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Intraspecific and interspecific variations in the swimming characteristics of snakes according to their lifestyle

Guillaume Fosseries[1], Anthony Herrel[2], Ramiro Godoy-Diana[3], Elie Gautreau[4], Karl Maroun[5], Philippe Traore[5], Nataniel Lekayi[5], Tom Fox[1], Shane Lombardo[1], David Hudry[1], Léa Patau[1], Fanny Aguilera[1], Sarah Alves Heleno[1], Olivier Chateau[6], Hugues Gossuin[6], Xavier Bonnet[1,*]

[1] *CEBC*, *Centre d'études Biologiques de Chizé*, *UMR*7372, *CNRS*, *La Rochelle University*, *Villiers-en-Bois* 79360, *France*
[2] *MNHN*, *National Museum of Natural History*, *CNRS*, *Paris* 75005, *France*
[3] *PMMH*, *Physique et Mécanique des Milieux Hétérogènes*, *UMR*7636, *CNRS*, *ESPCI Paris-PSL*, *Sorbonne Université*, *Université Paris Cité*, *Paris* 75005, *France*
[4] *Department of GMSC*, *Pprime Institute CNRS*, *ENSMA*, *University of Poitiers*, *UPR* 3346, *Chasseneuil-du-Poitou* 86360, *France*
[5] *Department of DFTC*, *Pprime Institute CNRS*, *University of Poitiers*, *UPR* 3346, *Chasseneuil-du-Poitou* 86360, *France*
[6] *Aquarium des Lagons*, *Nouméa* 98807, *Nouvelle-Calédonie*

ABSTRACT

Snakes exhibit extraordinary ecological diversity and occupy a broad range of terrestrial, aquatic, and intermediate environments. Despite their widespread capacity for swimming, quantitative assessments of their aquatic locomotion remain scarce. Furthermore, the roles of intraspecific variation in shaping swimming performance and kinematics have been largely overlooked, hindering robust interspecific comparisons. This study systematically investigated intraspecific and interspecific variation in 287 individuals representing seven snake species along a terrestrial to aquatic continuum. Nine conventional swimming traits were quantified, including swimming speed and undulation characteristics such as frequency, wavelength, lateral velocities (head, body and tail) and amplitudes (head, body and tail). Undulation frequency and lateral velocity exhibited strong positive correlations with swimming speed, whereas wavelength showed a strong negative correlation. Semi-aquatic taxa attained the highest swimming speeds, while fully aquatic snakes displayed the lowest speeds. Intraspecific variation in swimming performance and kinematics was moderately reduced in aquatic species. Morphological traits, sex, and reproductive status significantly influenced both speed and kinematic profiles within species. Principal component analyses further revealed distinct kinematic domains among certain species (e.g., no overlap between aspic viper and sea snakes), while others, such as the green whip snake, exhibited broad overlap with all taxa examined. These findings demonstrate that ecological specialization to aquatic habitats does not unilaterally dictate swimming speed or kinematic patterns. Moreover, conventional kinematic parameters alone are insufficient to study the evolutionary trajectories of aquatic locomotion in snakes. Integrating hydrodynamic, endurance capacity, and diving performance will be essential to better understand how natural selection has shaped locomotion in aquatic snakes.

Keywords: Evolution; Lateral undulation; Swimming kinematics; Swimming speed

INTRODUCTION

Snakes have repeatedly colonized both terrestrial and aquatic environments throughout their extensive evolutionary history, while retaining a streamlined, elongate body architecture (Hsiang et al., 2015). Of the more than 4 000 described species (Uetz et al., 2025), approximately 400 exhibit either semi-aquatic habits (e.g., *Natricidae*) or occupy fully aquatic niches (e.g., marine *Hydrophiinae*). Many species exploit freshwater and brackish environments such as rivers, lakes, swamps, and mangroves, where swimming plays a central role in foraging, dispersal, mate location, and predator avoidance (Madsen et al., 2006; Murphy, 2012). Remarkably, all snakes, even fossorial taxa and those inhabiting arid or otherwise water-limited environments appear to retain the capacity to swim (Fosseries et al., 2024).

Despite this widespread swimming ability, substantial interspecific variation in body form is evident across ecological

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*Corresponding author, E-mail: bonnet@cebc.cnrs.fr

types, suggesting a corresponding diversity in locomotor performance and mechanics (Gillis, 1996; Jayne, 1982; Mathou et al., 2023). Morphological extremes, such as long-tailed arboreal snakes and short-bodied fossorial or terrestrial forms, would not be expected to exhibit comparable swimming dynamics. Consequently, swimming ability alone cannot serve as a reliable proxy for aquatic specialization. Quantitative assessments of swimming kinematics and performance metrics are necessary to evaluate the extent of locomotor adaptation to aquatic habitats (Munk, 2008; Stin et al., 2024). For instance, if evolutionary transitions to aquatic life enhance swimming proficiency, one might predict that aquatic snakes should outperform terrestrial counterparts in traits such as velocity—just as no terrestrial bird approaches the aquatic efficiency of penguins (Kelley and Pyenson, 2015).

Snakes exhibit four main modes of locomotion, subdivided into 11 distinct subtypes (Jayne, 2020; Tingle et al., 2024). Among these, lateral undulation represents the most widespread and versatile, enabling effective movement across diverse terrestrial substrates, vegetation, and aquatic environments. The biomechanics of this locomotor mode have been extensively studied in elongated organisms such as fish (D'Août & Aerts, 1999; Di Santo et al., 2021; Gillis, 1997; Gray & Lissmann, 1950), amphibians, and snakes (Bulla, 2013; Jayne, 1985, 1986; Munk, 2008), offering foundational insights into undulatory propulsion. Anguilliform swimming, characterized by lateral undulations of the whole body, has received renewed attention, with recent reviews highlighting the relevance of parameters governing wave dynamics (Stin et al., 2024), including undulation frequency, wavelength, and amplitude (Gray, 1933; Lindsey, 1978; Tytell et al., 2023). At a given frequency, amplitude increases along the body to generate thrust, and the hydrodynamic consequences of variation in these parameters have been explored through theoretical and empirical modeling (Piñeirua et al., 2015; Tytell & Lauder, 2004). Notably, strong correlations between undulation frequency and swimming speed have been repeatedly documented (Brischoux et al., 2010; Gillis, 1998; Tack et al., 2021), underscoring its functional significance. More recently, volumetric particle imaging velocimetry has enabled high-resolution characterization of the three-dimensional (3D) vortex structures generated by swimming snakes, providing key insights into the hydrodynamic architecture of anguilliform propulsion (Stin et al., 2023). Despite these advances, comparative data on the interspecific diversity of swimming kinematics across snake taxa remain remarkably sparse. Quantitative measurements of swimming speed exist for fewer than 20 snake species, and detailed kinematic data are limited to just five species, four of which are aquatic and one terrestrial (Brischoux et al., 2010; Graham et al., 1987; Gray & Lissmann, 1950; Jayne, 1985; Munk, 2008). Moreover, all studied species belong to either *Colubridae* or *Elapidae*, leaving broad phylogenetic gaps, particularly among early-diverging lineages (e.g., *Scolecophidia*, *Aniliidae*), as well as among fossorial and arboreal specialists. Consequently, current understanding fails to capture the full spectrum of morphological and ecological variation across snakes, severely constraining evolutionary inferences regarding the emergence of secondarily aquatic lifestyles.

