
- Chuang, Y., Chang, H., Liu, G. and Chen, P.** (2017). Climbing upstream: multi-scale structural characterization and underwater adhesion of the Pulin river loach (*Sinogastromyzon puliensis*). *J. Mech. Behav. Biomed. Mater.* **73**, 76-85. doi:10.1016/j.jmbm.2017.01.029
- Crandell, K. E., Herrel, A., Sasa, M., Losos, J. B. and Autumn, K.** (2014). Stick or grip? Co-evolution of adhesive toepads and claws in *Anolis* lizards. *Zoology* **117**, 363-369. doi:10.1016/j.zool.2014.05.001
- Crisp, D. J., Walker, G., Young, G. A. and Yule, A. B.** (1985). Adhesion and substrate choice in mussels and barnacles. *J. Colloid Interface Sci.* **104**, 40-50. doi:10.1016/0021-9797(85)90007-4
- Denny, M. W. and Gosline, J. M.** (1980). The physical properties of the pedal mucus of the terrestrial slug, *Ariolimax columbianus*. *J. Exp. Biol.* **88**, 375-394.
- Ditsche, P. and Summers, A. P.** (2014). Aquatic versus terrestrial attachment: Water makes a difference. *Beilstein J. Nanotechnol.* **5**, 2424-2439. doi:10.3762/bjnano.5.252
- Ditsche, P. and Summers, A.** (2019). Learning from Northern clingfish (*Gobiesox maeandricus*): Bioinspired suction cups attach to rough surfaces. *Phil. Trans. R. Soc. B* **374**, 20190204. doi:10.1098/rstb.2019.0204
- Ditsche, P., Wainwright, D. K. and Summers, A. P.** (2014). Attachment to challenging substrates – fouling, roughness and limits of adhesion in the northern clingfish (*Gobiesox maeandricus*). *J. Exp. Biol.* **217**, 2548-2554. doi:10.1242/jeb.100149
- Ditsche, P., Hicks, M., Truong, L., Linkem, C. and Summers, A.** (2017). From smooth to rough, from water to air: The intertidal habitat of northern clingfish (*Gobiesox maeandricus*). *Sci. Nat.* **104**, 33. doi:10.1007/s00114-017-1454-8
- Endlein, T., Barnes, W. J. P., Samuel, D. S., Crawford, N. A., Biaw, A. B. and Grafe, U.** (2013). Sticking under wet conditions: The remarkable attachment abilities of the torrent frog, *Staurois guttatus*. *PLoS ONE* **8**, e73810. doi:10.1371/journal.pone.0073810
- England, M. W., Sato, T., Yagihashi, M., Hozumi, A., Gorb, S. N. and Gorb, E. V.** (2016). Surface roughness rather than surface chemistry essentially affects insect adhesion. *Beilstein J. Nanotechnol.* **7**, 1471-1479. doi:10.3762/bjnano.7.139
- Federle, W., Barnes, W. J. P., Baumgartner, W., Drechsler, P. and Smith, J. M.** (2006). Wet but not slippery: Boundary friction in tree frog adhesive toe pads. *J. R. Soc. Interface* **3**, 689-697. doi:10.1098/rsif.2006.0135
- Gorb, E. V., Lemke, W. and Gorb, S. N.** (2019). Porous substrate affects a subsequent attachment ability of the beetle *Harmonia axyridis* (Coleoptera, Coccinellidae). *J. R. Soc. Interface* **16**, 20180696. doi:10.1098/rsif.2018.0696
- Huber, G., Gorb, S. N., Hosoda, N., Spolenak, R. and Arzt, E.** (2007). Influence of surface roughness on gecko adhesion. *Acta Biomater.* **3**, 607-610. doi:10.1016/j.actbio.2007.01.007
- Irschick, D. J., Herrel, A. and Vanhooydonck, B.** (2006). Whole-organism studies of adhesion in pad-bearing lizards: Creative evolutionary solutions to functional problems. *J. Comp. Physiol. A* **192**, 1169-1177. doi:10.1007/s00359-006-0145-2
- Kappl, M., Kaveh, F. and Barnes, W. J. P.** (2016). Nanoscale friction and adhesion of tree frog toe pads. *Bioinspir. Biomim.* **11**, 035003. doi:10.1088/1748-3190/11/3/035003
- Kier, W. M. and Smith, A. M.** (2006). The structure and adhesive mechanism of octopus suckers. *Integr. Comp. Biol.* **42**, 1146-1153. doi:10.1093/icb/42.6.1146
- Langowski, J. K. A., Singla, S., Nyarko, A., Schipper, H., Van Den Berg, F. T., Kaur, S., Astley, H. C., Gussekloo, S. W. S., Dhinojwala, A. and Van Leeuwen, J. L.** (2019). Comparative and functional analysis of the digital mucus glands and secretions of tree frogs. *Front. Zool.* **16**, 19. doi:10.1186/s12983-019-0315-z
