

Tail morphology and Swimming Performance in *Ambystoma laterale* and *Plethodon cinereus*

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Ellen Johnson

Advisors: Drs. Michael J. Cramer & Vanessa Young

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ABSTRACT

Morphology is known to influence performance, specifically locomotion, in all organisms. Tail morphology can have aquatic and terrestrial locomotion implications. *Ambystoma laterale* is a species of salamander that has a laterally compressed tail, a shape commonly associated with aquatic species, despite only spending a short time in water to breed. *Plethodon cinereus* is a salamander species with a round tail due to it being fully terrestrial. I hypothesized that these differences in tail morphology and life history would lead to *A. laterale* have greater swimming performance capabilities compared to *P. cinereus* when faced with swimming against varying flow rates. After taking tail and body measurements and running swimming trials with 6 salamanders of each species, I found that *A. laterale* have longer swimming strides compared to *P. cinereus* due to their relatively larger tail surface area, but no difference in swimming velocity was found. These findings highlight one morphological advantage lateral tail compression provides in terms of swimming performance. They also show that other factors, such as tail beat amplitude, swimming gait, and tail beat frequency, may have a greater influence on swimming velocity than tail morphology alone.

The relationships between morphology, performance, and fitness have been documented and studied in a variety of groups, such as fish, salamanders, and snakes (Arnold, 1983; Fitzpatrick, *et al.*, 2003; Hawkins and Quinn, 1996; Irschick and Garland Jr, 2001). Quantifying these relationships can show how well adapted an organism is to its environment. Performance is often used as a quantifiable key intermediate to determine relationships between morphology and fitness (Arnold, 1983; Urban, 2010). Arnold (1983) addressed this by broadly outlining a strategy to directly measure the selection pressure on morphological traits based on variation in performance by quantifying the relationships between morphology, performance, and fitness.

When it comes to assessing how heavily performance is influenced by morphology, this is called the performance gradient, variation in the habitat of organisms must be considered. Habitat conditions influence how organisms behave and interact with their environment and community. Moermond (1979) looked at how habitat constrains behavior, morphology, and community structures of *Anolis* lizards. Using perch matrices as the habitat variable, Moermond

compared different *Anolis* lizard species in their movements, distribution, and related morphologies. Aubret and Shine (2008) demonstrated how habitat variation has led to morphological and performance differences between populations of aquatic snakes by artificially manipulating tail morphology and testing swimming performance measures. Their results demonstrated that particular morphologies allow organisms to perform better in certain habitats over others. This leads to natural selection favoring different characteristics based on habitat conditions, which could lead to similarities in the morphology among species found within a certain habitat (Storfer and White, 2004). Likewise, species found in differing habitats, even if only for part of their lives, can exhibit different morphologies to best fit their respective habitat conditions.

Habitat can influence some aspects of morphology because it influences the locomotion of organisms. Morphology is directly related to movement, so different habitats require specific morphologies for animals to adequately traverse them. Locomotion is part of most organisms' daily behaviors, making it an important aspect of performance to study (Irschick and Garland Jr, 2001). The relationship between locomotor performance and morphology can be quantified to analyze the strength of this relationship. Some key studies looked at the relationship between morphology and performance by assessing locomotion (Aubret and Shine, 2008; Irschick and Garland Jr, 2001). Ijspeert and Cabelguen (2006) modeled salamander locomotion by studying and measuring morphology as well as movement. Irschick and Garland Jr. (2001) used locomotion to explore the relationship between morphology and performance with respect to environmental variations. Instances where environmental variations influence performance and morphology can result in similar morphological trends between species that share a similar niche (Alberch, 1981).

The morphological aspects of tails are known to have an impact on the locomotor performance of some organisms, especially while swimming (Bennett, *et al.*, 1989; Hawkins and Quinn, 1996; Ijspeert and Cabelguen, 2006). Ijspeert and Cabelguen (2006) examined tail morphology in relation to walking and swimming in salamanders by modeling their movement and body measurements. Hawkins and Quinn (1996) looked at tail shape to assess swimming performance in various species of trout and found that tail size and certain aspects of shape had the most influence on performance. Laterally compressed tail shape is most often observed in aquatic species since lateral compression provides a large surface area for generating thrust when in water (Aubret and Shine, 2008). Round tail shape is more often observed in terrestrial species because it aids in locomotion and balance on land (Dawson, 2003).

Salamanders are a diverse group when it comes to tail morphology due to the variety of habitats inhabited by the different species. This variation can be partially explained by habitat variation and life history, as different environments contain different challenges and therefore require different morphologies. Many species of salamanders have an aquatic life stage, and therefore have morphologies related to aquatic locomotion such as laterally compressed tails and gills as efts (Ohio Divisions of Wildlife, 2012). Other salamander species are completely terrestrial and therefore have round tails and never have a life stage that possesses gills (Cochran, 1911). This study will investigate how tail morphology relates to swimming performance in two salamander species and see if salamanders with laterally compressed tails exhibit greater swimming performance compared to those with round tails.