Disentangling the evolutionary drivers of snake swimming traits remains challenging due to the complex interplay of ecological, morphological, and physiological variables across taxa and lifestyles. Locomotor performance, particularly swimming speed, is influenced by multiple factors, including body size, sex, feeding and reproductive state, and environmental exposure to contaminants (Finkler & Claussen, 1999; Hopkins & Winne, 2006; Shine et al., 2003; Webb, 2004), as well as marked phenotypic plasticity (Aubret et al., 2007). Beyond swimming speed, it is likely that these factors also play a role in swimming kinematics (Di Santo et al., 2021), but no previous studies focused on the effect of these biological and environmental factors on kinematic for snakes. Overall, it is important to consider the influence of intraspecific variability in snake swimming traits before making interspecific comparisons. The extent to which swimming traits documented in one or a few individuals are representative of a species and, therefore, its lifestyle or ecology is unknown.

Most available studies are constrained by small sample sizes (although exceptions exist: Brischoux et al., 2010; Shine et al., 2003; Wang et al., 2013), preventing a thorough understanding of the drivers of variation in swimming speed and kinematics. To overcome these limitations, the present study quantified swimming speed and kinematic parameters in 287 individuals across seven snake species spanning a gradient from terrestrial to aquatic lifestyles (Figure 1), including a marine representative of Hydrophiinae) as a representative of the most aquatic-adapted species. All individuals were wild-caught and tested immediately under standardized conditions. For six species, sample sizes exceeded 20 individuals (range: 5–103 per species), enabling robust assessments of intraspecific variability. Key traits examined included body length, body condition, sex, and—when possible—reproductive status. An important objective was to assess the extent to which these factors influence swimming performance and kinematics across species. Although overall locomotor capacity was expected to differ between semi-arboreal, terrestrial, semi-aquatic, and fully aquatic species, individual-level variation, such as greater muscle mass in males (Bonnet et al., 1998), may exert equally strong effects. This framework enabled a comprehensive evaluation of both inter- and intraspecific contributions to swimming performance and kinematics and allowed direct testing of the hypothesis that swimming speed increases progressively from terrestrial to fully aquatic lineages.

MATERIALS AND METHODS

Study species and field sites

This study included seven snake species representing a range of ecological types, including semi-arboreal, terrestrial, semi-aquatic, and fully aquatic (Table 1). All individuals were captured by hand in the wild. Cover boards were used to detect four species in a forest in France (N46.14°, W0.42°), including the Aesculapian snake (*Zamenis longissimus* (ZL)), asp viper (*Vipera aspis* (VA)), green whip snake (*Hierophis viridiflavus* (HV)), and grass snake (*Natrix helvetica* (NH)). These species were tested during the active seasons of 2022 and 2023. *Zamenis longissimus* exhibits both terrestrial and semi-arboreal behaviors, *V. aspis* and *H. viridiflavus* are primarily terrestrial, and *N. helvetica* is semi-aquatic (Gregory & Isaac, 2004; Laurence et al., 2024; Lelièvre et al., 2012). While *Z. longissimus*, *V. aspis*, and *H. viridiflavus* predominantly consume small mammals, *N. helvetica* feeds mainly on amphibians. Although *H. viridiflavus* is regularly observed swimming in areas with water bodies, it remains

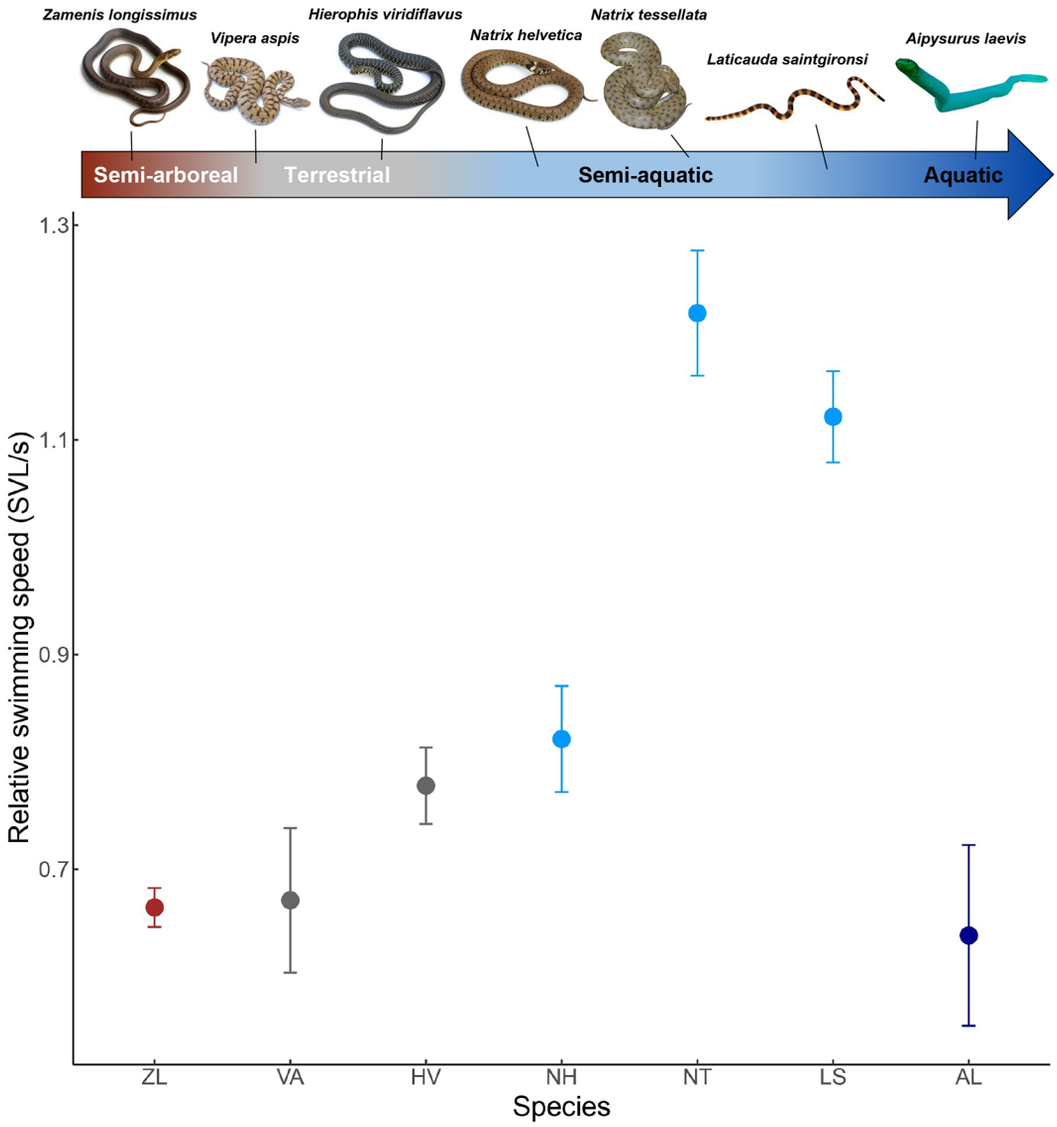

Figure 1 Mean relative swimming speed (±se) (SVL/s) for each species of snake

ZL: *Zamenis longissimus*; VA: *Vipera aspis*; HV: *Hierophis viridiflavus*; NH: *Natrix helvetica*; NT: *Natrix tessellata*; LS: *Laticauda saintgironsi*; AL: *Aipysurus laevis*. Species are classified along a terrestrial-to-aquatic lifestyle gradient. Colored symbols indicate lifestyle of each species according to this gradient.

largely terrestrial across its range. An additional species, the dice snake (*Natrix tessellata* (NT)) was studied in July 2022 along the shore of Lake Prespa in North Macedonia (N40.52°, W20.59°). This semi-aquatic, piscivorous species is highly associated with freshwater habitats (Ajtić et al., 2013). Two species were investigated in November 2023 near Nouméa, New Caledonia (N22.18°, W166.26°): the sea-krait (*Laticauda saintgironsi* (LS)) and olive sea snake (*Aipysurus laevis* (AL)). *L. saintgironsi* is a semi-aquatic, piscivorous species that divides its activity between marine and terrestrial environments. Individuals were captured while on land (Bonnet, 2012). In contrast, *A. laevis* is a fish-eating, fully aquatic species that never ventures ashore (Burns & Heatwole, 1998). Consequently, individuals were captured during scuba diving.

