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Aquatic Locomotor Kinematics of the Eastern Water Dragon (*Intellagama lesueurii*)

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Abstract.—**Quantitative studies of the axial undulatory swimming techniques used by secondarily aquatic vertebrates have been largely restricted to crocodilians. Numerous members of the suborder Lacertilia (lizards) are also known to swim using axial undulatory techniques, but how they do so has received minimal attention from the scientific community. We investigated the morphology and undulatory locomotor kinematics adopted by the Eastern Water Dragon (*Intellagama lesueurii*) through observation of natural swimming and filming of animals in a flume tank with a high speed camera. We found that morphological modifications associated with improved swimming ability and correlations between wave characteristics and swimming velocity are limited to the tail. The shape of dorsal spines and the reduction in the width of transverse processes of the caudal vertebrae result in a mediolaterally compressed tail instead of the typically rounded or dorsoventrally compressed tail seen in other Australian agamids. Axial undulatory swimming in *I. lesueurii* was found to be conceptually similar to that of crocodilians, but the relatively long and thin terminal part of the tail produces a different shaped undulatory wave. Unlike crocodilians and fishes, *I. lesueurii* does not use frequency moderated velocity control. Instead, changes in velocity are solely controlled by the phase speed of the propagating wave. The combined effect of these traits is comparable efficiency and performance in the water relative to that of crocodilians and an improvement relative to terrestrial lizards.**

Although no extant members of the suborder Lacertilia (lizards) are known to be fully aquatic, some species are known to have close associations with freshwater, brackish and marine habitats (Bartholomew et al., 1976; Bauer and Jackman, 2008). These associations range from dependence on riparian vegetation to active foraging in the water (Dawson et al., 1977; Shine, 1986; Mayes et al., 2005). Aquatic dependence is found with increased frequency among varanids, iguanids, scincids, and agamids from tropical latitudes, and it is among these species that improved aquatic locomotor capabilities relative to more terrestrial species are likely to occur.

When presented with the challenge, most terrestrial lizards have some capacity to swim (Braun and Reif, 1985). The action of walking can often be coopted for swimming (Snyder, 1962; Gray, 1968; Ritter, 1996); however, in the absence of morphologies associated with aquatic locomotion, this technique is highly inefficient (Braun and Reif, 1985). Morphological traits such as streamlining help to reduce drag (Lighthill, 1969, 1970) and webbed limbs can increase propulsive force. Animals may further adapt to the aquatic environment by changing their locomotor technique altogether. Key to this study is the tendency for secondarily aquatic tetrapods to posses flattened tails (Bedford and Christian, 1996) that are used as an aquatic locomotor organ.

Braun and Reif's (1985) review of vertebrate swimming grouped aquatic locomotor techniques into two broad categories: axial and paraxial. Axial techniques use the cyclic beating of the trunk to propagate a travelling sinusoidal wave while paraxial techniques use appendages such as arms and legs. Axial undulatory techniques are considered to provide the most efficient method for aquatic propulsion (Braun and Reif, 1985), and animals that use them usually rely on the tail as the main locomotor organ. Typically, axial undulation incorporates a travelling sinusoidal wave, generated rostrally and travelling caudally. Tails or fins are used to amplify the effect of the undulation. The shape of the sinusoidal wave can be used to further define the type of axial undulation (Breder, 1926; Braun and Reif, 1985). The propulsive wave type is categorized by two factors: the relative length of the sinusoidal wave, and to which part of the body the wave is confined. Propulsive techniques that use wavelengths shorter than the animal's body length are defined as undulatory, and wavelengths longer than the animal's body length are said to be oscillatory. Hence, a complete wave is observed within the length of an animal in undulatory swimming where as an incomplete wave is observed in oscillatory swimming. Where pronounced changes in wave amplitude are observed between the animal's trunk and caudal section, they are said to be refined to a subset of the animal's body. Based on these observations Braun and Reif's (1985) proposed the following categories: undulatory, subundulatory, oscillatory, and suboscillatory.

Axial undulatory swimming in semi-aquatic tetrapods is of particular interest from an evolutionary perspective. Traditionally, studies of undulatory swimming in secondarily aquatic vertebrates have been restricted largely to crocodilians (Manter, 1940; Fish, 1984; Frey and Salisbury, 2001; Seebacher et al., 2003). Crocodilians have a long association with the aquatic environment and possess well-documented morphological traits that improve their aquatic locomotor capabilities (Frey and Salisbury, 2001). However, much can be learned of the evolution of undulatory swimming in secondarily aquatic vertebrates by studying reptiles other than crocodilians. We aim to address this knowledge gap by investigating the swimming kinematics and morphologies of a semi-aquatic lizard, the Eastern Water Dragon, *Intellagama* (formerly *Physignathus*) *lesueurii* (Gray, 1831).

Although spending much of its time out of the water, *I. lesueurii* is known to actively traverse and feed within the aquatic component of its habitat space (Thompson, 1993; Christian and Conley, 1994; Christian et al., 1996; Mayes et al., 2005). *Intellagama lesueurii* is also known to possess a mediolaterally compressed tail, a morphological trait common to swimmers that use lateral undulation (Bedford and Christian, 1996; Frey and Salisbury, 2001), along with numerous physiological adaptations associated with a semi-aquatic lifestyle (Courtice, 1981a,b). Aquatic dependence, evidence of morphological and physiological adaptation and the abundance of *I. lesueurii* around urban areas in southeastern Queensland make it an ideal species for investigating the evolution of undulatory swimming in secondarily aquatic reptiles.

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The purpose of this study was to describe and quantify the efficiency and performance of axial undulatory techniques in a semi-aquatic lizard. Also, we attempted to identify morphological features conducive to improved locomotor performance. We hypothesized that locomotor techniques in *I. lesueurii* would be similar to those seen in crocodilians given their comparable body plans but at lower efficiencies and performances attributable to less pronounced morphological modifications of the locomotor organs and natural history suggestive of less aquatic dependence.