When assessing the relationship between swimming performance and tail morphology in salamanders, many studies focus on the larval stage since this is the stage during which many salamanders must live in water and rely on swimming to survive. Fitzpatrick *et al.* (2003),

Storfer and White (2004), and Urban (2010) all explore aspects of this relationship in salamander larvae because, in this life stage, swimming performance relates directly to fitness as it is a key factor in escaping predators. Though some have looked at the tails of adult salamanders, including Bennett *et al.* (1989) and Ijspeert and Cabelguen (2006), there is less focus on swimming performance compared to terrestrial locomotion when dealing with adult salamanders. This study aims to assess swimming performance measures in adults and compare salamanders that are fully terrestrial to salamanders with an aquatic larval stage and which breed in water. I also aim to assess swimming performance of salamanders swimming against flowing water at varying rates.

Plethodon cinereus and *Ambystoma laterale* are salamander species with different life histories and tail morphologies. *A. laterale*, the blue-spotted salamander, has a laterally compressed tail, which is commonly associated with aquatic organisms, and may best be explained by their return to vernal pools for breeding each year (Ohio Divisions of Wildlife, 2012). *P. cinereus*, the redback salamander, has a round tail because it is a fully terrestrial salamander that does not have an aquatic larval stage, and therefore does not require adaptations associated with increased swimming performance (Cochran, 1911). Assessing the swimming performance of *P. cinereus* and *A. laterale* is important for understanding the performance gradient associated with laterally compressed tails and swimming performance. Testing their swimming performance against a variety of flow rates could be useful despite neither species having a major ecological role in flowing water bodies. This is because with events such as heavy rain or habitat change, these salamanders may have to interact with flowing water as vernal pools drain or connect to other bodies of water (Pennsylvania Natural Heritage Program, 2015). It is important to address these ideas as they will help in the understanding of the

relationship that the laterally compressed tail morphology has with swimming velocity and efficiency and the ecology of these salamanders.

This study investigates the performance gradient in *P. cinereus* and *A. laterale* by focusing on tail morphology and using swimming velocity and tail stride length, defined here as how far an individual travels with a single beat of their tail, as a proxy for locomotor performance. The factors of tail morphology that I measured were length, depth, and surface area. The first hypothesis I tested is that salamanders with greater relative tail surface area would exhibit higher swimming velocities and travel farther with each beat of their tail compared to those with relatively smaller tails. This research also assesses the influence of varying water flow rates on the swimming performance of these salamanders, so I also hypothesized that salamanders that swim against increasing flow rates would exhibit decreased swimming velocities and tail stride lengths. The third hypothesis is that *A. laterale* would exhibit higher swimming velocities and have longer tail stride lengths than *P. cinereus* because of their differences in tail morphology and life history.

MATERIALS AND METHOD

I collected 16 total salamanders from forested areas at the University of Notre Dame Environmental Research Center (UNDERC), and these locations were noted so they could be returned to the appropriate locations. Collection took place in late June through early July. I housed individual salamanders in plastic containers that contained leaf litter taken from the area of collection as well as a moistened paper towel in each of them. Paper towels were dampened daily. Containers were cleaned after each salamander was released so they could be reused. Salamanders were fed a slug or wireworm found in the field after three days of holding if the individual was kept for that long. No individual was held for more than 6 days. Salamanders

were returned to the area in which they were found on UNDERC property after data collection was complete.

I tested the swimming performance of each salamander against four different set flow rates (0, 2, 3.5, and 5.3 cm/sec) with an artificial stream. Each salamander was tested for swimming velocity at all four water flow rates. Salamanders did two swim trials per day to avoid exhaustion and the order in which individuals swam against the four flow rates varied.

The set-up for the trials consisted of a swimming lane in an artificial stream. The swim lane was made from a laterally cut PVC pipe and had lines drawn on to indicate distances from 0-50 cm at 10 cm intervals. This provided a scale with which to calculate swimming velocity and tail stride length. The swim lane also had fine plastic mesh glued to either end to prevent salamanders from escaping or being swept away by the water flow. The stream used a motor to move a paddle wheel at different controllable speeds to produce water flow inside a container where the PVC swim lane was secured with rocks at either end (Figure 1). Flow rates were assessed and determined using a float made from folded duct tape before trials. A video camera recorded each trial and video analysis was conducted using PowerDirector to determine average swimming velocity and tail stride length performed by each salamander at each flow rate. Salamanders were continuously prompted to swim the entire length of the lane by gentle poking of their tails from behind. Forty-eight swimming trials were run, four trials for each of the twelve salamanders. Average swimming velocities of each salamander at each flow rate were used in data analysis. Pauses while swimming across the lane that were greater than 0.5 seconds or that required further prompting were exempted from velocity and stride length calculations.

