

Feeding Underground: Kinematics of Feeding in Caecilians

ANTHONY HERREL^{1*} AND G. JOHN MEASEY²

¹UMR 7179, Muséum National d'Histoire Naturelle, Département d'Ecologie et de Gestion de la Biodiversité, Paris, France

²Department of Zoology, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa



ABSTRACT

Caecilians are limbless amphibians that have evolved distinct cranial and postcranial specializations associated with a burrowing lifestyle. Observations on feeding behavior are rare and restricted to above-ground feeding in laboratory conditions. Here we report data on feeding in tunnels using both external video and X-ray recordings of caecilians feeding on invertebrate prey. Our data show feeding kinematics similar to those previously reported, including the pronounced neck bending observed during above-ground feeding. Our data illustrate, however, that caecilians may be much faster than previously suspected, with lunge speeds of up to 7 cm sec⁻¹. Although gape cycles are often slow (0.67 ± 0.29 sec), rapid jaw closure is observed during prey capture, with cycle times and jaw movement velocities similar to those observed in other terrestrial tetrapods. Finally, our data suggest that gape angles may be large (64.8 ± 18°) and that gape profiles are variable, often lacking distinct slow and fast opening and closing phases. These data illustrate the importance of recording naturalistic feeding behavior and shed light on how these animals are capable of capturing and processing prey in constrained underground environments. Additional data on species with divergent cranial morphologies would be needed to better understand the co-evolution between feeding, burrowing, and cranial design in caecilians. *J. Exp. Zool.* 317A:533–539, 2012. © 2012 Wiley Periodicals, Inc.

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Caecilians are an elongate and completely limbless group of amphibians, most of which are soil-dwelling predators of the wet tropics. In association with their burrowing habit, most terrestrial species have sturdy, compact skulls, recessed mouths, and reduced eyes sometimes covered by the bones of the skull roof (Taylor, '68; Nussbaum, '98). As the head-first burrowing lifestyle of caecilians puts severe constraints on maximal head diameter (Wake, '93; O'Reilly, 2000), the external adductors, positioned at the side of the head, are strongly reduced compared to those of other amphibians (Bemis et al., '83; Nussbaum, '83; O'Reilly, 2000). However, the presence of a mobile quadrate (streptostyly) and a unique jaw-closing system involving the large and well-developed interhyoideus posterior muscle, positioned in line with the head (and thus not increasing the head diameter), suggests that these animals can generate considerable bite forces (Summers and Wake, 2005; Kleinteich et al., 2008a,b).

Dietary accounts indicate that most caecilians are generalist predators with the majority of prey items being earthworms and subterranean arthropods, suggesting no need for high bite forces (Wake, '80; Verdade et al., 2000; Delêtre and Measey, 2004; Gaborieau and Measey, 2004; Kupfer et al., 2005). Moreover, the use of long-axis rotations to reduce prey may effectively alleviate

constraints on the need for large jaw muscles and bite forces (Measey and Herrel, 2006). Actual observations of feeding behavior in caecilians are, however, rare due to the subterranean existence of these animals (Tanner, '71; O'Reilly, 2000; Summers and Wake, 2005). Consequently, the information we have on caecilian feeding kinematics is derived from animals feeding above ground in laboratory conditions (Bemis et al., '83; O'Reilly, 2000). Of note has been the extremely slow nature of caecilian prey capture compared to that of other terrestrial amphibians, in which the prey is contacted before feeding is initiated, and jaw opening appears to be modified by sensory feedback throughout prey prehension (O'Reilly, 2000). Yet, the

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*Correspondence to: Anthony Herrel, C.N.R.S/M.N.H.N., Département d'Ecologie et de Gestion de la Biodiversité, 57 rue Cuvier, CP 55, 75231 Paris, France. Email: anthony.herrel@mnhn.fr

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Table 1. Dimensions of animals used in this study.

Species	Ind.	Snout-vent length (mm)	Head length (mm)	Mass (g)	Body diameter (mm)
<i>Boulengerula taitana</i>	10	262	6.0	5.84	5.3
<i>Boulengerula taitana</i>	5	207	5.6	2.96	4.0
<i>Boulengerula taitana</i>	2	299	7.3	6.95	5.7
<i>Schistometopum thomense</i>	3	237	10.2	9.65	7.6
<i>Schistometopum thomense</i>	2	224	8.7	8.21	6.7

Individuals for which cycles could be digitized are indicated in bold. Ind, individual.

constrained tunnel environment of caecilians may affect their feeding kinematics. For example, the pronounced neck bending during biting observed in previous studies (Bemis et al., '83; O'Reilly, 2000) may be absent when feeding in tunnels due to space constraints. In this study, we use external and X-ray video recordings of unrestrained live animals feeding in tunnels to explore how feeding kinematics may be affected by the tunnel environment and compare these data to previously published data for feeding in caecilians (Bemis et al., '83; O'Reilly, 2000).