MATERIALS AND METHODS

Morphology.—Morphological data were collected from both preserved specimens and live animals. Preserved spirit and skeletal specimens were supplied by the Queensland Museum. Specimens showing obvious signs of desiccation were not used for morphological analysis. Whole body measurements were recorded to the nearest millimeter using either a tape measure or ruler. Fine scale measurements were recorded with a Kincrome 150-mm vernier calliper to the nearest 10th of a millimeter. Measurements taken were as follows: skull length (from tip of the nose to rear of the cranium); snout–vent length; vent to tail tip; tail height and width at standard increments from the vent to tail tip. Tail vertebrae were measured for height and width from the base of the centrum to the top of the spinal process, and across the maximum width of the transverse processes, respectively. For live animals, tail and limb flexibility was recorded by photographing the maximum range of motion under manual manipulation. As a comparison to *I. lesueurii*, these measures were conducted on the following species: Mertens's Water Monitor, *Varanus mertensi* (Glauert 1951); Lace Monitor, *Varanus varius* (White ex Shaw, 1790); Sand goanna, *Varanus gouldii* (Gray 1838); Inland Bearded Dragon, *Pogona vitticeps* (Ahl, 1926); Eastern Bearded Dragon, *Pogona barbata* (Curvier, 1829); Frill-Necked Lizard, *Chlamydosaraus kingii* (Gray 1825); and Rainforest Dragon *Hypsilurus spinipes* (Duméril and Duméril, 1851).

Intellagama lesueurii are abundant on The University of Queensland St. Lucia Campus. Specimens were captured using a noose pole apparatus and contained in a hessian sack. When animals were held for more than a few hours, they were kept in a lined plastic bin containing a suitable amount of water. No animal was kept for longer than one day before being returned to its location of capture.

Flume Tank Studies.—Kinematic studies were conducted in a flume tank facility at The University of Queensland, St. Lucia Campus. The study sampled *I. lesueurii* of the full range of sizes encountered on the St. Lucia Campus, captive *P. vitticeps* as a terrestrial control, and a single captive *V. mertensi* as a comparison to another semi-aquatic lizard. Only animals with minimal damage to the tail were used in the primary data set to reduce the effect of tail length confounding results. Animals with damaged tails were treated separately to test the importance of tail length. Male *I. lesueurii* attain larger sizes and once mature are more robustly built than females. Females and immature males are morphologically indistinguishable. Both sexes were used in the study to allow for sampling of a larger range of sizes and so that the study was representative of the species as a whole.

To measure swimming technique and performance, specimens were enclosed in a 1.5-m × 0.6-m section of a flume tank powered by twin Minn Kota electric motors. To prevent temperature-dependent performance from confounding data, water temperature was maintained at 30°C, a temperature that generally produces optimal performance in a wide variety of reptiles (Bartholomew et al., 1976; Courtice, 1981c; Turner et al., 1985; Seebacher et al., 2003). To ensure constant and consistent body temperature between individuals, specimens were given 15 min for their body temperature to equalize with the water before the experiment commenced (Bell, 1979; Grigg et al., 1979; Fraser and Grigg, 1984). When measuring burst speed, specimens were allowed to recover between takes to counter the effects of fatigue. If specimens did not spontaneously take to swimming, they were held in the direction of flow until they showed signs of readiness. Animals were encouraged to swim either by splashing the water behind them or by touching their tail. Maximum burst speed was used as a measure of performance, and phase speed to forward velocity ratio was used as a measure of efficiency. A top view of surface swimming was recorded by filming a mirror positioned at a 45° angle above the tank. The tank was lit with a single 150-W incandescent work light aimed at the mirror so as to reflect down on the subject; a single 20-W waterproof halogen garden light was also submerged at the rear of the swimming chamber to provide additional illumination and contrast. For ease of recognition of key sections of the animal's spine, white, nontoxic acrylic paint was used to mark reference points. Each animal was marked with lines or dots on the tip of the nose, the interception of the spine with the pectoral girdle, the interception of the spine with the pelvic girdle, at the tail spine bifurcation and tail tip (Fig. 1). Paint either washed off or was shed by animals shortly after release.

Video Analysis.—Video footage was filmed with a Casio Exilim EX-F1 digital camera at 300 frames per second. MOV files were converted to high resolution AVI files using Quicktime Pro (version 7) for analysis using Redlake MotionScope PCI. Water speed was calculated by measuring the progress of a neutrally buoyant object. The object was allowed to accelerate to match water velocity before being measured toward the rear of the swim chamber. This process was repeated three times before each test and the average was assumed as water velocity. Variability between the three estimates was low and typically within the error margins of the recoding technique. The section of the flume used for experiments was baffled to reduce localized variability in water velocity. Furthermore, swimming footage was only analyzed from the central section of the flume. Sections of swimming footage where the animal contacted or came into close proximity with walls were excluded from analysis. Instantaneous velocity was calculated by adding the animal's velocity relative to the tank to the average water velocity. Manter (1940) found that undulatory swimmers do not maintain true constant velocity but go through a cycle of acceleration and deceleration about an average velocity. To account for this variability, velocities were measured over the time frame of half a complete cycle such that a true representation of thrust output for the wave characteristics of a given tail beat could be calculated. Wave characteristics including phase speed, amplitude, frequency, and wavelength were determined by tracking the peak amplitude of predetermined landmarks over time.