- Liechti, K. M., Schnapp, S. T. and Swadener, J. G.** (1997). Contact angle and contact mechanics of a glass/epoxy interface. *Int. J. Fract.* **86**, 361-374. doi:10.1023/A:1007472628431
- Lister, B. C.** (1976). The nature of niche expansion in West Indian *Anolis* lizards II: evolutionary components. *Evolution (N. Y.)* **30**, 677-692. doi:10.2307/2407809
- Maie, T., Schoenfuss, H. L. and Blob, R. W.** (2007). Ontogenetic scaling of body proportions in waterfall-climbing gobiid fishes from Hawai'i and Dominica: Implications for locomotor function. *Copeia* **2007**, 755-764. doi:10.1643/0045-8511(2007)2007[755:OSOBPI]2.0.CO;2
- Maie, T., Schoenfuss, H. L. and Blob, R. W.** (2012). Performance and scaling of a novel locomotor structure: adhesive capacity of climbing gobiid fishes. *J. Exp. Biol.* **215**, 3925-3936. doi:10.1242/jeb.072967

- Maie, T., Schoenfuss, H. L. and Blob, R. W.** (2013). Musculoskeletal determinants of pelvic sucker function in Hawaiian stream gobiid fishes: Interspecific comparisons and allometric scaling. *J. Morphol.* **274**, 733-742. doi:10.1002/jmor.20130
- Moody, K. N., Kawano, S. M., Bridges, W. C., Blob, R. W., Schoenfuss, H. L. and Ptacek, M. B.** (2017). Contrasting post-settlement selection results in many-to-one mapping of high performance phenotypes in the Hawaiian waterfall-climbing goby *Sicyopterus stimpsoni*. *Evol. Ecol.* **31**, 489-516. doi:10.1007/s10682-017-9889-0
- Naylor, E. R. and Higham, T. E.** (2019). Attachment beyond the adhesive system: the contribution of claws in gecko clinging and locomotion. *Integr. Comp. Biol.* **59**, 168-181. doi:10.1093/icb/icz027
- Ozkan, A. and Berberoglu, H.** (2013). Adhesion of algal cells to surfaces. *Biofouling J. Bioadhesion Biofilm Res.* **29**, 469-482. doi:10.1080/08927014.2013.782397
- Peng, Z. L., Wang, C. and Chen, S. H.** (2014). Effects of surface wettability on gecko adhesion underwater. *Colloids Surfaces B Biointerfaces* **122**, 662-668. doi:10.1016/j.colsurfb.2014.07.047
- Persson, B. N. J. and Gorb, S.** (2003). The effect of surface roughness on the adhesion of elastic plates with application to biological systems. *J. Chem. Phys.* **119**, 11437-11444. doi:10.1063/1.1621854
- Price, S. A., Wainwright, P. C., Bellwood, D. R., Kazancioglu, E., Collar, D. C. and Near, T. J.** (2010). Functional innovations and morphological diversification in parrotfish. *Evolution* **64**, 3057-3068. doi:10.1111/j.1558-5646.2010.01036.x
- Riskin, D. K. and Fenton, M. B.** (2001). Sticking ability in Spix's disk-winged bat, *Thyroptera tricolor* (Microchiroptera: Thyropteridae). *Can. J. Zool.* **79**, 2261-2267. doi:10.1139/z01-192
- Russell, A. P.** (2017). The structure of anoline (Reptilia: Dactyloidae: *Anolis*) toe pads in relation to substratum conformity. *Acta Zool.* **98**, 300-309. doi:10.1111/azo.12180
- Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C., Saalfeld, S., Schmid, B. et al.** (2012). Fiji: An open-source platform for biological-image analysis. *Nat. Methods* **9**, 676-682. doi:10.1038/nmeth.2019
- Schoenfuss, H. L. and Blob, R. W.** (2003). Kinematics of waterfall climbing in Hawaiian freshwater fishes (Gobiidae): Vertical propulsion at the aquatic-terrestrial interface. *J. Zool.* **261**, 191-205. doi:10.1017/S0952836903004102
- Schoenfuss, H. L. and Blob, R. W.** (2007). The importance of functional morphology for fishery conservation and management: applications to Hawaiian amphidromous fishes. *Bish. Museum Bull. Cult. Environ. Stud.* **3**, 125-141.