MATERIALS AND METHODS

Animals and Husbandry

Three *Boulengerula taitana* and two *Schistometopum thomense* were used in the experiments (Table 1). Animals were housed in Plexiglas cages (60 cm × 40 cm × 3 cm) filled with a mixture of sand and potting soil. The caecilians were kept individually or in pairs and were fed weekly with earthworms (*Eisenia fetida*, diameter: 2.8 mm) and crickets (*Acheta domestica*, diameter: 3.4 mm) ad libitum. All the animals established well-defined tunnel systems in which they moved when foraging.

Video Recordings

Animals were filmed using a Redlake MotionPro high-resolution digital camera (Redlake IDT, Tallahassee, FL, USA) set at 50 or 125 frames sec⁻¹. Two custom-made arrays of eight ultrabright red light-emitting diodes were used to provide the necessary illumination. The red light did not disturb the animals and the feeding behavior could be recorded in tunnels adjacent to the Plexiglas (Fig. 1). The animals were filmed between 18.00 hr and midnight as they showed most interest in food during these times. X-ray video recordings were made using Redlake MotionPro digital high-resolution camera attached to the image intensifier of a Philips Optimas M200 X-ray system (Philips International B.V., Amsterdam, The Netherlands). X-rays were generated at 40 kV and animals were filmed at 50 frames sec⁻¹ while feeding in the soil (Fig. 2).

Video Analysis

Twenty X-ray clips and 55 external videos were recorded for the three *B. taitana* and two *S. thomense* included in our study. Of

those, 15 (14 for three *B. taitana* and 1 for one *S. thomense*; nine X-ray videos and five external ones) were in good lateral view and could be digitized. In addition, seven lunges of two *B. taitana* toward prey were visible and could be digitized. Moreover, for six sequences we were able to quantify the head angle during biting. For feeding sequences, we digitized the tips of the upper and lower jaws on both external and X-ray videos; for lunges we digitized the distal tip of the snout only. All videos were analyzed using Didge (Image Digitizing Software v. 2.2.0; Alistair Cullum, Omaha, Nebraska, USA) and X,Y coordinates were exported to a spreadsheet. Raw coordinates were scaled to metric units, and the gape angle, head angle, and gape distance were calculated for feeding sequences. The displacement of the snout tip was calculated for lunges. Next, the gape distance and lunge profiles were smoothed using a zero phase shift, fourth-order low pass Butterworth filter at 4 Hz (Winter, 2004). From the smoothed gape profiles we extracted peak gape angle and gape distance, the velocity of jaw opening and closing, the duration of the total cycle, and the duration of the slow opening (SO), fast opening (FO), fast closing (FC), and slow closing (SC) phases (see Bramble and Wake, '85; Bemis et al., '83). From the smoothed lunge profiles we extracted the distance moved and the peak velocity of the animal. No qualitative differences were detected between cycles in which animals were feeding on earthworms versus crickets. However, due to our small sample sizes, we did not statistically test for differences between feeding on different prey types. Head angle was calculated from the same videos by calculating the angle between the dorsal surface of the head and the long axis of the body in ImageJ (Rasband, 2011).

RESULTS

Animals rapidly established tunnel systems in the filming cages (Himstedt and Simon, '95). During movement in the tunnels animals often stopped and showed increased frequency of buccal pumping. Prey detection was sometimes dependent on tactile stimuli (i.e., the animal touching the prey), but often animals attacked prey without prior contact. Feeding consisted of a rapid lunge toward and seizure of the prey in the jaws. During lunging, animals moved an average of 82 ± 19 mm, with peak velocities of up to 71.2 ± 18.0 m msec⁻¹ (Table 2). Often prey capture was