Ventral and lateral photographs were taken of each individual on graph paper next to a ruler to gather morphometric data. Salamanders were chilled in a refrigerator for up to 10

minutes before photos were taken to reduce movement during photographing. The images were used to analyze and measure snout-vent length (SVL), tail length, depth, and calculate tail surface area. The mass of each salamander was also taken. I analyzed morphological measurements regarding swimming performance with data from 12 of the 16 total salamanders caught, 6 *Ambystoma laterale* and 6 *Plethodon cinereus*. Three of the remaining salamanders, 2 *Ambystoma laterale* and 1 *Plethodon cinereus*, provided incomplete data, and the fourth was not the appropriate species, *Ambystoma maculatum*, so these salamanders were not considered for analysis.

Shapiro-Wilks tests were used to test for normality in tail morphology characteristics, average swimming velocity, and tail stride length. One-way ANCOVAs were conducted to determine a statistically significant difference in tail morphometrics between *A. laterale* and *P. cinereus* controlling for SVL. ANCOVAs were also used to determine if tail surface area has a relationship with average swimming velocity and the tail stride length of each species. 2-way ANOVAs were used to determine if there was a difference in average swim velocity and tail stride length between the four different flow rates against which the two species swam. All statistics were done in R (R Core Team, 2018) and all figures made in Microsoft Excel (Microsoft Corporation, 2016).

RESULTS

Tail morphology characteristics, average swimming velocities, and tail beat stride lengths were all found to be normal except for mass ($p=0.013$). There was a significant difference between the proportion of tail surface area and SVL between the two species ($df=8$, $F=309.4$, $p<0.001$). *A. laterale* had proportionally larger tails compared to *P. cinereus* ($df=4$, $F=366.8$, $R^2=0.9892$, $p<0.001$; $df=4$, $F=109.3$, $R^2=0.9647$, $p<0.001$; Figure 2). There was a significant

difference between the proportion of tail depth and SVL between the two species (df=8, F=158.9, $p<0.001$). *A. laterale* had proportionally deeper tails compared to *P. cinereus* (df=4, F=103.3, $R^2=0.9627$, $p<0.001$; df=4, F=39.48, $R^2=0.908$, $p=0.003$; Figure 3). There was not a significant difference between the proportion of tail length and SVL between the two species (df=8, F=17.64, $p<0.001$; df=4, F=62.81, $R^2=0.9401$, $p=0.001$; df=4, F=16.8, $R^2=0.8077$, $p=0.00115$; Figure 4).

Tail surface area does not have a significant effect on average swimming velocity in either species (df=8, F=1.713, $p=0.241$; df=4, F=0.6601, $R^2=0.1416$, $p=0.4621$; df=4, F=28.03, $R^2=0.8751$, $p=0.006$; Figure 5). SVL also does not have a significant effect on average swimming velocity in either species (df=8, F=2.259, $p=0.15587$; df=4, F=1.118, $R^2=0.2185$, $p=0.350$; df=4, F=56.38, $R^2=0.9338$, $p=0.002$; Figure 6), but does have a significant positive relationship with tail stride length in both *A. laterale* and *P. cinereus* (df=8, F=52.48, $p<0.001$; df=4, F=25.65, $R^2=0.8651$, $p=0.007$; df=4, F=21.44, $R^2=0.8428$, $p=0.010$; Figure 7). Tail surface area was found to have a significant effect on the tail stride length of each species (df=8, F=40.09, $p<0.001$). *A. laterale* had significantly greater stride lengths compared to *P. cinereus* (df=4, F=18.68, $R^2=0.8236$, $p=0.012$; df=4, F=16.72, $R^2=0.8069$, $p=0.015$; Figure 8).

Average swimming velocity did not significantly differ between the two species (df=3, F=0.435, $p=0.729$) but did significantly vary with changing flow rates (df=3, F=2.938, $p=0.045$, Figure 9). The average swimming velocities at the highest flow rate, 53mm/sec, were found to be significantly less than the velocities at the other flow rates ($p=0.036$, Figure 9). Average tail stride length significantly differed between the two species (df=1, F=26.252, $p<0.001$) but did not significantly vary with changing flow rates (df=3, F=0.049, $p=0.986$, Figure 10).

DISCUSSION

This paper investigated the relationship tail morphology has with swimming performance in *Ambystoma laterale* and *Plethodon cinereus*. The results from this study support the hypothesis that salamanders with greater tail surface area travel farther with each beat of their tail compared to those with smaller tails. Salamanders with relatively larger tails, regardless of species, were found to exhibit greater tail stride length (Figure 6). This can be explained, like in other papers, by the fact that greater tail surface area can generate greater thrust, so a greater stride can be achieved (Aubret and Shine, 2008; Hawkins and Quinn, 1996). The results do not support the hypothesis that salamanders with greater tail surface exhibit higher swimming velocities. Though there were differences in stride length among different tail surface areas, no significant change in swimming velocities was seen (Figure 4). This means that tail surface area is not the controlling factor in determining swimming velocity. Other factors such as tail beat frequency and amplitude may be more significantly influential to swimming velocity (Storfer and White, 2004).