Data Analysis.—Morphological and kinematic data were compiled and analyzed using Microsoft Excel 2007 and R (version 2.15.1). We used separate linear mixed effects models to assess the relationship between each wave characteristic and swimming velocity. All models accommodated nonindependent

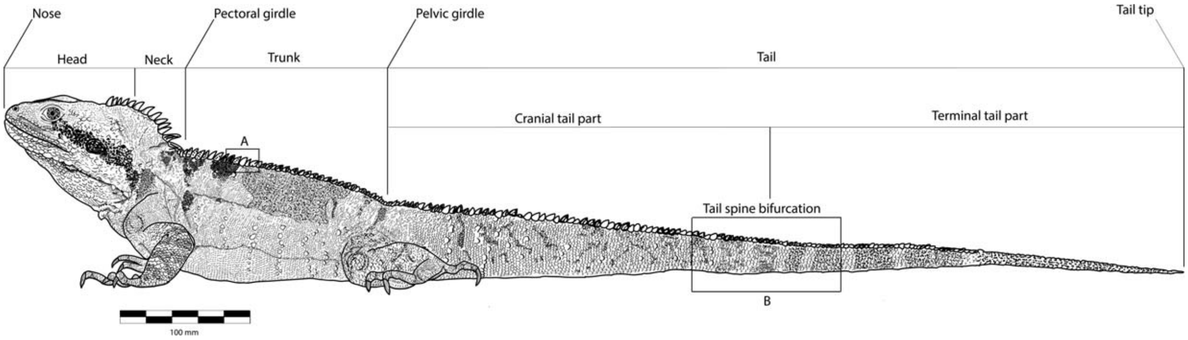

FIG. 1. Lateral view of an adult male *Intellagama lesueurii*. A and B are areas shown in detail in Figures 3 and 4, respectively. The cranial tail part is described as the section of tail spanning from the pelvic girdle to the tail spine bifurcation. The section, which is typically one snout–vent length long supports the bulk of the muscle mass of the tail and is relatively stiff compared to the terminal tail part. The terminal tail part is the remaining span of the tail. It varies in relative length from individual to individual and can also be reduced in size from naturally accrued damage.

measures from the same animal using a random intercept term. Model assumptions of residual normality and homoscedasticity were graphically confirmed. Stepwise term deletion routines, using likelihood ratio tests, were used to assess the significance of each term. Models were fit using maximum likelihood for hypothesis testing, and minimal adequate models were refit using restricted maximum likelihood for parameter estimation. Mean performance ratios were calculated for each animal and then averaged to provide a mean ratio for each body section. Likewise, standard errors for performance ratios for each animal were pooled to generate a standard error for each body section. These analyses were performed using the R-package nlme (Pinheiro et al., 2012).

RESULTS

Morphology.—Examination of the morphology of *I. lesueurii,* relative to other agamids reveals a number of characteristics indicative of improved aquatic locomotor ability. The feet of *I. lesueurii* lack webbing (Fig. 2), and the limbs are of similar appearance to those of other terrestrial agamids. The undamaged tail of *I. lesueurii* ranges from 2.2–2.7 times the snout–vent length. Tail height reduces evenly along its length, reducing to a thin cord-like strand terminally (Fig. 1). The cranial part of the tail supports the bulk of the axial and hypaxial muscle mass, reducing rapidly in cross-section further terminally. Scales are keeled but otherwise smooth and without protrusions. A row of spines runs from a scale-crest down the midline from the interorbital region through to the tail tip. On the head and dorsum, the spines are separate from each other (Fig. 3), but commencing at the pelvis they begin to interlock, with the space between spines decreasing (Fig. 4). At approximately one snout–vent length along the tail, the row of spines bifurcates and the tail becomes squarer in cross-section (Fig. 4). It is at this point that the tail is most mediolaterally compressed, being approximately twice as high as its maximum width (Figs. 4 and 5). As a result of this compression, the tail retains lateral flexibility but resists dorsoventral flexion. Mediolateral compression of the tail is associated with osteological features of the caudal vertebrae (Fig. 6), including the width of transverse processes and the height of the spinal process. The spinal processes are markedly higher than in other agamids (*P. vitticeps*, *P. barbata*, *C. kingii*, *H. spinipes*), whereas the transverse processes are relatively narrower and reduce in width until absent. This graduation was found to occur over fewer vertebrae than in other agamids. The result is a proportionately long and mediolaterally compressed tail, with a cranially positioned muscle mass and rectangular cross-section terminally (Fig. 5).

Swimming Kinematics.—The primary aquatic locomotive technique for *I. lesueurii* is axial undulatory swimming on the water's surface. Diving and hybridized paraxial/axial swimming was also observed but not paraxial on its own. We analyzed footage of axial surface swimming only. Undulations are generated in the head and travel caudally before continuing toward the tail. However, the propulsive component of the sinusoidal wave does not fully develop until the pelvic girdle (Figs. 7 and 8). No relationship between body size and absolute speed was found ($F_{1,11} = 2.089$, $P = 0.176$).

The amplitude of undulations originating from the head reduces to a node just caudal to the pectoral girdle. It then increases in size at the pelvic girdle and continues to do so until it reaches the tail tip (Fig. 8). The amplitude of undulations

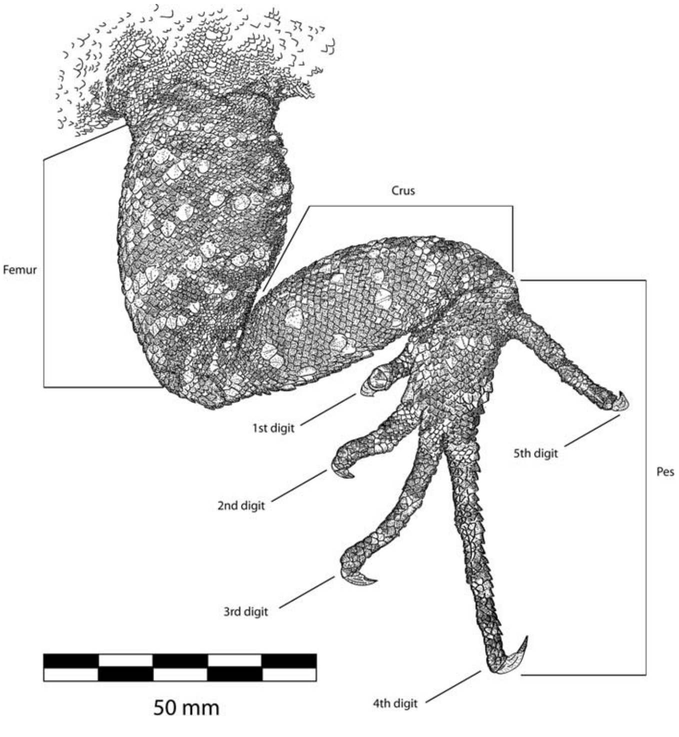

FIG. 2. The left hind limb of *Intellagama lesueurii*, showing no sign of morphological adaptation to swimming.

