



The effects of stroke frequency on swimming across frog species



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Introduction

- While swimming styles vary across animals, two fundamental forces affect swimming performance across all types: drag on the body that slows a swimmer down, and thrust from limbs or fins that propel a swimmer forward².
- Drag is dependent on the resistance encountered by a body in water, while propulsive thrust is derived from feet pushing against water. The proportional strength of one force over the other can be quantified as a body's "drag ratio".
- Drag slows a body down, possibly requiring more frequent strokes to achieve a given average velocity when swimming in the case of organisms without large foot areas to provide thrust to counteract drag.
- Frogs show high diversity in body form⁴, which may affect swimming. Because of their broad set of ecological ranges, frog species have developed varying styles of aquatic locomotion to fit with varying body proportions¹. This leads to aspects such as stroke frequency possibly varying greatly among anuran species.

Research Questions

- How does capacity for body drag encountered by an organism's frontal cross-sectional area relate to its potential for propulsive thrust from the foot based on its foot area?
- Does this "drag ratio" correlate with stroke frequency?
- Is there a relationship between stroke frequency and velocity?
- Does the kind of velocity (peak velocity vs. average velocity) matter?

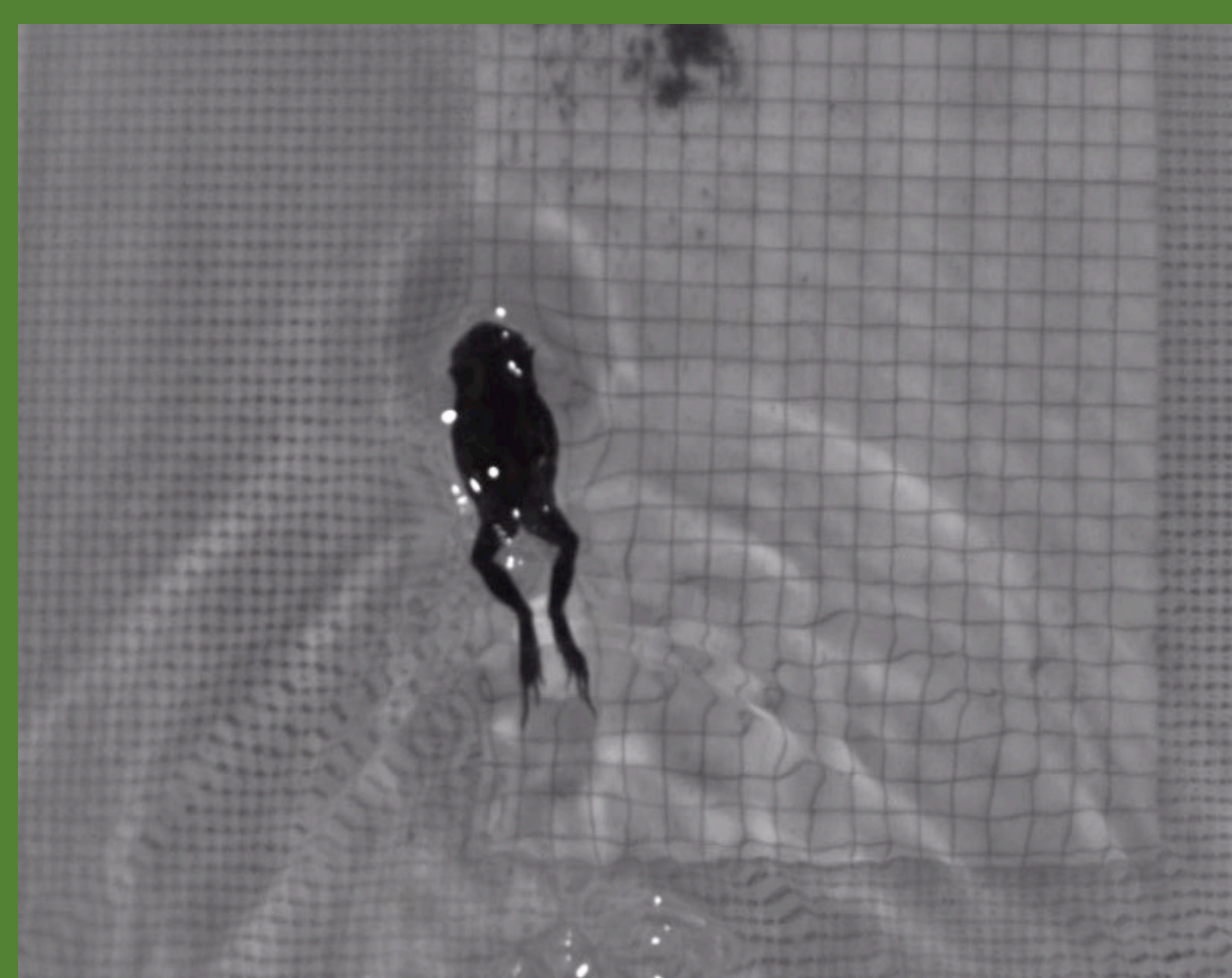
We hypothesized that if an organism encounters both increased drag and decreased propulsion (thus a higher drag ratio), it will increase its swimming stroke frequency in order to achieve similar velocity as a species with a lower drag ratio.