The hypothesis that salamanders that swim against increasing flow rates would exhibit decreased swimming velocities was partially supported by these results, but the results reject the hypothesis that increased flow rates lead to decreased tail stride lengths in these salamanders. Only the highest flow rate of 53mm/sec affected swimming velocity in either species of salamander (Figure 8). This is likely due to the relatively slow flow rates used because of the limitations of the artificial stream. The intermediate flow rates were slow enough to not have a significant effect on swimming velocity compared to the 0mm/sec flow rate. The flow rate against which the salamanders swam did not have a significant effect on their tail stride length (Figure 9). This could mean that the salamanders generate a constant thrust and therefore stride length when faced with subtle flow rate changes, or that the opposing water flow cancels out any

additional thrust they may be generating to result in a significantly unchanging stride length. Ideally, the salamanders were performing at maximum swimming capabilities for each trial, which would make the former a more possible explanation, but there was no way to guarantee the constant maximum performance of each salamander.

The third hypothesis that *A. laterale* would have longer tail stride lengths than *P. cinereus* was supported by the results, but the hypothesis that *A. laterale* swim at greater velocities than *P. cinereus* was rejected. Even when adjusted for body size, it was found overall that *Ambystoma laterale* have a greater stride length which can be explained by their different tail morphometrics to body size ratios and increase tail surface area (Figure 10, 1 and 2). This means that to go the same distance, *P. cinereus* must beat its tail more often than *A. laterale*. Interestingly, the swimming velocities did not significantly differ between species. This could indicate that *P. cinereus* has a great tail beat frequency and therefore needs to exert greater energy to travel the same distance and speed as *A. laterale*, though a formal analysis would be needed to verify this.

The analysis of tail morphometrics and body size shows that *Ambystoma laterale* differ significantly from *Plethodon cinereus* in size, tail shape, and body proportions (Figures 1-3). There is a particularly notable difference in relative tail depth and surface area between the two species, since it is these that relate most to the shape difference between the tails of the two species laterally compressed and round tails. These differences are both visually and statistically significant, and they have some swimming performance implications as found in this study. These results also showed that these morphological differences have an impact on swimming performance, specifically stride length. This supports the claim that lateral tail compression in *A. laterale* has an evolutionary purpose of improving swimming performance that would be applied

to their return to vernal pools to breed (Collins and Wilbur, 1979; Ohio Divisions of Wildlife, 2012; Shine and Shetty, 2001).

P. cinereus was still found to maintain significantly similar swimming velocities with *A. laterale* despite not having any ecological necessity or indicative morphology for swimming (Cochran, 1911). This differing morphology is likely the explanation for the observed difference in swimming style between the two species. *P. cinereus* appeared to laterally undulate their whole body in one continuous motion from body to tail. *A. laterale* appeared to undulate their tails more than their bodies and movement seemed to have a more jointed transitioning between body and tail. They sometimes also seemed to augment lateral undulation with walking-like motions. Ijspeert and Cabelguen (2006) modelled salamander locomotion on land and water and demonstrated that different morphological aspects and gaits are adopted for terrestrial and aquatic locomotion. *P. cinereus* being more terrestrially adept than *A. laterale* could explain the observed differences in gait while swimming. This difference in morphology and possibly swimming gait applies to the reported difference in stride length. Differing swimming styles and stride length could indicate a difference in energy output and overall swimming efficiency between the two species, which is plausible considering the ecological need for swimming in *A. laterale* and not in *P. cinereus*, but would need further studies and analysis to verify.

These results also support the finding that lateral tail compression is associated with increased swimming performance (Aubret and Shine, 2008; Fitzpatrick *et al.* 2003; Hawkins and Quinn, 1996; Irschick and Garland, 2001). *Ambystoma laterale* having aquatic breeding habits, unlike *Plethodon cinereus*, combined with greater swimming stride length and greater tail surface area of *A. laterale* is supportive of the relationship that morphology has with performance and fitness in this species (Arnold, 1983; Collins and Wilbur, 1979). In general,

these results indicate that larger body size as well as tail size influences swimming performance, but even when adjusting for body size, greater relative tail surface area has a positive effect on swimming performance. These support claims that *A. laterale* and other salamanders with aquatic breeding habits can be considered to have greater swimming performance than those like *P. cinereus* that are strictly terrestrial.

There is the possibility that the lack of significant difference in swimming velocity between the two species and varying tail morphometrics could simply be explained by the limited data set of 6 salamanders per species. Further data collection and more time for data collection and analysis would be needed to verify the results found here more definitively. Wilson *et al.* (2000) found that thermal variation can influence the mechanics of muscles in vertebrates, which could affect locomotor performance. With this in mind, it is possible that varying air and water temperature interfered with swimming performance results since the artificial stream and swimming lane were outdoors.