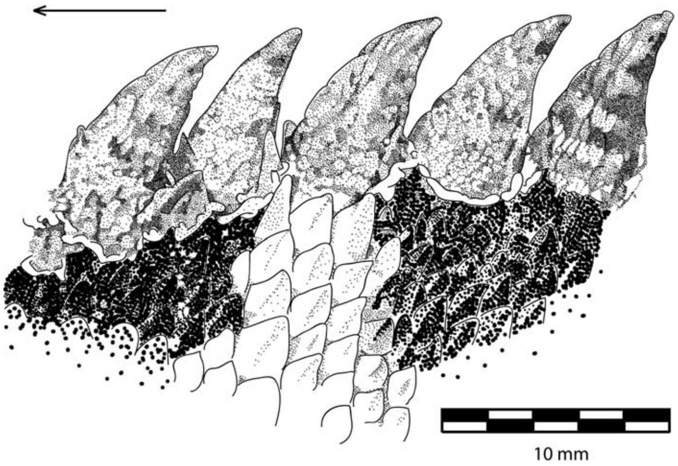

FIG. 3. Spines on the middorsum of an adult male *Intellagama lesueurii* (as seen in Fig. 2A). Cranial is shown by the arrow.

increased in relation to the size of the animal and, as such, amplitude was scaled in relation to body length. Amplitude was found to have no statistically significant correlation with changes in velocity (Table 1).

Frequency was found to vary both between and within individuals. However, on average the frequency between sections remained relatively similar. Changes in frequency did not correlate with changes in velocity in any body section (Table 1). Larger animals undulated at a lower frequency than did small animals; however, when combined with amplitude as a function of lateral velocity, the speed of undulations was roughly equivocal relative to body size.

Variable wave amplitude and phase speed made measuring a complete wave difficult and inconsistent. Instead the wavelength (λ) was calculated mathematically as a function of phase speed (v) and frequency (f) so that $\lambda = v/f$. Wavelength was then scaled to body length and plotted as a regression. There was a tendency for overall wavelength to increase with velocity, approaching 0.9 body lengths at maximum velocity, but, at a significance indicating need for greater replication ($F_{1,19} = 4.259$, $P = 0.053$). No correlation between velocity and wavelength was identified at the pectoral girdle, pelvic girdle, and tail tip (Table 1) but was found to correlate at the tail spine bifurcation ($F_{1,19} = 9.899$, $P = 0.0053$; Fig. 9).

The propagation of the sinusoidal wave was found to vary along the length of the body and in accordance with changes in velocity. The front and rear of the head oscillates as a single unit. As a consequence, the phase speed of the span between the nose tip and pectoral girdle appears much faster than the rest of the body at 2.98 ± 0.74 SE times the forward velocity. The phase speed of the span between the pectoral girdle and the pelvic girdle was the lowest at 1.20 ± 0.16 SE times the forward velocity. The phase speed of the span between the pelvic girdle and tail spine bifurcation, and tail spine bifurcation and tail tip, were 1.66 ± 0.18 SE and 1.54 ± 0.23 SE times the forward velocity. Phase speed was found to only correlate with forward velocity with statistical significance in the section between the pelvis and tail spine bifurcation ($F_{1,19} = 8.443$, $P = 0.0091$; Table 1). The phase speed of the whole animal was found to correlate over the entire range of recorded forward velocities (0.403–1.067 m/sec) with statistical significance ($F_{1,24} = 19.690$, $P < 0.001$; Fig. 10) at a performance ratio of at 1.77 ± 0.247: 1 to the forward velocity.

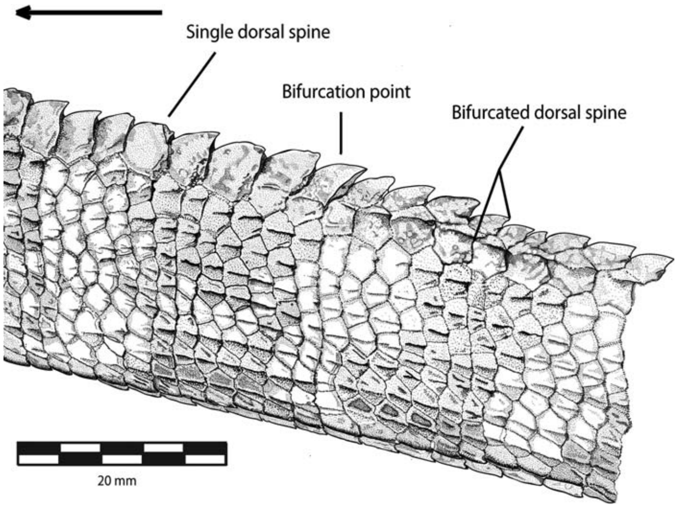

FIG. 4. The section of tail from an adult male *Intellagama lesueurii* where the dorsal spine bifurcates (as seen in Fig. 2B). Cranial is shown by the arrow.

DISCUSSION

Aquatic Locomotion in Intellegama lesueurii. Both the limbs and the tail of *I. lesueurii* provide propulsion during swimming. The limbs lack webbing (Fig. 2) and are only used as a locomotor organ during rapid acceleration from a static start or for steering purposes. In most cases, changes in direction are achieved independent of the limbs through adjustments in the position of the head relative to the tail. For rapid bursts or during sustained swimming, the legs remain retracted against the trunk in a streamlined position (Fig. 7). The digits are thin and elongate and similar in proportion to fully terrestrial agamids, in which they are used mainly to clasp branches while climbing. Correlations between wave characteristics and velocity were consistently found to be significant in the proximal sections of the tail, indicating that this section is likely to be responsible for thrust production and velocity control. All evidence points toward the tail as the single most important structure for improved aquatic locomotor performance in this species.