Methods

- We collected data from 83 different species of frogs ($n = 379$ individuals, predominantly adult males) collected from the field in China, Colombia, Australia, Madagascar, and the United States (Oklahoma and Arkansas).
- From each individual, we measured snout-to-vent length (SVL), live mass, and total overall foot area (including webbing). The latter was measured by taking photographs of the individuals' feet and measuring their area in ImageJ (see below).



Still foot images of feet pressed against glass were used to measure foot and webbing areas.

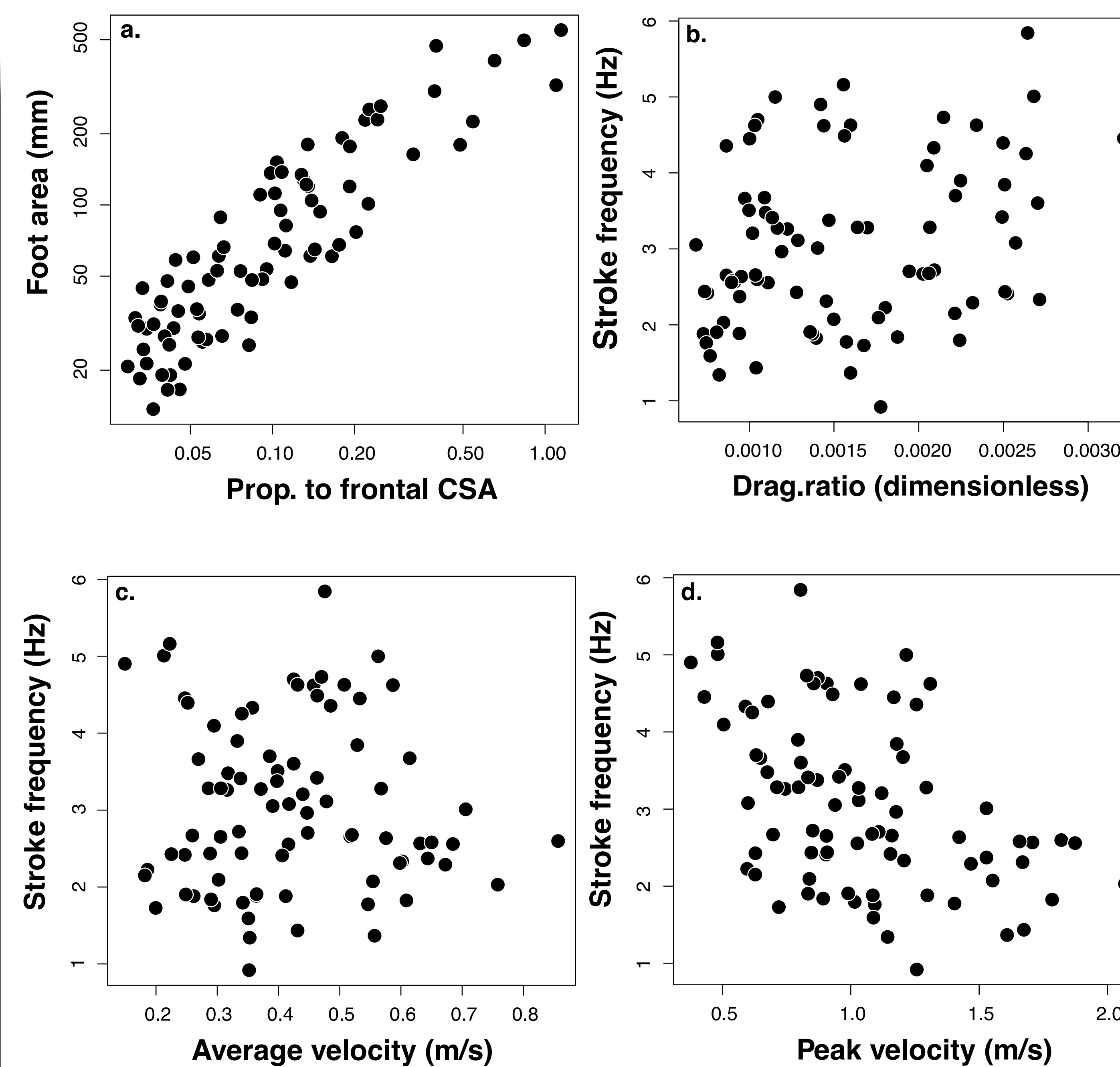


Swimming videos of individuals were used to measure peak and average velocities achieved over a swim stroke.

Methods (cont.)

- For the purposes of this study, we defined an organism's drag ratio as being equal to its frontal cross-sectional area (CSA) divided by its total foot area. Frontal CSA was approximated by dividing live mass (assumed to be proportional to volume) by its SVL.
- We calculated swimming performance data from high-speed videos of swimming in frogs collected in the field (see below left). All data were collected from single, complete strokes. These data included stroke frequency, peak velocity obtained during the stroke, and average velocity over the complete stroke. Methods largely followed previously published research^{3,5}.
- Following data collection, we analyzed the data with the program JMP Pro 14. We calculated bivariate Pearson product-moment correlations between variables and considered relationships significant when $P < 0.05$.

Results



Results: Figure 1

(a) Plotting our approximation of frontal cross-sectional area against total foot area shows a wide range of foot areas for any frontal CSA value. (b) Stroke frequency and drag ratio were significantly positively related ($P = 0.0089$), though their correlation was low ($r = 0.2853$). (c) No significant correlation was found between stroke frequency and average velocity ($P = 0.6338$; $r = -0.0531$). (d) We found that stroke frequency and peak velocity were significantly negatively correlated ($P < 0.0001$; $r = -0.4461$).

Discussion

- We showed that foot area (potential for propulsive thrust) varies widely at a given frontal CSA (potential for drag). This motivated using those variables' ratio (drag ratio) to understand the need to stroke frequently or not.