Further studies of salamander swimming performance could be beneficial in gaining more support and insight to the results found here. Other topics relating to salamander swimming performance could be explored such as the effect of tail autotomy on swimming performance. Since surface area has been found to influence swimming performance, a loss or partial loss of a tail should have implications relating to swimming performance. Further studies looking at swimming strategy, tail beat frequency, and swimming efficiency could be done to assess in more detail which species of salamander is the more efficient swimmer. A similar study could also be done to address similar questions but in a terrestrial setting to get a broader understanding of locomotor performance in *Ambystoma laterale* and *Plethodon cinereus*.

FIGURES



Figure 1: Swimming lane and artificial stream for locomotor performance trials. Ten-centimeter intervals are marked by black lines.

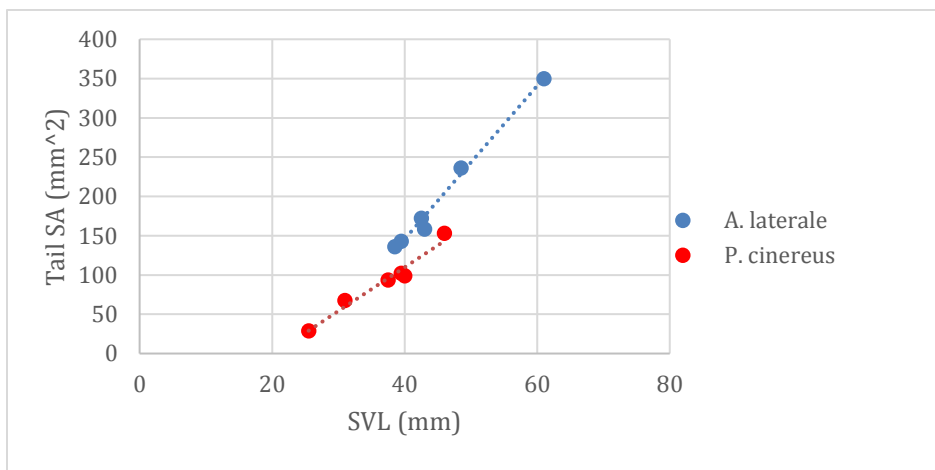


Figure 2: Snout-vent length (SVL) and tail surface area (SA) proportions in *A laterale* and *P. cinereus* individuals. An ANCOVA comparing body proportions of SVL and tail surface area reveals that *A laterale* and *P. cinereus* differed in tail surface area relative to SVL, yielding values: $df=8$, $F=309.4$, $p<0.001$. *A. laterale* had proportionally larger tails compared to *P. cinereus* ($df=4$, $F=366.8$, $R^2=0.9892$, $p<0.001$; $df=4$, $F=109.3$, $R^2=0.9647$, $p<0.001$).

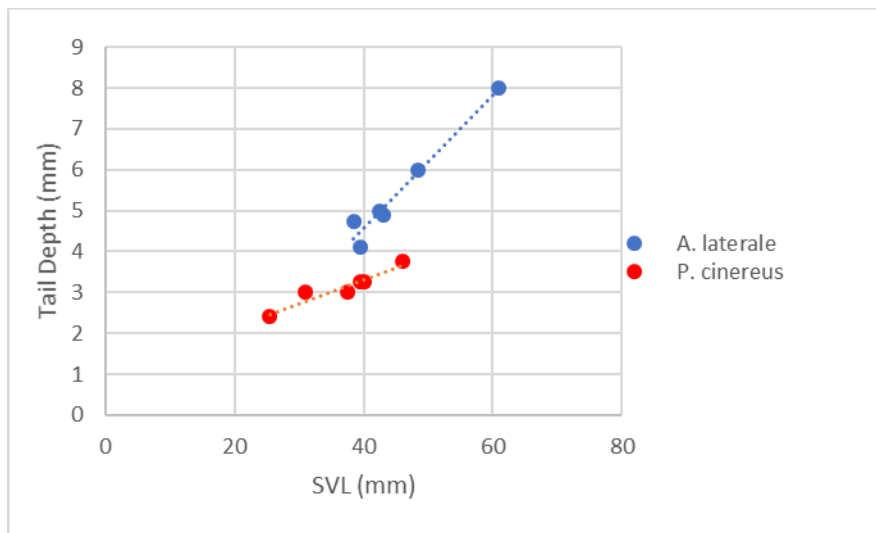


Figure 3: Snout-vent length (SVL) and tail depth proportions in *A laterale* and *P. cinereus* individuals. An ANCOVA comparing body proportions of SVL and tail depth reveals that *A laterale* and *P. cinereus* differed in tail depth relative to SVL, yielding values: $df=8$, $F=158.9$, $p<0.001$. *A. laterale* had proportionally deeper tails compared to *P. cinereus* ($df=4$, $F=103.3$, $R^2=0.9627$, $p<0.001$; $df=4$, $F=39.48$, $R^2=0.908$, $p=0.003$).