At up to 2.7 times the snout–vent length, the undamaged tail of *I. lesueurii* is proportionately one of the longest tails of any semi-aquatic lizard. Comparatively the tail of the Australian varanid *V. mertensi* was observed to be 1.3–1.5 times the snout–vent length, whereas other semi-aquatic agamids such as *Amblyrhynchus cristatus* at approximately 1 (Dawson et al., 1977). The ability to regenerate the terminal part of their tail, an uncommon feature for agamids (Arnold, 1984), suggests that the length bears some importance to fitness. It seems likely that tail length provides significant benefits to *I. lesueurii* on an evolutionary scale for it to have reached such lengths and for the animal to invest energy in the growth of a replacement if part of the tail is lost. One possible explanation for its proportionately greater length relative to other agamids is increased locomotor performance.

Ratios of phase speed to forward velocity are commonly used as a measure of performance in undulatory swimming (Manter, 1940; Fish, 1984). Reduced locomotor performance is common in lizards that have experienced tail loss (Bateman and Fleming, 2009). In the case of *I. lesueurii*, reduced tail length was observed to influence both wave form and performance. In investigating one particular animal for which its tail had been reduced to a

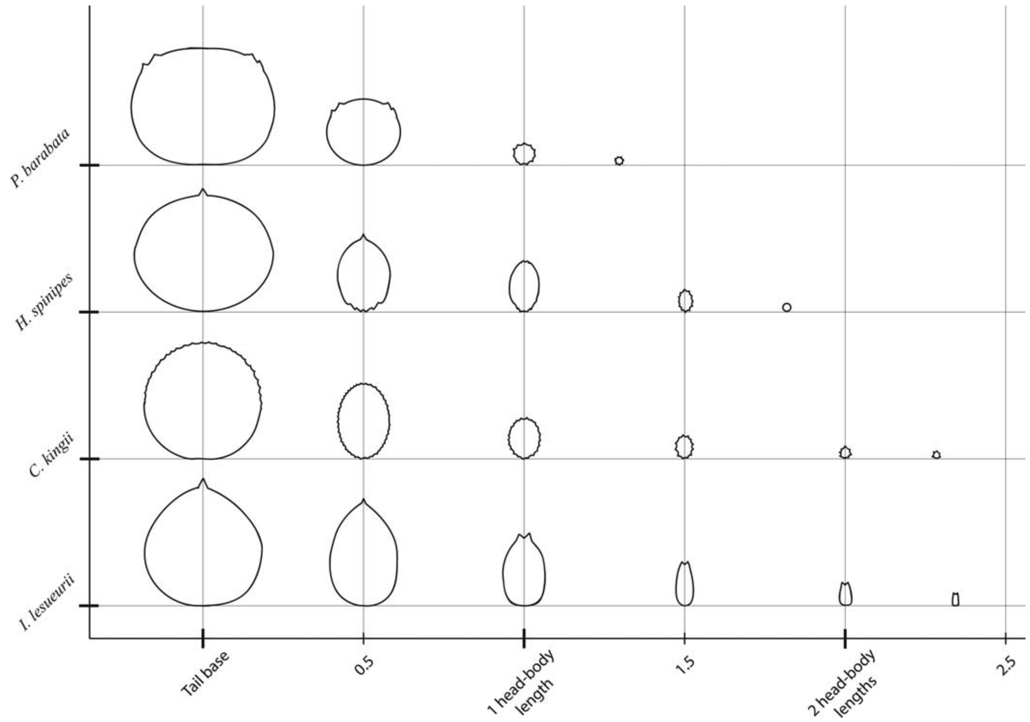

FIG. 5. The differences in cross-sectional shape in the tail of four Australian agamids: *Pogona barbata, Hypsilurus spinipes, Chlamydosaraus kingii,* and *Intellagama lesueurii*. Tails are scaled so that the heights are even at their base/vent.

third of the normal size the phase speed to forward velocity ratio in this animal was 1.99 ± 0.11 : 1, which compared to 1.77 ± 0.24 : 1 seen in normal animals. We compared this animal to the remaining population and found that it differed significantly (linear mixed effects model comparing phase speed with swimming velocity; $F_{1,30} = 9.808$, $P = 0.0039$). When compared visually to animals with complete tails, the tail of this individual was no longer observed to undulate in the same manner. The stiffness of the remaining part prevented a sinusoidal wave from effectively propagating, such that the tail's oscillations formed only a partially complete wave. Angles of flexion were more comparable to what is seen at the terminal part of the complete tails of the terrestrial control, *P. vitticeps*. An increase in water turbulence is seen at the tip, suggesting excess energy is being inefficiently expended. In animals with a complete tail, this energy appears to continue further down the tail through the propagation of the sinusoidal wave. Improved locomotor performance in animals with complete tails is likely to result from either an increase in forward thrust by virtue of a larger propulsive surface, improved streamlining, and drag reduction or a combination. Although the animal was able to compensate for the loss of part of its tail, the alternative locomotor technique appears inefficient and compromises performance.