In addition to the seven species selected above, one individual from eight additional species was tested to broaden the ecological and morphological gradient without evaluating intraspecific variation. These included: an extremely elongated, strictly arboreal species (*Ahaetulla prasina,* captive specimen); two stocky fossorial and one semi-fossorial species (*Eryx colubrinus*, *Loxocemus bicolor*, and *Rhamphiophis oxyrhynchus*, captive specimens), a terrestrial/semi-arboreal species (*Chironius carinatus*, captured and tested in French Guyana), a semi-aquatic species (*Eunectes murinus*, captive specimen), and two fully aquatic snakes (*Emydocephalus annulatus* and *Aipysurus duboisii*, captured and tested in New Caledonia).

Because fully aquatic snakes are highly sensitive to handling and confinement, individuals were tested immediately and released at the capture site following measurements. For other species, most individuals were also tested rapidly and released. A subset was temporarily housed in cotton bags for one to three days, and then either released at the place of capture or returned to their enclosures after all procedures were completed.

Ethics statement and permits

Permission to conduct this study was obtained from the authorities in each country. Capture, handling, and measurement of snakes were approved by the respective

governmental authorities (Permit No. DREAL/2021D/8647, 09/346/DEROG in France, Permit No. 03-246 in Northern Macedonia, and Permit No. 4011-2023/ARR/DDDT (Province Sud) in New Caledonia). No invasive procedures were performed, and all individuals were released promptly following testing and measurement.

Experimental setup and swimming tests

Swimming trials were conducted using custom-built aquatic tracks consisting of longitudinally halved pipes filled with still water. Two configurations were used depending on field conditions: a 12 m×0.6 m track for *Z. longissimus*, *H. viridiflavus*, *N. helvetica*, and *V. aspis* and a 6 m×0.5 m track for *L. saintgironsi*, *N. tessellata*, and *A. laevis* (Supplementary Figure S1). Track dimensions were determined by the constraints of space and material availability at each field site. Sidewalls were installed to prevent escape and direct the snakes along a straight path. The initial and terminal sections of the track, used for initial acceleration and stopping were excluded from swimming performance and kinematic analyses to isolate steady-state swimming sequences. The measured swimming distances were set at 10 m and 5 m for the 12 m and 6 m tracks, respectively. Two overhead cameras (Sony DSC-RX0M2G, Japan) were positioned above the first and final thirds of the swimming area to capture each trial from different segments of the swim. The cameras were positioned to avoid overlapping fields of view, thereby maximizing the chances of obtaining an appropriate video to extract kinematic sequences. Recordings were made at 50 frames per second with a resolution of 1 920×1 080 pixels. Water temperature was adjusted to reflect the natural conditions of each species. For non-aquatic snakes, freshwater temperatures matched ambient air (20–30°C). For semi-aquatic and fully aquatic species, water temperatures reflected local field conditions: seawater at 22–24°C for marine species and freshwater between 14–30°C for others. Captive tropical species were tested in warmer freshwater (24–28°C). The water and the swimming tracks were kept disinfected using a solution of Virkon® (a 90% biodegradable broad-spectrum disinfectant effective against viruses, bacteria, fungi and mycoplasmas).

Each snake had to perform 10 consecutive trials, resulting in a maximum of 20 video recordings. Between trials, the snakes were returned to the starting point and swam in the same direction each time. At the start of each trial, the snake placed in the introduction zone began to swim spontaneously (all semi-aquatic and fully aquatic species) or was gently stimulated by touching its tail if necessary. Filming commenced when the head crossed the line delimiting the swimming zone and ended when the head reached the recapture zone. Most individuals placed in the starting zone tried to escape from the experimenter and thus swam in a straight line toward the end of the track, but several individuals turned back or tried to climb the sidewalls. They were immediately placed/pushed back in the water to continue the trial. When an individual stopped during a trial, the experimenter motivated it to start again by touching the tip of its tail. As soon as the animal crossed the finish line, it was immediately returned to the beginning of the track to begin a new trial. If the snake showed signs of exhaustion (i.e. stopped frequently, lost its balance, or refused to swim) the test was stopped before the 10 trials were completed.

At the end of the trials, snakes were allowed to recover in cotton bags before measurement and release. Each animal was measured for snout-vent length (SVL), total length, and body mass. Body condition index (BCI) was calculated as the residual from a linear regression of log-transformed body mass against log-transformed SVL. Sex was determined visually from the shape of the tail in adults and by hemipenis eversion in juveniles. Female reproductive status was determined by ventral palpation. No gravid females were found in *H. viridiflavus*, *L. saintgironsi*, or *A. laevis*. Sample sizes for each species are provided in Table 1.

Extraction of swimming speed and kinematic parameters

Kinematic data were extracted using Software for the Analysis of Anguilliform Swimming (SAAS), a high-throughput video analysis algorithm that we have developed to rapidly quantify 2D undulatory kinematics from overhead footage of swimming snakes (Gautreau et al., 2023). Swimming speed was calculated as the linear distance traveled by the head along the main axis of the track, ignoring lateral movements; i.e. the speed at which the snake moves through the water rather than the absolute speed of the head movements. Eight additional kinematic parameters were measured to capture key aspects of wave propagation, including frequency, wavelength, lateral amplitude, and transverse speed of the waves. Because, amplitude and associated transverse speed vary along the body as the undulatory wave propagates backward, three regions were analyzed: head, center of gravity (CG, i.e., middle of the body), and tail (Brischoux et al., 2010; Jayne, 1985; Munk, 2008). A full list and description of extracted parameters are provided in Table 2.

Prior to SAAS extraction, all video sequences were reviewed and edited using the Shotcut video editor (v.22.12.21) to retain only those in which the entire body of the snake remained fully visible throughout the swim (Supplementary Figure S2). Only sequences in which the animal swam in a relatively straight line and at a steady pace

Table 1 Summary of total sample composition for each species

Species	N-males	N-females	Nr	Nj	Ntot	SVL (cm)	BCI
ZL	61	42	10	12	103	21.0–115	−0.66–0.11
VA	6	12	4	3	18	20.8–61.5	0.20–1.21
HV	31	14	0	6	45	23.4–102.5	0.90–0.25
NH	11	23	3	6	34	35.6–96.5	−0.32–0.61
NT	16	26	18	6	42	24.5–92	−0.49–0.53
LS	31	9	0	0	40	62–81.5	−0.26–0.17
AL	3	2	0	1	5	46–84	0.70–1.16

ZL: *Zamenis longissimus*; VA: *Vipera aspis*; HV: *Hierophis viridiflavus*; NH: *Natrix helvetica*, NT: *Natrix tessellata*; LS: *Laticauda saintgironsi*; AL: *Aipysurus laevis*. N-males and N-females represent number of males and females tested, respectively. Nr is the number of gravid or pregnant females and Nj is the number of juveniles tested. Ntot is the total number of snakes tested. Range of snout-vent length (SVL) and body condition index (BCI) are also specified.