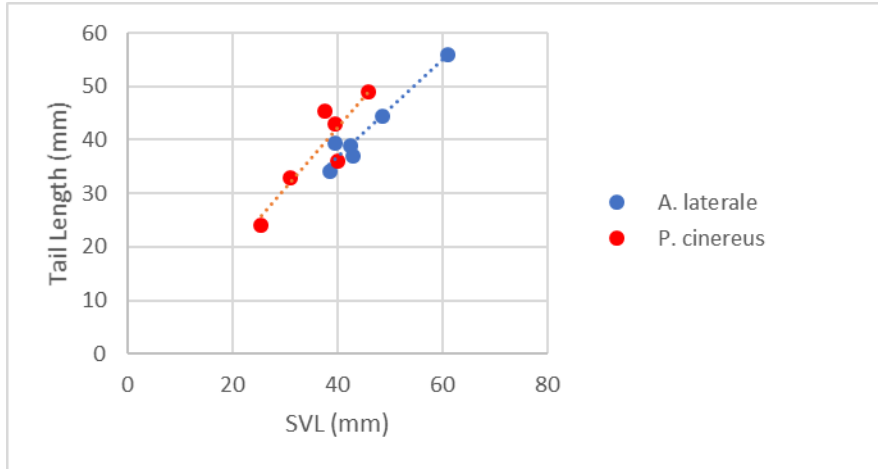


Figure 4: Snout-vent length (SVL) and tail length proportions in *A. laterale* and *P. cinereus* individuals. An ANCOVA comparing body proportions of SVL and tail length reveals that *A. laterale* and *P. cinereus* did not differ in tail length relative to SVL, yielding values: $df=8$, $F=17.64$, $p<0.001$; $df=4$, $F=62.81$, $R^2=0.9401$, $p=0.001$; $df=4$, $F=16.8$, $R^2=0.8077$, $p=0.00115$.

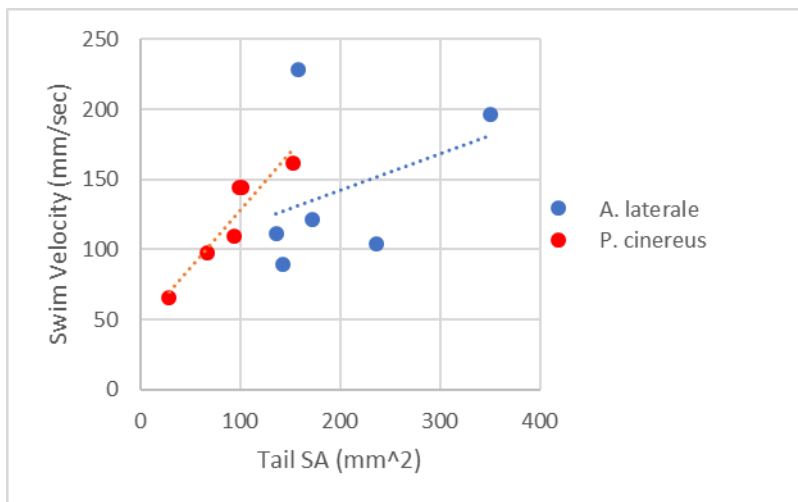


Figure 5: Effect of tail surface area (SA) on average swimming velocity in *A. laterale* and *P. cinereus* individuals. An ANCOVA assessing the influence tail surface area had on swimming velocity reveals tail surface area did not have a significant effect on average swimming velocity in either species, yielding values: $df=8$, $F=1.713$, $p=0.241$; $df=4$, $F=0.6601$, $R^2=0.1416$, $p=0.4621$; $df=4$, $F=28.03$, $R^2=0.8751$, $p=0.006$.

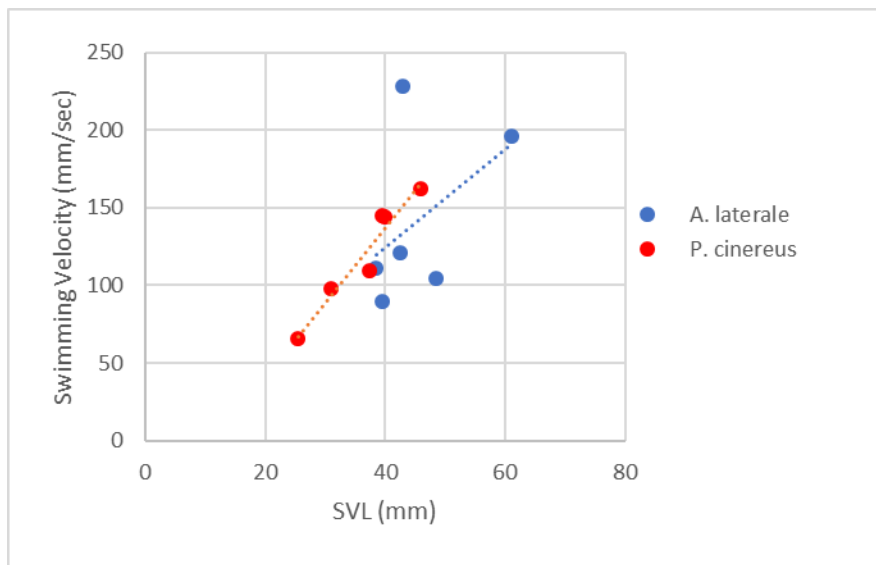


Figure 6: Effect of snout-vent length (SVL) on average swimming velocity in *A. laterale* and *P. cinereus* individuals. An ANCOVA assessing the influence SVL had on swimming velocity reveals SVL did not have a significant effect on average swimming velocity in either species, yielding values: $df=8$, $F=2.259$, $p=0.15587$; $df=4$, $F=1.118$, $R^2=0.2185$, $p=0.350$; $df=4$, $F=56.38$, $R^2=0.9338$, $p=0.002$.