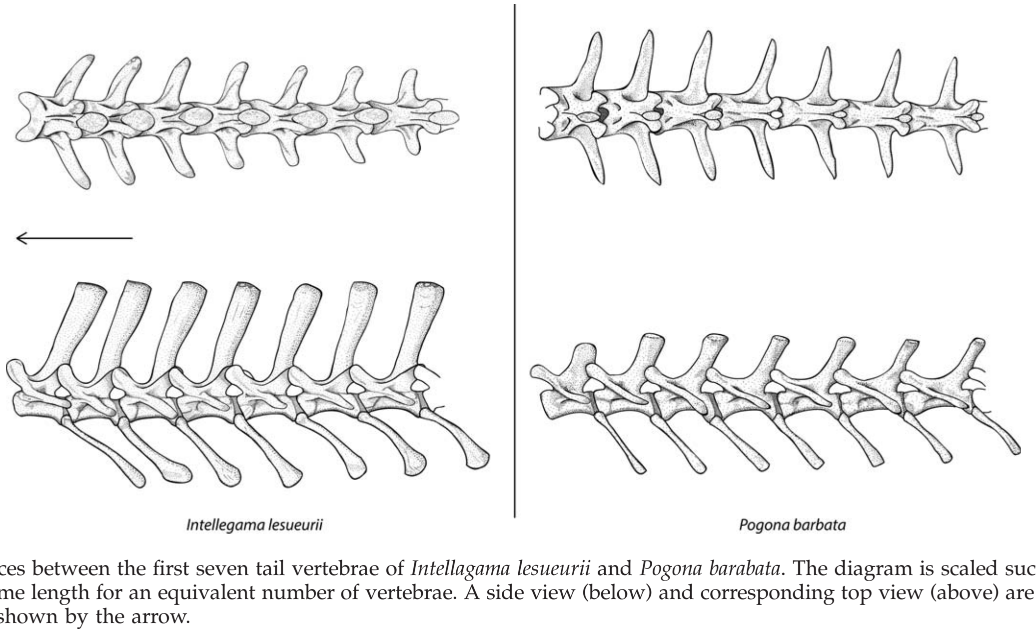

FIG. 6. Differences between the first seven tail vertebrae of *Intellagama lesueurii* and *Pogona barabata*. The diagram is scaled such that the sections depicted are the same length for an equivalent number of vertebrae. A side view (below) and corresponding top view (above) are provided for both species. Cranial is shown by the arrow.

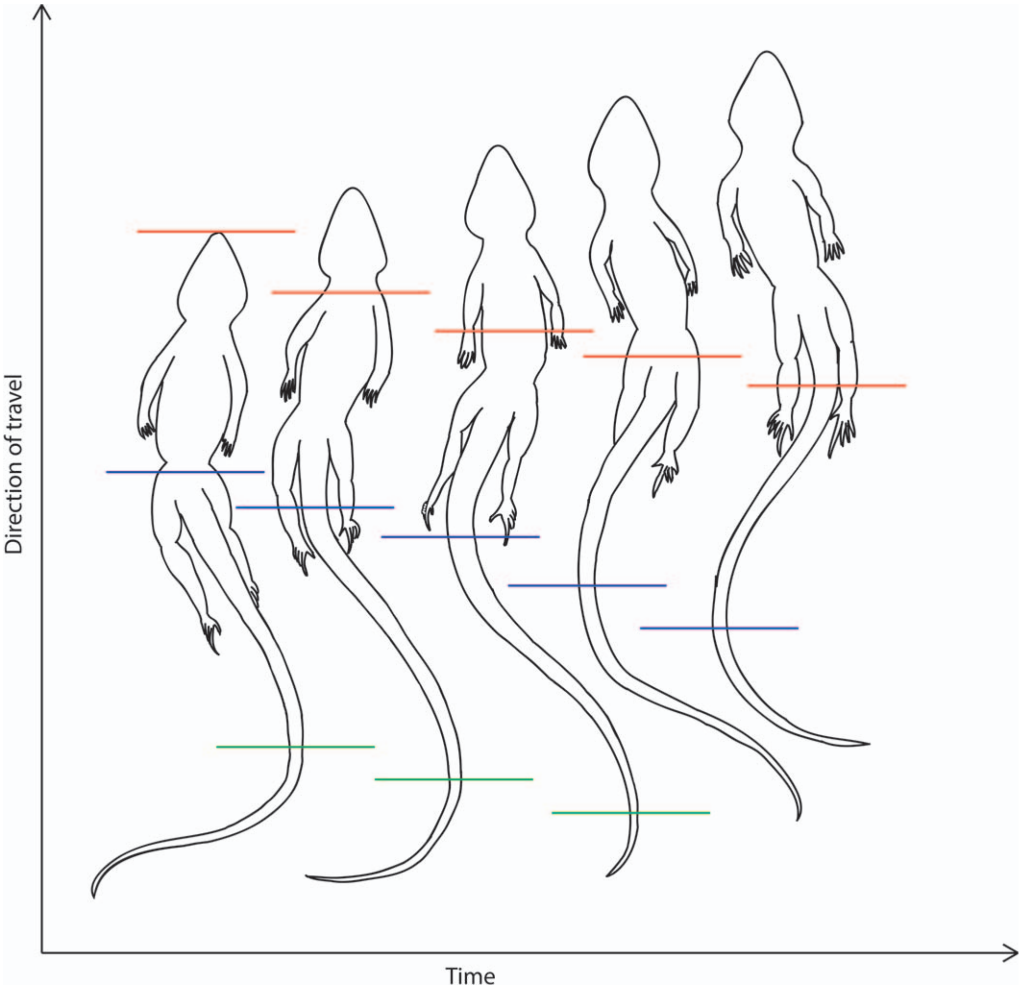

FIG. 7. The undulatory cycle of *Intellagama lesueurii* at 1/15 second intervals swimming at a speed of approx 0.7m/sec. The locomotor technique is anguilliform in nature; however, the section terminal of the pelvic girdle shows the steepest increase in amplitude. Each series of colored bars depicts the propagation of a wave front.

Despite numerous similarities, aspects of *I. lesueurii*'s locomotor technique differ from that of crocodilians (see Manter, 1940; Fish, 1984; Frey and Salisbury, 2001). The most notable disparity is that, in *I. lesueurii*, frequency does not vary with velocity. In crocodilians and fishes, frequency has been found to covary with phase speed in controlling velocity (Manter, 1940; Fish, 1984). This technique is adopted to maintain optimal wave form throughout the entire range of swimming velocities. The different technique observed in *I. lesueurii* has several implications regarding the relationship between size and absolute speed.