Table 2 Means of nine conventional swimming parameters of seven snake species

Sp	V	f	Vt (h)	Vt (CG)	Vt (t)	λ	A (h)	A (CG)	A (t)
ZL	0.67	1.09	0.19	0.47	0.76	0.82	0.108	0.120	0.204
VA	0.67	1.16	0.20	0.52	0.86	0.78	0.114	0.119	0.220
HV	0.78	1.52	0.27	0.52	0.79	0.76	0.044	0.093	0.131
NH	0.82	1.74	0.22	0.59	0.90	0.67	0.044	0.087	0.126
NT	1.22	2.40	0.34	0.76	1.18	0.63	0.059	0.079	0.126
LS	1.12	1.80	0.32	0.64	0.83	0.71	0.040	0.091	0.122
AL	0.64	0.93	0.13	0.29	0.38	0.86	0.045	0.076	0.113

ZL: *Zamenis longissimus*; VA: *Vipera aspis*; HV: *Hierophis viridiflavus*; NH: *Natrix helvetica*, NT: *Natrix tessellata*; LS: *Laticauda saintgironsi;* AL: *Aipysurus laevis*. First line provides the initial of the nine swimming parameters: V: Swimming speed (snout-vent length (SVL)/s); f: Frequency (Hz); Vt: Transverse speed (SVL/s, h: Head, CG: Center of gravity, t: Tail); λ: Wavelength (SVL); A: Amplitude (SVL, h: Head, CG: Center of gravity, t: Tail).

were included. Videos were excluded if the snake touched the edge of the track, stopped, or exhibited irregular behavior (e.g., directional changes, hesitation, or fatigue) that could compromise kinematic accuracy. Because snakes did not always follow a trajectory parallel to the longitudinal axis of the track, the orientation of each trajectory was automatically adjusted by translating and rotating the extracted images based on X/Y coordinates of all points calculated by SAAS for each frame along the midline of the snake's back. Kinematic parameters were extracted from the corrected coordinates. The accuracy of extraction was verified visually for each sequence. In total, kinematic data were extracted from 2 498 swimming sequences from 287 individuals (*Z. longissimus*: *n*=103 individuals, 734 videos, *H. viridiflavus*: *n*=45, 214 videos, *N. helvetica*: *n*=34, 309 videos, *V. aspis*: *n*=18, 62 videos, *N. tessellata*: *n*=42, 797 videos, *L. saintgironsi*: *n*=40, 341 videos, *A. laevis*: *n*=5, 41 videos).

Statistical analyses

Compared to previous studies, this experimental design incorporated substantially longer swimming tracks, multiple consecutive trials per individual (up to 10), and dual-camera recordings. Depending on the species and individual, snakes exhibited different levels of fatigue after several consecutive trials. The influence of fatigue on kinematics has never been studied in snakes. To minimize bias related to fatigue, only the best trial of each individual was used in the analyses, resulting in a total of 287 videos. The best trial was defined as the one with the highest swimming speed, which typically coincided with consistent, steady-state locomotion. In most cases, this occurred within the first three trials, before the onset of fatigue, although some individuals achieved optimal performance in later trials (e.g. once the snake no longer hesitated or slowed down after initial panic). The number of swimming sequences filmed for each individual (up to 20) was sufficient to allow reliable selection of maximum performance trials, enabling clear differentiation between acceleration, maximal speed, cruising speed, and signs of fatigue.

Larger snakes swam faster than smaller ones in absolute terms (d/t); therefore, swimming speed was not expressed in m/s but as SVL/s (Van Damme & Van Dooren, 1999). SVL was positively correlated with most kinematic traits (Supplementary Figure S3), except frequency. Therefore, relative values were calculated per unit SVL for all analyses. Descriptive statistics for each species are reported in Supplementary Table S1.

To evaluate intraspecific drivers of swimming speed and kinematics, linear regressions were used to assess the effects of SVL and body condition on each swimming parameter. Separate analyses of covariance (ANCOVA) were then conducted for each species, with sex and reproductive status as factors, the swimming parameter as the dependent variable, and SVL as a covariate (Table 3). The assumption of homogeneity of regression slopes was satisfied in all cases.

For interspecific comparisons, ANCOVA was performed with each kinematic trait as the dependent variable, snake species as the independent variable, and SVL as a covariate where applicable. Homogeneity of regression slopes was confirmed for four kinematic variables (head and tail amplitude, frequency, and wavelength), allowing for the use of additive models. *Post-hoc* Tukey tests were performed to identify significant pairwise differences among species. For the remaining five kinematic variables, models incorporating interactions between SVL and species were used. Principal component analysis (PCA) was also conducted on the full set of nine swimming variables to explore the occupancy of each species in a kinematic domain. Analyses were performed using R v.4.0.5 (Posit Team, 2025).

Water temperature was excluded from statistical models. Body temperature equilibrated rapidly to water temperature, and within-species comparisons revealed no detectable effects of temperature on swimming speed. In most trials, water temperature did not vary. Furthermore, no positive correlation was observed between water temperature and average swimming performance across species. For example, *N. tessellata* achieved the highest speeds while swimming in relatively cold water (14–21°C), whereas *A. laevis* was the slowest species, despite being tested in tropical seawater at the same temperature as the much faster *L. saintgironsi*. In our experimental design, where we avoided varying water temperature interspecifically and intraspecifically as much as possible, interspecific differences species were much more important than temperature in explaining swimming characteristics.

RESULTS

Description of swimming speed and kinematics

Descriptive statistics per species are presented in Supplementary Table S1. For each trait and species, variance was usually very low and always lower than the mean, with modest coefficients of variation. Kurtosis values were predominantly close to zero or positive, with all negative values greater than −2.4. Overall, the data were not over scattered. These distributional characteristics suggest that kinematic parameters were measured with sufficient precision to support robust interspecific comparisons.