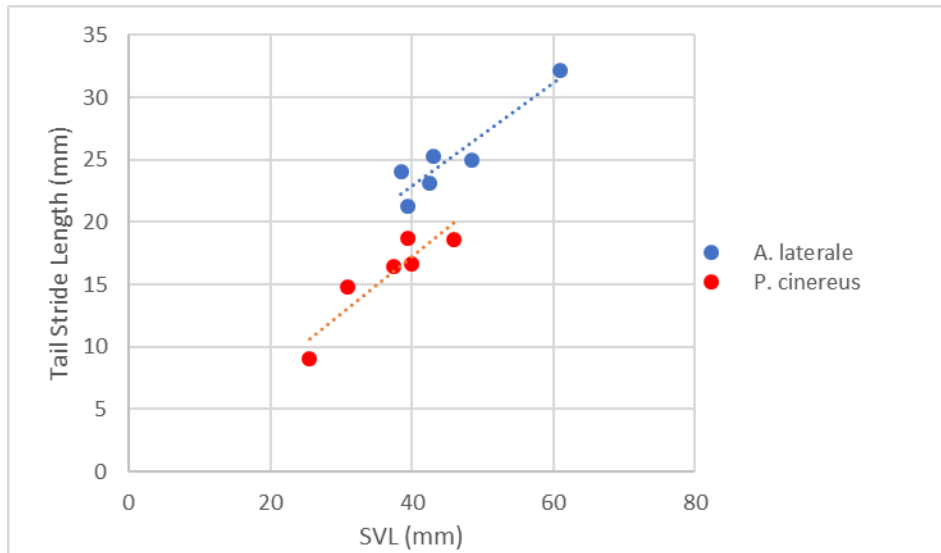


Figure 7: Effect of snout-vent length (SVL) on average tail stride length in *A. laterale* and *P. cinereus* individuals. An ANCOVA assessing the influence SVL had on average stride length reveals SVL had a significant effect on average swimming velocity in both species and stride lengths significantly differed between species, yielding values: $df=8$, $F=52.48$, $p<0.001$; $df=4$, $F=25.65$, $R^2=0.8651$, $p=0.007$; $df=4$, $F=21.44$, $R^2=0.8428$, $p=0.010$.

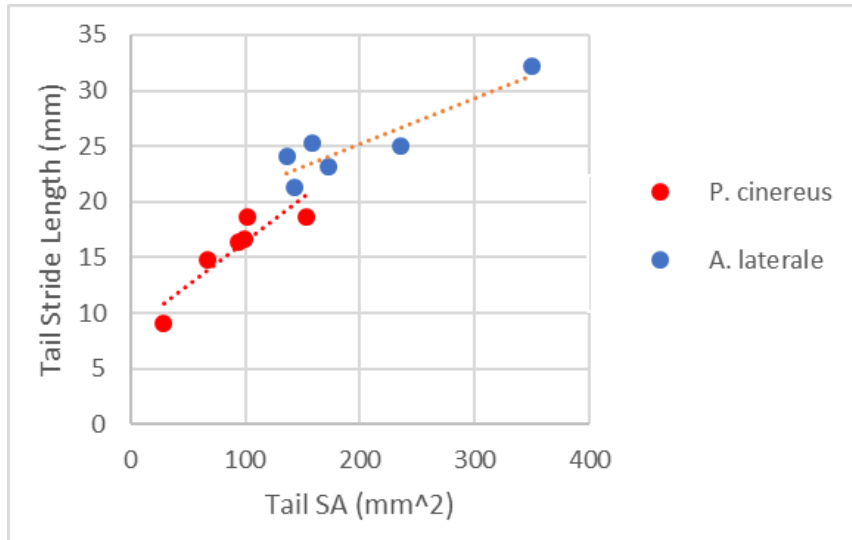


Figure 8: Effect of tail surface area (SA) on average tail stride length in *A. laterale* and *P. cinereus* individuals. An ANCOVA assessing the influence tail surface area had on average stride length reveals tail surface area had a significant effect on average stride length in both species and stride lengths significantly differed between species, yielding values: $df=8$, $F=40.09$, $p<0.001$. *A. laterale* had significantly greater stride lengths compared to *P. cinereus* ($df=4$, $F=18.68$, $R^2=0.8236$, $p=0.012$; $df=4$, $F=16.72$, $R^2=0.8069$, $p=0.015$)