Typically, the maximum absolute speed of swimming increases with body length (Bainbridge, 1960; Videler and Wardle, 1991). The relationship is generally allometric, where smaller individuals perform proportionately better than larger animals. In this study, it was found that larger animals performed the same as or slightly poorer than smaller individuals. Because the average frequency and relative amplitude was found to vary with size, it seemed likely that these differences in wave form were the contributing factors to this unexpected observation. Although larger animals generated larger wave amplitudes they did so at lower frequencies. These two parameters effectively cancelled each other out, such that the velocity of lateral movements for the same forward velocity was markedly similar between small and large individuals. When coupled with comparable phase speed to velocity ratios, the performance of the locomotive technique of *I. lesueurii* does not scale relative to body size. Instead of increasing with length, the maximum absolute lateral and longitudinal velocities of wave generation are the same regardless of an animal's length. With these similarities between size classes in mind, the findings of Seebacher et al. (2003) suggest that the Reynolds number should bear little effect since the difference in length between the smallest and largest animals does not span orders of magnitude. This explains why the observed performance is independent of size but not why larger individuals lack the capacity to increase their outputs. Physiological limitations of muscle contraction rates are also a likely explanation that deserves further investigation.

When compared to the wave form of an alligator (Manter, 1940; Fish, 1984), it is clear that the sinusoidal wave of *I. lesueurii* propagates differently (Fig. 7). Fish (1984) suggests that in alligators, a modified sinusoidal wave that increases in amplitude at the pelvic girdle continues to propagate evenly to the tail tip. The attack angle (Fig. 8) of the propulsive surface in crocodilians appears to increase but remains at an oblique angle to forward movement. A dependant relationship between frequency, amplitude, and phase speed means that, as each component varies, other components are required to covary to maintain constant attack angles. For example, if phase speed,

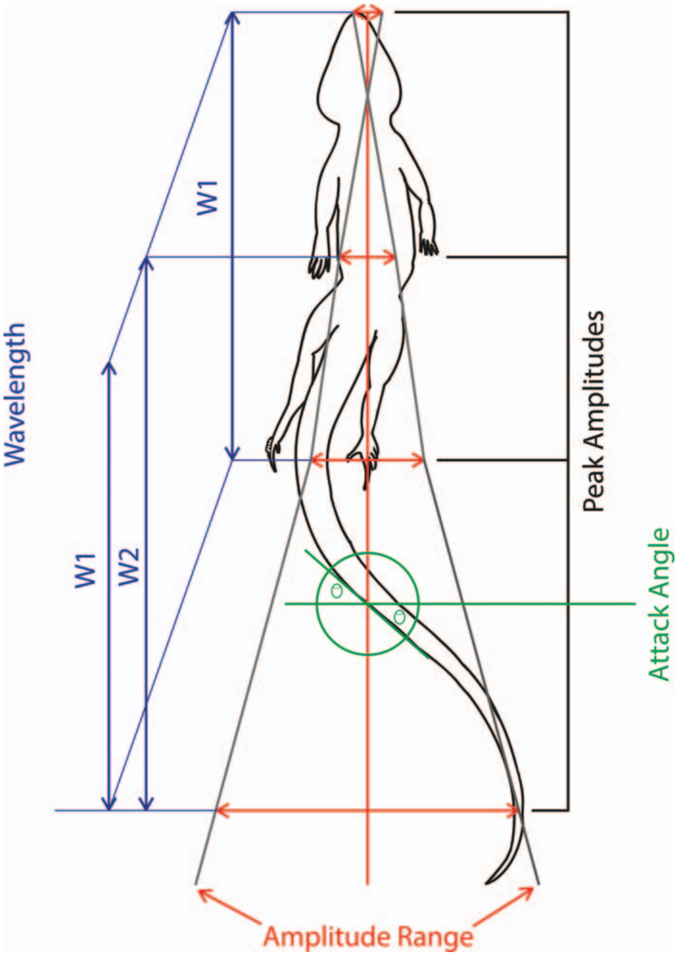

FIG. 8. The undulatory characteristics of a swimming *Intellagama lesueurii*. Amplitude range depicts how the width of lateral motion varies along the length of the animal. Peak amplitude was used to track wave propagation. Wavelength depicts the length of a complete wave, the differences between W1 and W2 show that wavelength varies along the length of the body. Attack angle is the offset of the tail's propulsive surface from perpendicular to the animal's trunk.

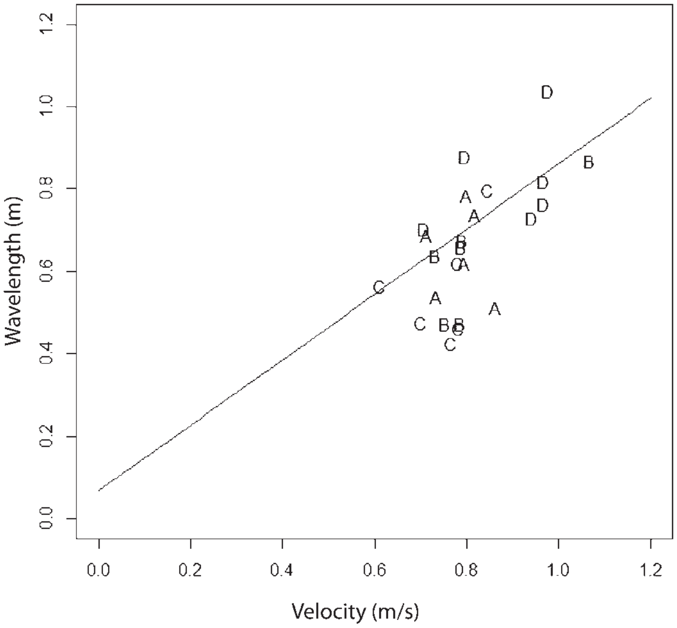

FIG. 9. Change in wavelength with forward velocity at the tail spine bifurcation in *Intellagama lesueurii* ($F_{1,19} = 9.899$, $P < 0.01$). A Linear Mixed Model was used to account for the numerous animals used in the experiment. Data were collected from swimming observation from four individuals; letters indicate different individuals.