Mean relative swimming speed varied by a factor of 1.91

Table 3 Linear regressions between nine swimming variables and four independent variables for each species

Variables	ZL	VA	HV	NH	NT	LS	AL
Mean speed (SVL/s)	**SVL** / BCI	SVL / BCI	**SVL** / BCI	**SVL** / BCI	**SVL** / **BCI**	**SVL** / BCI	SVL / BCI
	SEX / RS	**SEX** / RS	SEX	**SEX** / RS	SEX / **RS**	SEX	SEX
Mean amplitude of head (SVL)	SVL / BCI	SVL / BCI	**SVL** / BCI	SVL / BCI	**SVL** / **BCI**	SVL / BCI	SVL / BCI
	SEX / RS	SEX / RS	SEX	**SEX** / RS	SEX / RS	SEX	SEX
Mean amplitude of CG (SVL)	**SVL** / BCI	SVL / BCI	SVL / BCI	**SVL** / BCI	**SVL** / **BCI**	SVL / BCI	SVL / BCI
	SEX / RS	SEX / RS	SEX	SEX / RS	SEX / **RS**	SEX	SEX
Mean amplitude of tail (SVL)	SVL / BCI	SVL / BCI	SVL / BCI	**SVL** / **BCI**	SVL / BCI	SVL / BCI	SVL / BCI
	SEX / RS	SEX / RS	SEX	SEX / RS	SEX / RS	SEX	SEX
Mean frequency (Hz)	SVL / BCI	SVL / BCI	SVL / BCI	**SVL** / BCI	SVL / BCI	**SVL** / BCI	SVL / BCI
	SEX / RS	**SEX** / RS	SEX	SEX / RS	SEX / RS	SEX	SEX
Mean wavelength (SVL)	SVL / BCI	SVL / **BCI**	SVL / BCI	SVL / BCI	**SVL** / **BCI**	SVL / BCI	SVL / BCI
	SEX / RS	SEX / RS	SEX	SEX / RS	SEX / RS	SEX	SEX
Mean transverse speed of head (SVL/s)	**SVL** / **BCI**	SVL / BCI	SVL / BCI	**SVL** / BCI	**SVL** / BCI	SVL / BCI	SVL / BCI
	SEX / RS	SEX / RS	SEX	SEX / RS	SEX / RS	SEX	SEX
Mean transverse speed of CG (SVL/s)	SVL / BCI	SVL / BCI	**SVL** / **BCI**	**SVL** / BCI	**SVL** / **BCI**	**SVL** / BCI	SVL / BCI
	SEX / RS	SEX / RS	SEX	SEX / RS	**SEX** / **RS**	SEX	SEX
Mean transverse speed of tail (SVL/s)	**SVL** / BCI	SVL / BCI	SVL / BCI	**SVL** / BCI	SVL / BCI	SVL /BCI	SVL / BCI
	SEX / RS	SEX / RS	SEX	SEX / RS	**SEX** / RS	SEX	SEX

SVL: Snout-vent length; BCI: Body condition index; SEX: Sex; RS: Reproductive status. ZL: *Zamenis longissimus*; VA: *Vipera aspis*; HV: *Hierophis viridiflavus*; NH: *Natrix helvetica*, NT: *Natrix tessellata*; LS: *Laticauda saintgironsi*; AL*: Aipysurus laevis*. SVL and BCI were included alone to test their influence on each dependent variable. To test the influence of SEX and RS, SVL was included as a covariate in the model. Bold indicates a statistically significant result.

across the ecological gradient (Figure 1), while the other eight kinematic traits exhibited interspecific variation from 1.37-fold (wavelength) to 3.11-fold (tail transverse speed). The highest relative swimming speeds were recorded in the semi-aquatic species (*N. tessellata*, *L. saintgironsi*, and *N. helvetica*), the lowest mean value was recorded in the fully aquatic snake (*A. laevis*). The other species fall between these limits. The semi-arboreal species (*Z. longissimus*) swam more slowly than terrestrial snakes (*V. aspis* and *H. viridiflavus*), which occupied an intermediate position (Table 2; Supplementary Table S2A). As expected, the rank order of species by swimming speed exactly matched the order observed for undulation frequency, resulting in a strong positive correlation between these two parameters (r=0.86, $F_{1,5}$=30.86, P<0.005; Supplementary Table S3 and Figure S4). In contrast, species ranking was nearly reversed for mean wavelength, with semi-aquatic species exhibiting the shortest wavelengths, fully aquatic *A. laevis* the longest, and semi-arboreal and terrestrial species intermediate values (Table 2; Supplementary Table S2A). Consequently, mean wavelength showed strong negative relationships with swimming speed (r=−0.65; Supplementary Table S3) and undulation frequency (r=−0.91).

Mean relative transverse speed of the head, CG, and tail followed a consistent ecological pattern, corresponding well to swimming speed and undulation frequency (Table 2; Supplementary Table S2A). The lowest values were recorded for the fully aquatic snake, followed by the semi-arboreal snake, while the highest values were observed in the semi-aquatic species, in particular *N. tessellata*. Terrestrial species again occupied intermediate positions. Regarding the mean relative amplitudes of the head, the CG, or the tail, the higher values were systematically observed in some semi-aquatic (*Natrix* species) or in the most terrestrial snakes (*Z. longissimus* and *V. aspis*) and the lowest values in the most semi-aquatic and fully aquatic snakes, with other terrestrial snakes (*H. viridiflavus*) occupying an intermediate position (Table 2; Supplementary Table S2A).

Patterns of intraspecific variation also differed among ecological groups (Supplementary Table S2A–C). Fully aquatic and highly aquatic semi-aquatic snakes (*L. saintgironsi* and *N. tessellata*) frequently exhibited the lowest coefficients of variation and moderate to high kurtosis values for most traits, except for head transverse speed. In contrast, terrestrial species (*V. aspis* and *H. viridiflavus*) tended to show the highest coefficients of variation and the lowest kurtosis, except for CG and tail amplitudes. Mean coefficients of variation and kurtosis across the nine kinematic traits were 31.5 and 0.18, respectively, for the three semi-arboreal and terrestrial species, compared to 26.8 and 0.32 for the four semi-aquatic and fully aquatic species. However, these lifestyle trends are less clear than for the means of the kinematic traits (e.g. swimming speed and frequency). Among all traits, mean wavelength exhibited the lowest coefficient of variation. Within each species, amplitude and transverse speed at the head showed greater variability than corresponding values at the CG or tail, except for *A. laevis*.

Effects of SVL, body condition, sex, and reproductive status

The influence of individual-level traits on swimming performance and kinematics is summarized by species in Table 3. For conciseness, only statistically significant results are reported below.

Swimming speed: Relative swimming speed generally decreased with increasing body length across species, except for *A. laevis* and *V. aspis*, but SVL accounted only for approximately half of the variance in swimming speed (r^2<0.52). In *N. tessellata*, body condition had a significant positive effect on swimming performance. Males swam faster than females in *Z. longissimus*, *N. helvetica*, and *V. aspis* (r^2<0.5). Gravid *N. tessellata* females swam more slowly than non-reproductive females, a pattern not observed in *Z. longissimus*, *V. aspis,* or *N. helvetica*.

Kinematics: Undulation frequency was negatively correlated with SVL in *L. saintgironsi* and *N. helvetica* (r^2<0.2). Shorter individuals in *N. tessellata* exhibited greater relative wavelength (r^2<0.2). Relative transverse speed was negatively correlated with SVL in *Z. longissimus*, *N. helvetica*, *N. tessellata*, and *H. viridiflavus* (r^2<0.5). In *N. tessellata* and *H. viridiflavus*, smaller individuals showed higher relative head amplitude (r^2<0.2). Higher relative CG amplitude was also associated with smaller size in *N. tessellata* and *N. helvetica* (r^2<0.5), as well as tail amplitude in *N. helvetica* (r^2<0.5). Conversely, in *Z. longissimus*, larger individuals displayed

greater relative CG amplitudes (r^2<0.2).

Body condition was negatively correlated with relative head and CG amplitude in *N. tessellata* (r^2<0.2; r^2<0.5), and with tail amplitude in *N. helvetica* (r^2<0.2). Body condition was negatively correlated with relative wavelength in both *N. tessellata* and *V. aspis* (r^2<0.5), positively correlated with relative transverse speed at the head in *Z. longissimus* (r^2<0.2), and negatively correlated with relative transverse speed at the CG in *H. viridiflavus* (r^2<0.2) and *N. tessellata* (r^2<0.5).