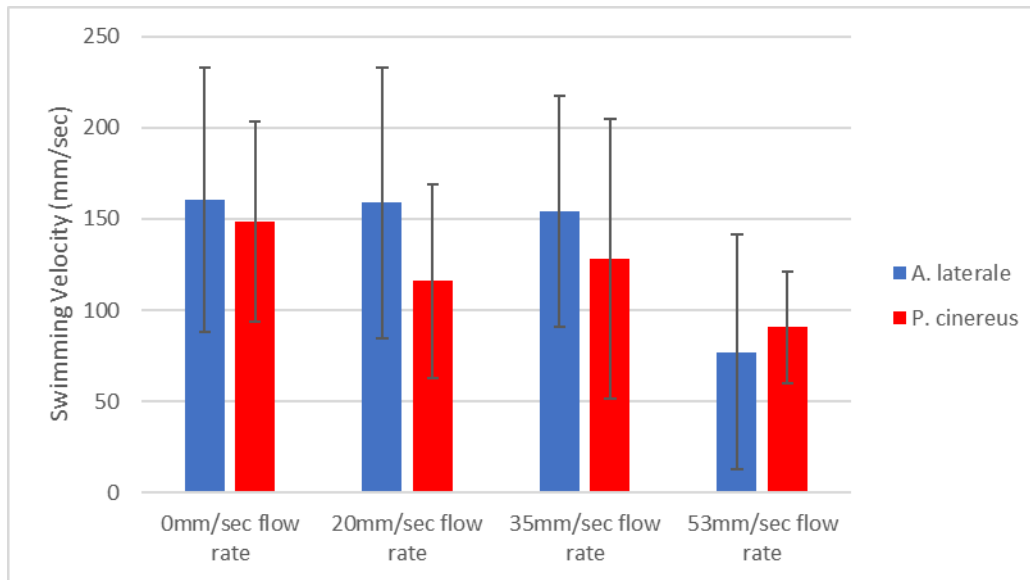


Figure 9: Average swimming velocity of *A. laterale* and *P. cinereus* swimming against different flow rates. A 2-way ANOVA comparing average swimming velocities at each flow rate between *A. laterale* and *P. cinereus* reveals that there was no significant difference in swimming velocities between *A. laterale* and *P. cinereus*, and that flow rate had a significant effect on swimming velocity, yielding values: $df=3, F=0.435, p=0.7293$; $df=3, F=2.938, p=0.0448$. A Tukey post hoc test reveals that the swimming velocities at the 53mm/sec flow rate significantly differed from those at the other flow rates yielding the value $p=0.036$. Error bars represent standard deviations.

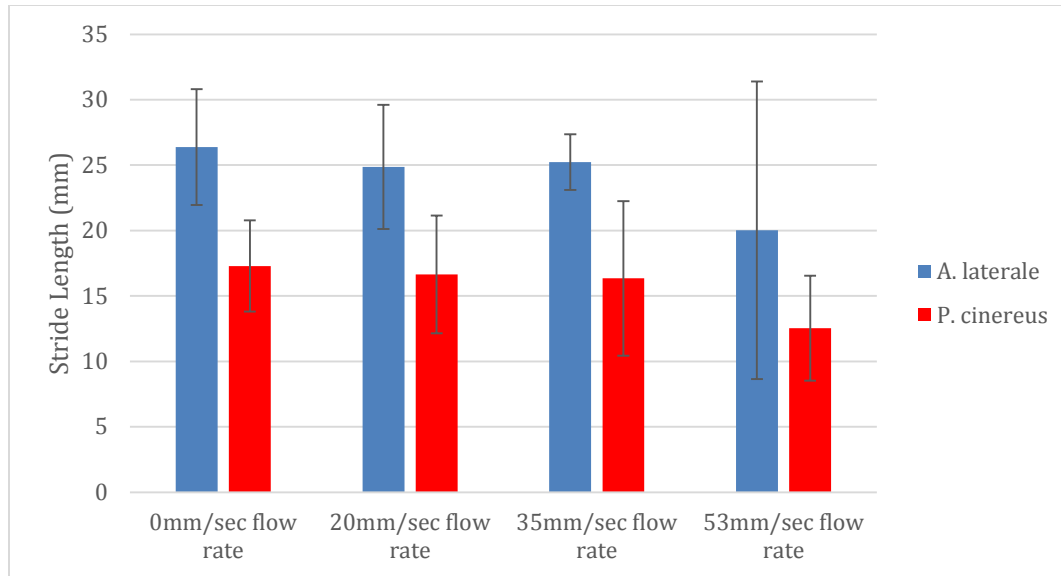


Figure 10: Average tail stride length of *A. laterale* and *P. cinereus* swimming against different flow rates. A 2-way ANOVA comparing average stride lengths at each flow rate between *A. laterale* and *P. cinereus* reveals that flow rate did not have a significant effect on stride length in either species, yielding values: $df=3$, $F=0.435$, $p=0.986$; $df=1$, $F=26.252$, $p<0.001$. Error bars represent standard deviations.

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