- Despite significant results for stroke frequency and drag ratio ($P = 0.0089$), the correlation value was low ($r = 0.2853$), indicating that these morphologies do not explain stroke frequency as much as expected.
- We found different effects of peak velocity and average velocity on stroke frequency. Average velocity is determined by both peak velocity and stroke frequency, which themselves were negatively related. This suggests that frogs with different peak velocities modify their stroke frequency in order to achieve similar average velocities, which may be what matters more ecologically (e.g. escaping predators).
- Future studies can look into differences in the types of and proportions of muscle mass between species, in order to determine if muscle qualities have a more direct effect on stroke frequency than the variables tested in this study.
- Ecomorph (a body form that fits a certain environment) analysis could be beneficial in future research, as previous studies have shown that species' microhabitat can influence performance³.
- Phylogenetic comparative analysis may also be a useful tool in future research, as evolutionary history could influence the patterns that we found in this study^{3,4}.

Literature Cited

- Abourachid, A. and D. M. Green. 1999. Origins of the frog-kick? Alternate-leg swimming in primitive frogs, families Leiopelmatidae and Ascaphidae. *Journal of Herpetology* 33:657-663.
- Biewener, A. A. and S. N. Patek. 2018. *Animal Locomotion*. Oxford University Press, New York, NY, USA.
- Moen, D. S., D. J. Irschick, and J. J. Wiens. 2013. Evolutionary conservatism and convergence both lead to striking similarity in ecology, morphology and performance across continents in frogs. *Proceedings of the Royal Society B* 280:20132156.
- Moen, D. S., H. Morlon, and J. J. Wiens. Testing convergence versus history: convergence dominates phenotypic evolution for over 150 million years in frogs. *Systematic Biology* 65:146-160.
- Peters, S. E., L. T. Kamel, and D. P. Bashor. 1996. Hopping and swimming in the leopard frog, *Rana pipiens*: I. step cycles and kinematics. *Journal of Morphology* 230:1-16.

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Anodonthyla pollicaris, demonstrating a large frontal CSA and little webbing area.



Boophis madagascariensis, demonstrating a small frontal CSA and a large proportion of webbing area.