In *V. aspis*, males showed higher undulation frequency than females (r^2<0.5). In *N. helvetica*, male head amplitude was reduced compared to females (r^2<0.2), while in *Z. longissimus*, males exhibited lower tail amplitude (r^2<0.2). In *N. tessellata*, males displayed higher transverse speeds at both CG and tail compared to females (r^2<0.5).

Gravid *N. tessellata* females exhibited lower relative CG amplitude and transverse speed compared to non-reproductive females (r^2=0.51 and r^2=0.58, respectively).

Analyses of covariance

Mean relative swimming speed differed significantly among species (*P*<0.001; Supplementary Tables S4, S5; Figure 1). *Post-hoc* comparisons identified *N. tessellata* and *L. saintgironsi* as the faster swimmers. *Natrix helvetica* exhibited higher swimming speed than both *H. viridiflavus* and *Z. longissimus*. The decline in swimming speed with increasing SVL was most pronounced in *N. helvetica*, *N. tessellata*, and *L. saintgironsi.*

Species-specific undulation frequencies also differed significantly (*P*<0.001; Supplementary Tables S4, S5 and Figure S5). *Natrix. tessellata* swam at the highest frequency, whereas *A. laevis* and *Z. longissimus* swam at the lowest. Mean wavelength also varied significantly across species (*P*<0.001; Supplementary Table S1 and Figure S6), with *N. tessellata* exhibiting the shortest wavelength and *A. laevis*, *Z. longissimus*, and *V. aspis* showing the longest wavelengths.

Amplitudes also varied markedly among species (*P*<0.001; Supplementary Tables S4, S5 and Figure S7). For head and tail amplitudes, *Z. longissimus* and *V. aspis* exhibited consistently higher values than other taxa. At the CG level, *Z. longissimus* showed greater amplitudes than *N. helvetica* and *N. tessellata*. The relationship between CG amplitude and SVL varied significantly across species, showing an increase in CG amplitude with increasing SVL in *Z. longissimus* and *V. aspi*s but the opposite pattern in other species.

Significant interspecific variation in mean transverse speed was observed across all body segments (*P*<0.001; Supplementary Tables S4, S5 and Figure S8). *N. tessellata* and *L. saintgironsi* exhibited elevated transverse speeds compared to non-aquatic species. In contrast, *Z. longissimus* and *V. aspis* tended to show the lowest transverse speeds. Notably, *N. helvetica* and *N. tessellata* showed the steepest reductions in transverse speed with increasing SVL across all body regions.

Principal component analyses

The PCA results revealed that the first two axes accounted for 51.6% and 28.4% of the total variance, respectively (Figure 2A; Supplementary Figure S9). All nine kinematic variables contributed meaningfully to the factor map (Supplementary Figure S9). Undulation frequency, swimming speed, and wavelength loaded heavily on the first principal axis, where amplitudes strongly contributed to the second principal axis. Transverse speed exhibited more balanced contributions to both axes.

Species occupied distinct yet partially overlapping regions of this multivariate domain. To better visualize and compare the kinematic domains of species with the most specialized and contrasting lifestyles, *H. viridiflavus* and *N. helvetica*—two species positioned near the midpoint of the lifestyle gradient—were removed (Figure 2B). This refinement revealed a clear separation between the three most aquatic taxa (*N. tessellata*, *L. saintgironsi*, and *A. laevis*) and the more terrestrial *V. aspis*. Notably, fully aquatic *A. laevis* even seems to stand out compared to the semi-aquatic snakes (but sample size is small). Despite this, some overlap existed between aquatic species and the semi-arboreal *Z. longissimus*. Species classified as intermediate along the lifestyle gradient (*H. viridiflavus* and *N. helvetica*) occupy kinematic domains that overlapped extensively with both aquatic and terrestrial forms, including the fully aquatic species. The structure of the kinematic space remained unchanged when additional species, each represented by a single individual, were incorporated across the lifestyle gradient (Supplementary Figure S10).

DISCUSSION

As far as we know, tetrapods that returned to a marine life evolved adaptations that drastically increased their swimming ability; sea mammals, birds, and turtles swim much faster than their land-dwelling relatives. The results obtained with snake species distributed along a lifestyle gradient spanning from arboreal to fully aquatic species do not fit well with this swimming speed scenario. Despite the tendency for semi-aquatic snake species to swim relatively fast with relatively high undulation frequency, the strong overlap between species with contrasting ecologies, as well as the marked slowness of the fully aquatic snakes, means that swimming speed and associated kinematics cannot be clearly categorized along the terrestrial-aquatic gradient.

This discrepancy likely stems from fundamental biomechanical differences. Unlike mammals, birds, and turtles, snakes employ anguilliform swimming—also found in other limbless tetrapods such as various elongated fish, amphibians, and reptiles. In fish, the modalities of this swimming mode vary between lineages and species (Di Santo et al., 2021). Given the extensive morphological diversity among snakes, ranging from very elongated arboreal forms with tapered tails to robust aquatic snakes with short, dorsoventrally flattened tails, marked ecological differentiation in swimming kinematics was also expected. However, our results, particularly the counterintuitive swimming speeds and interspecific overlaps, do not align well with these expectations and suggest a more complex pattern. Several non-exclusive reasons may explain this evolutionary puzzle. First, the data may not have been of sufficient quality to allow for an effective comparison of species. Second, other important sources of variation may have confounded the results. Third, the conventional measurements we have recorded are not suitable for dealing with the problem.

Technical caveats

During the swimming trials, the experimenter functioned as a simulated predator, prompting snakes to exhibit escape behavior. Behavioral differences were observed between terrestrial and semi-arboreal *versus* aquatic species. In the