- Schoenfuss, H. L., Maie, T., Moody, K. N., Lesteberg, K. E., Blob, R. W. and Schoenfuss, T. C.** (2013). Stairway to heaven: Evaluating levels of biological organization correlated with the successful ascent of natural waterfalls in the hawaiian stream goby *Sicyopterus stimpsoni*. *PLoS ONE* **8**, 1-14. doi:10.1371/journal.pone.0084851
- Smith, A. M.** (1991). The role of suction in the adhesion of limpets. *J. Exp. Biol.* **161**, 151-169.
- Smith, A. M.** (2002). The structure and function of adhesive gels from invertebrates. *Integr. Comp. Biol.* **42**, 1164-1171. doi:10.1093/icb/42.6.1164
- Stark, A. Y., Badge, I., Wucinich, N. A., Sullivan, T. W., Niewiarowski, P. H. and Dhinojwala, A.** (2013). Surface wettability plays a significant role in gecko adhesion underwater. *Proc. Natl. Acad. Sci. USA* **110**, 6340-6345. doi:10.1073/pnas.1219317110
- Stark, A. Y., Palecek, A. M., Argenbright, C. W., Bernard, C., Brennan, A. B., Niewiarowski, P. H. and Dhinojwala, A.** (2015). Gecko adhesion on wet and dry patterned substrates. *PLoS ONE* **10**, e0145756. doi:10.1371/journal.pone.0145756
- Taft, N. K., Taft, B. N., Henck, H., Diamond, K. M., Schoenfuss, H. L. and Blob, R. W.** (2017). Comparative morphology and mechanical properties of the lepidotrichia of climbing and non-climbing Hawaiian gobioid fishes. *Cybium* **41**, 107-115.
- Thewissen, A. J. G. M. and Etnier, S. A.** (1995). Adhesive devices on the thumb of vespertilionoid bats (Chiroptera). *J. Mammal.* **76**, 925-936. doi:10.2307/1382762
- Thomas, L. A. and Hermans, C. O.** (1985). Adhesive interactions between the tube feet of a starfish, *Leptasterias hexactis*, and substrata. *Biol. Bull.* **169**, 675-688. doi:10.2307/1541309
- Wainwright, D. K., Kleinteich, T., Kleinteich, A., Gorb, S. N. and Summers, A. P.** (2013). Stick tight: suction adhesion on irregular surfaces in the northern clingfish. *Biol. Lett.* **9**, 1-5. doi:10.1098/rsbl.2013.0234
- Watson, G. S., Watson, J. A., Hu, S., Brown, C. L., Cribb, B. W. and Myhra, S.** (2010). Micro and nanostructures found on insect wings - Designs for minimising adhesion and friction. *Int. J. Nanomanuf.* **5**, 112-128. doi:10.1504/IJNM.2010.029929
- Wicaksono, A., Hidayat, S., Damayanti, Y., Jin, D. S. M., Sintya, E., Retnoaji, B. and Alam, P.** (2016). The significance of pelvic fin flexibility for tree climbing fish. *Zoology* **119**, 511-517. doi:10.1016/j.zool.2016.06.007
- Zhou, Y., Robinson, A., Steiner, U. and Federle, W.** (2014). Insect adhesion on rough surfaces: analysis of adhesive contact of smooth and hairy pads on transparent microstructured substrates. *J. R. Soc. Interface* **11**, 20140499. doi:10.1098/rsif.2014.0499