frequency, and wavelength remain constant, the increasing amplitude would progressively increase the attack angle as the wave propagates terminally. Therefore, to retain optimal attack angles, one or multiple wave components need to be altered to counter the effect of the increasing amplitude. It is apparent that crocodilians have done so by covarying frequency, whereas *I. lesueurii* does not and simply controls velocity with phase speed (Fig. 10). That phase speed is the only control mechanism for swimming velocity in *I. lesueurii* is further supported by the increase in wavelength in the tail, which is consistent with frequency not being a covariate.

Oscillation of the pelvis and stiffened cranial part of the tail of *I. lesueurii* is ultimately the source of increasing amplitude in the remainder of the tail (Figs. 7 and 8). Although the overall shape of the undulatory curve over the entire body forms a sinusoidal wave, in stiffer parts, the movement is restricted, thereby resulting in increasing amplitudes. Because the stiffened part restricts flexion, the tail instead sweeps in an arc scribed from the pelvis to proximal section of the tail. At the end of this arc, the tail once again becomes flexible and resumes fluid propagation as a sinusoidal wave. The increase in amplitude between these two points continues at a similar rate in the more flexible terminal part of the tail. Wavelength remains constant as

TABLE 1. Summary of significance tests of relationships between swimming velocity and wave characteristics. Amplitude and frequency were measured at each node, whereas phase speed and wavelength were measured across the span of two nodes. Asterisk marks statistical significance where $P < 0.05$.

	Nose	Pectoral girdle	Pelvic girdle	Tail spine bifurcation	Tail tip
Amplitude	$F_{1,19} = 0.424$, $P = 0.523$	$F_{1,19} = 0.179$, $P = 0.677$	$F_{1,19} = 0.909$, $P = 0.352$	$F_{1,19} = 2.163$, $P = 0.158$	$F_{1,19} = 0.075$, $P = 0.788$
Frequency	$F_{1,19} = 0.424$, $P = 0.523$	$F_{1,19} = 1.208$, $P = 0.286$	$F_{1,19} = 0.471$, $P = 0.501$	$F_{1,19} = 0.302$, $P = 0.589$	$F_{1,19} = 0.036$, $P = 0.852$
	Nose-pect	Pect-pelv	Pelv-bif	Bif-tip	Whole body
Phase speed	$F_{1,19} = 2.912$, $P = 0.104$	$F_{1,19} = 0.909$, $P = 0.352$	$F_{1,19} = 8.443$, $P = 0.0091$*	$F_{1,19} = 1.900$, $P = 0.184$	$F_{1,24} = 19.690$, $P < 0.001$*
Wavelength	$F_{1,19} = 0.263$, $P = 0.614$	$F_{1,19} = 0.599$, $P = 0.449$	$F_{1,19} = 9.899$, $P = 0.0053$*	$F_{1,19} = 2.179$, $P = 0.156$	$F_{,19} = 4.259$, $P = 0.053$

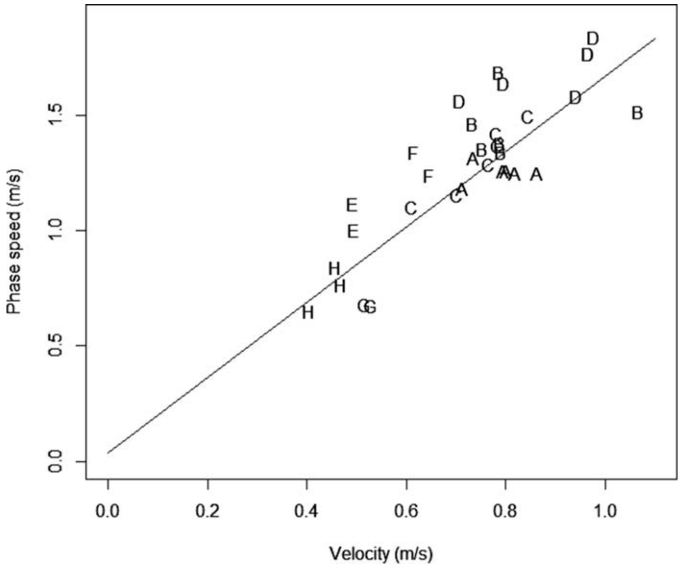

FIG. 10. Change in whole body phase speed with forward velocity in *Intellagama lesueurii* at swimming speeds ranging from 0.403–1.067 m/sec ($F_{1,24} = 19.690$, $P < 0.001$). A Linear Mixed Model was used to account for the numerous animals used in the experiment. Data were collected swimming observations from eight individuals; letters indicate different individuals.

the peak of the wave propagates down the tail. As the peak propagates, the terminal part in front of the peak becomes compressed like a spring decreasing in wavelength until the attack angle approaches 90°. At this point the loaded tail appears to recoil, expending the remaining energy of the wave in a rapid flick. This technique is only possible and efficient on account of the extended length of the tail. Individuals with shorter tails adopted a locomotor technique similar to that described in crocodilians, except that, without the extended height of the tail, they are much less efficient swimmers.

From these findings, it is reasonable to conclude the *I. lesueurii* is an effective swimmer relative to other semi-aquatic vertebrates. Although the locomotor techniques employed by *I. lesueurii* are functionally similar to crocodilians, differences in morphology and swimming technique are apparent enough to differentiate the two. These contrasting elements of morphology about a similar body plan highlight the radial nature of evolutionary pathways. Similar studies into lizards with more pronounced morphological modifications are likely to reveal more information into the evolution of axial undulatory locomotor techniques.

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