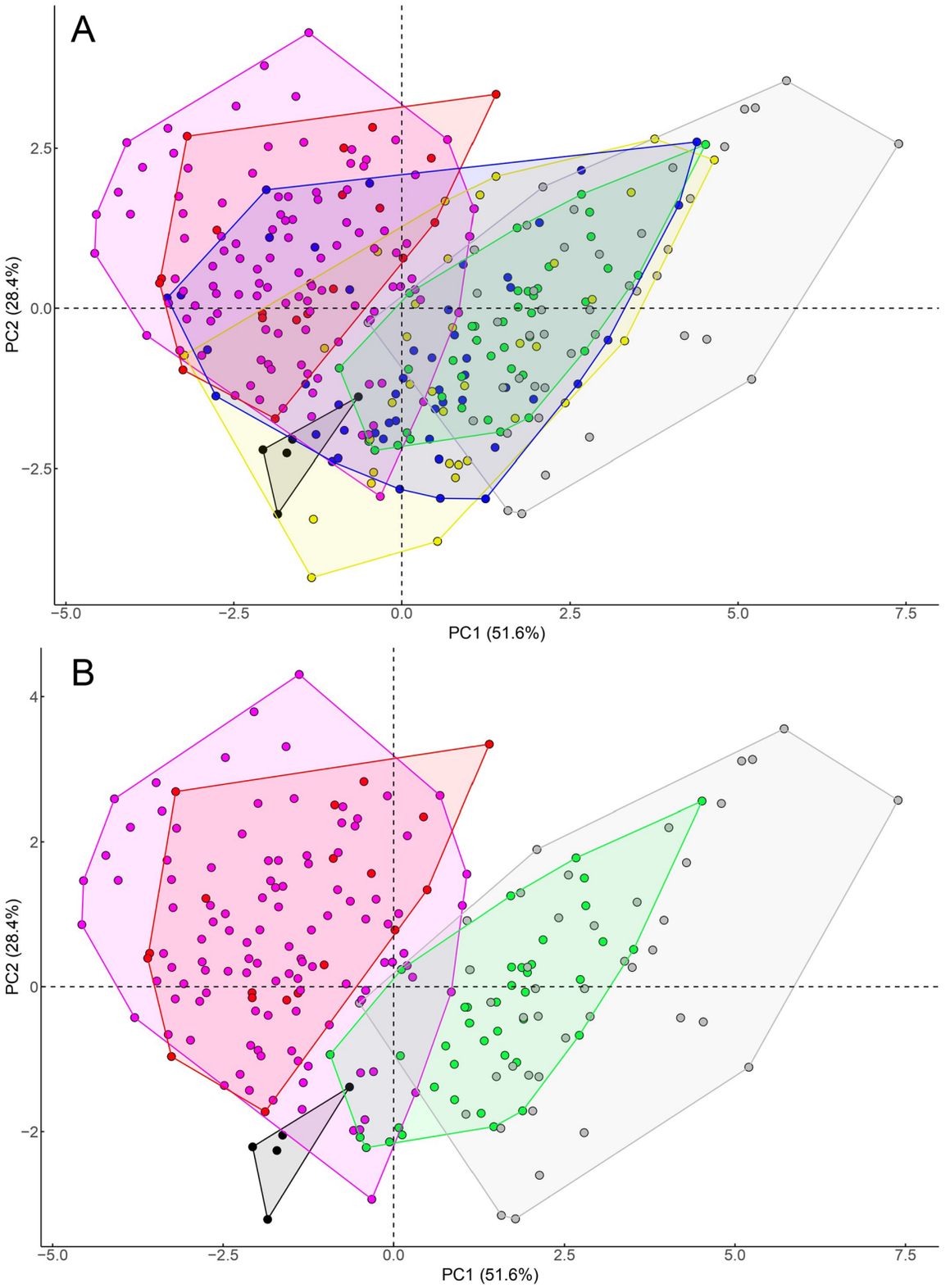

Figure 2 Principal component analysis of nine kinematic parameters for each individual of the seven snake species

Convex polygons show kinematic space occupied by each species. Each species is represented by a color: *Zamenis longissimus*: pink, *Vipera aspis*: red, *Hierophis viridiflavus*: blue, *Natrix helvetica*: yellow, *Natrix tessellata*: gray, *Laticauda saintgironsi*: green, *Aipysurus laevis*: black. A: Kinematic domain of each species. B: Individuals of *N. helvetica* and *Hierophis viridiflavus* were removed to improve visualization of domain separation or minor overlap.

former, several individuals attempted to climb the sidewalls to leave the track rather than swim directly forward, whereas aquatic species typically swam in a straight line from the onset, potentially introducing procedural artifacts. Nonetheless, no strict pattern emerged, as several non-aquatic species, such as *C. carinatus* and *A. prasina*, immediately initiated straight, sustained swimming. More importantly, by selecting only the best sequences from a large

initial dataset, any flawed or erratic trials were excluded from subsequent analyses. Descriptive analyses indicated that within-species data distributions were not notably affected by overdispersion or outliers. Despite variation in experimental track dimensions, all setups were long enough to allow snakes to attain a steady cruising speed within the filmed segment. Automatic trajectory correction and kinematic extraction procedures further limited potential measurement errors. A residual problem is that the tip of the tail of species with very tapered tails may have been poorly tracked by the software (e.g., "cut" by surface waves), but the absence of anomalous results suggests that this problem remained minor.

Influence of morphology, sex, and reproductive status

Body size exhibited consistent and biologically logical effects both within and between species. Larger individuals swam faster in absolute terms but slower in relative terms. Within species, individuals exhibiting higher undulation frequencies and shorter wavelengths achieved the highest relative speeds. Across species, swimming speed was strongly positively correlated with undulation frequency and negatively correlated with wavelength, in line with previous studies (Brischoux et al., 2010; Gillis, 1998; Jayne, 1985; Stin et al., 2024). However, no consistent associations emerged between body size and kinematic parameters at the head, CG, or tail, likely reflecting a complex interplay among morphology, kinematics, and hydrodynamics.

In species sampled across a broad size range and with sufficient sample size (Table 1; Supplementary Figure S3), body condition, sex, and reproductive status significantly influenced swimming traits. Body condition positively influenced swimming performance in *N. tessellata*, and in two other snakes, two parameters associated with fast swimming: low amplitude and low wavelength (less clear results were obtained for transverse speeds). Males exhibited faster swimming speeds than females, and in three species showed high values for the kinematic characteristics associated with fast swimming, which is consistent with their greater development of locomotor musculature than females (Bonnet *et al.*, 1998). In *N. tessellata*, females nearing oviposition swam more slowly, likely due to the drag and mass associated with large ovarian follicles (Webb, 2004). In contrast, no such effect was observed in *Z. longissimus*, *V. aspis*, or *N. helvetica*, where females were tested during early vitellogenesis, before follicle size imposed a significant physical burden. Collectively, these results indicate that the nine conventional swimming parameters employed in this study provided sufficiently precise information for comparing the swimming performance and kinematics of the selected species. However, often only half or less of the variance was explained by the physical traits considered.

Phenotypic plasticity

Early aquatic experience can influence swimming performance in snakes (Aubret et al., 2007). The semi-aquatic grass snake *N. helvetica* showed swimming characteristics more typical of terrestrial species than of its closest relative *N. tessellata*. The individuals were captured in a forested area of France lacking large water bodies or rivers, an unusually dry habitat for this species (although this snake is sometimes categorized as terrestrial). It is likely that these grass snakes were encountering aquatic conditions for the first time during our trials. Individuals sampled from wetland environments may have produced different results. However, swimming parameters recorded from two grass snakes sampled in a lake in North Macedonia fell within the overall kinematic domain of the species. In any case, this species was placed in the middle of the lifestyle gradient, and possible effects of phenotypic plasticity likely do not strongly influence our interpretations. These considerations do not apply to the other species, which were sampled within their typical native habitats.

Lifestyle gradient

Thanks to (or in spite of) the various sources of biological and technical variation outlined above, consistent macroevolutionary trends emerged across the lifestyle gradient. Disregarding fully aquatic species, semi-aquatic snakes exhibited the fastest relative swimming speeds and showed consistent kinematic parameters, such as high undulation frequencies, short wavelengths, and low head, CG, and tail amplitudes. These patterns likely reflect improved neuromuscular control over undulations, minimizing excessive lateral displacements that may reduce hydrodynamic efficiency. Furthermore, the degree of aquatic dependence (Figure 1) closely mirrored both swimming performance and associated kinematic parameters, with a clear terrestrial-to-aquatic ecological gradient corresponding to progressive shifts in conventional swimming parameters. In addition, aquatic snakes also exhibited reduced interindividual variability, a pattern expected given their swimming traits are likely more constrained and optimized compared to that of non-aquatic species.

However, fully aquatic species, those that spend their entire lives in the sea, did not conform to the general trends observed across the terrestrial-to-aquatic continuum (Figures 2 and S10). Contrary to expectations, these species swam slowly with relatively large head undulations, yet, as expected they showed relatively little intraspecific variability, indicating a consistent but distinct locomotor strategy. Comparable results for *Hydrophis* (*Pelamis*) *platurus* reinforce this pattern (Graham et al., 1987; Figure S10). These findings suggest that fully aquatic snakes have evolved a unique mode of swimming, supported by specialized morphological, physiological, and behavioural adaptations, rather than representing a mere extension of semi-aquatic locomotion. In the multivariate space (Figure 2), fully aquatic snakes are not located at the end of the putative trajectory formed by terrestrial and semi-aquatic species. Instead, they occupy a partially divergent position. It seems that swimming in fully aquatic snakes has evolved into relatively slow and wide undulations, including the wide undulations of the front part of the animal. Semi-aquatic snakes that spend most of their life in water (e.g., anacondas) may conform to the fully aquatic category, revealing a possible convergence (but our sample size is minimal for this speculative category).

Beyond these general trends, it is important to note both the large size of the kinematic domain occupied by most lifestyle and the substantial overlap between them. This broad picture underscores the complexity of snake locomotion. In many cases, differences between two terrestrial and thin-tailed taxa (e.g., *Z. longissimus* and *V. aspis*) exceeded those between a fully aquatic paddle-tailed snake (*A. laevis*) and a thin-tailed terrestrial species (*Z. longissimus*). Remarkably, the swimming speed of *A. laevis* was indistinguishable from that of *Z. longissimus* and *V. aspis*, both non-aquatic species likely naïve to aquatic environments. Expanded sampling that

included nine additional species, ranging from strictly arboreal and fossorial forms to three fully aquatic snakes (data from one species obtained from literature), supported this complex picture (Supplementary Figure S10). For example, the semi-aquatic *E. murinus* was among the slowest swimmers, comparable to the fossorial *E. colubrinus*, whereas the arboreal and filiform *A. prasina* and fossorial *L. bicolor* swam rapidly. Although the strong intraspecific variability observed limits these comparisons, it is important to highlight the fact that species with contrasting lifestyles and morphologies (e.g. *V. aspis* vs. *L. saintgironsi*) occupy completely separate kinematic domains (Figure 2). There are also strong differences between other species, e.g. *E. colubrinus* is particularly stocky and has a very small tail, whereas *A. prasina* is extremely slender, elongated and has a very long tail.

Adaptations to an aquatic lifestyle

Key morphological and anatomical traits likely contribute to aquatic locomotion but were not explicitly incorporated into the present analyses. Among anguilliform swimmers, a laterally compressed body likely facilitates the formation of vortices to generate thrust while minimizing drag. However, the influence of the degree of body flattening in anguilliform swimmers on their kinematics and swimming performance is poorly known; previous work has indeed focused on the role of the dorsal and ventral fins and the tail (van Rees et al., 2013). Fully aquatic snakes exhibit permanent lateral compression along the body axis (Heatwole, 1999), while various semi-aquatic species can actively flatten the posterior body region during swimming (Brischoux et al., 2010; Pattishall & Cundall, 2008). The epi-axial muscles are relatively more developed in semi-aquatic snakes than in terrestrial or arboreal snakes, probably providing an advantage for movement through viscous and dense media (Mathou et al., 2023). However, comparative data between semi-aquatic and fully aquatic snakes is lacking. These distinct morphological and anatomical adaptations may underlie the observed differences in performance and kinematics in fully aquatic snakes, which are unable to move on land, as opposed to semi-aquatic species with amphibious habits. Other aquatic adaptations, particularly to the marine environment, such as specialized salt glands, palm-shaped tails, or thicker skin, should also be considered (Aubret & Shine, 2008; Rautsaw et al., 2021; Shine et al., 2019; Webb, 1988). Specific work on these considerations is clearly needed.

CONCLUSIONS

This study highlights the difficulties in understanding the evolution of swimming in snakes. Here, integrated analysis of nine conventional kinematic parameters involving a large number of individuals and covering species spread across a wide range of lifestyles provided key insights into the relationship between swimming kinematics and speed. The analysis revealed two distinct evolutionary trajectories: one associated with semi-aquatic snakes that retain terrestrial locomotor capacity, and another defined by fully aquatic taxa incapable of land movement. Although both lineages likely stem from ancestrally amphibious forms, it remains uncertain whether extant semi-aquatic snakes actually represent the transitional stage towards fully marine snakes. We hypothesize that the elongated snake body form imposes functional constraints on swimming kinematics: in cylindrical-bodied snakes, large undulations may be less effective than smaller, high frequency undulations, while in laterally compressed snakes, larger, slower undulations may confer greater propulsive advantage. Our results also highlight the limitations of conventional measures focused solely on swimming speed and align with emerging evidence in other taxa, such as coral fish, demonstrating that morphology alone does not reliably predict swimming behavior and performance (Satterfield et al., 2023).

Snakes that have adapted to aquatic environments tend to feed on fish, but they still breathe air. Thus, their diving performance, duration and depth, which influence their ability to find food, are likely to be critical ecological adaptations (Brischoux et al., 2008). Amphibious snakes can rest on land for extended periods (e.g. during digestion), sometimes for weeks. The reverse is not true for fully aquatic species, although they can rest on the sea floor underwater (XB, personal observation), they must regularly come to the surface to breathe. Fully aquatic snakes are therefore forced to swim frequently. Accordingly, endurance capacity may represent another key adaptation distinguishing these groups. Investigating the relationships among morphology, swimming kinematics, speed, endurance, and energy expenditure is crucial for understanding aquatic specialization. Regarding swimming efficiency, hydrodynamic analysis offers a particularly powerful framework (Lighthill, 1969, 1971). Anguilliform swimming is energetically efficient, with snakes widely recognized as low-energy specialists (McCue et al., 2012; Palstra et al., 2008). However, quantifying the energy expenditure of undulatory wave patterns is technically challenging, particularly because the swimmer's body undergoes active and passive deformation while it progresses through water (Piñeirua et al., 2015; Stin et al., 2023, 2024). One promising avenue for the calculation of propulsive and drag forces, and thus estimation of the energy expenditure, is the characterization of the vortex structures produced at each body undulation, as recently quantified in snakes (Stin et al., 2023).

However, advancing this field will require expanded comparisons spanning diverse morphologies and ecologies across snake phylogeny, including fossorial taxa. Combining hydrodynamic analyses from representative species with broad kinematic datasets will enable the refinement of evolutionary and functional models. Such efforts will enable targeted digital simulations and the development of snake robots with undulatory profiles and structural parameters inspired by the particularly fluid swimming motion of real snakes (Gautreau et al., 2022; Maroun et al., 2024). Through this combined experimental and modeling approach, it will become possible to test key hypotheses regarding the biomechanical and energetic bases of aquatic locomotion in snakes.

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

X.B. conceived the original idea, obtained the funds, and administrated the project. X.B. and G.F. conceived the protocol and swimming tracks. G.F., E.G., T.F., X.B., K.M., P.T., and N.L. developed the analytical methodology. G.F., S.L., D.H., X.B., T.F., L.P., F.A., S.A.H., H.G., and O.C. collected the

data. G.F. and X.B. analyzed the data. G.F. and X.B. led the writing of the manuscript. A.H. and R.G.D. participated in the scientific development of the project and revised the manuscript. All authors read and approved the final version of the manuscript.

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