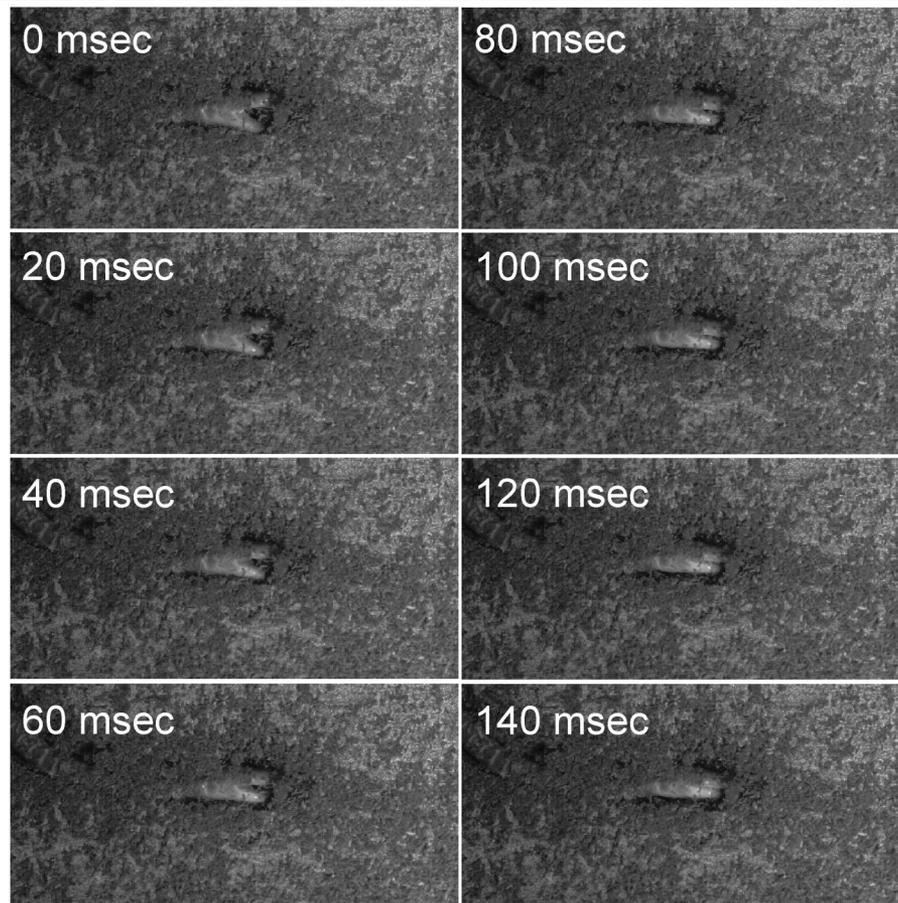


Figure 1. Representative image sequence of a *Boulengerula taitana* feeding on a cricket recording using external video. Note how the jaws are maximally opened at 0 msec and closed at 140 msec. The cricket is no longer visible in between the jaws and is being swallowed.

followed by long-axis rotation of the animals (Measey and Herrel, 2006). Prey transport took place with the animal in all possible orientations (upside down, on its side, right side up, head up, and head down), rendering many cycles unsuitable for analysis. All capture cycles showed a simple gape profile with undivided opening and closing phases (Fig. 3).

Both species showed a typical tetrapod gape profile during prey transport (Bramble and Wake, '85), with distinct opening and closing phases sometimes differing in the velocity profile and often consisting of multiple opening and closing movements (Figs. 3 and 4; see O'Reilly, 2000). Of the 15 sequences analyzed, 33% showed a slow open phase and 50% showed a distinct slow close phase; others consisted of a single opening and closing phase only. Cycle duration was much greater in *S. thomense* compared to *B. taitana*, largely due to the much longer slow opening phase in the former species (Table 2). Yet, gape angle, gape distance, and opening and closing velocities were similar in both species

(Table 2). Gape angles were relatively high (around 60°; see Table 2) resulting in gape distances of about one head length in both species. Fast opening and fast closing phases were comparatively slow with peak jaw speeds of only about 1 cm sec⁻¹ (Table 2). Yet, at least *B. taitana* is capable of rapid jaw movements of up to 7 cm sec⁻¹, as indicated by the one failed capture attempt analyzed (Table 2). Peak head flexion angles for *B. taitana* at the end of closing were 34.2 ± 11.1° on average (Table 2).

DISCUSSION

Although caecilians are often considered to be slow (Bemis et al., '83; O'Reilly, 2000), our data show that these animals can be fast, with the velocity of the lunge being close to the average peak velocity of the animals when moving underground (7.4 cm sec⁻¹; see Herrel and Measey, 2010), and much faster than previously thought. Our data for *B. taitana* show that jaw movements can

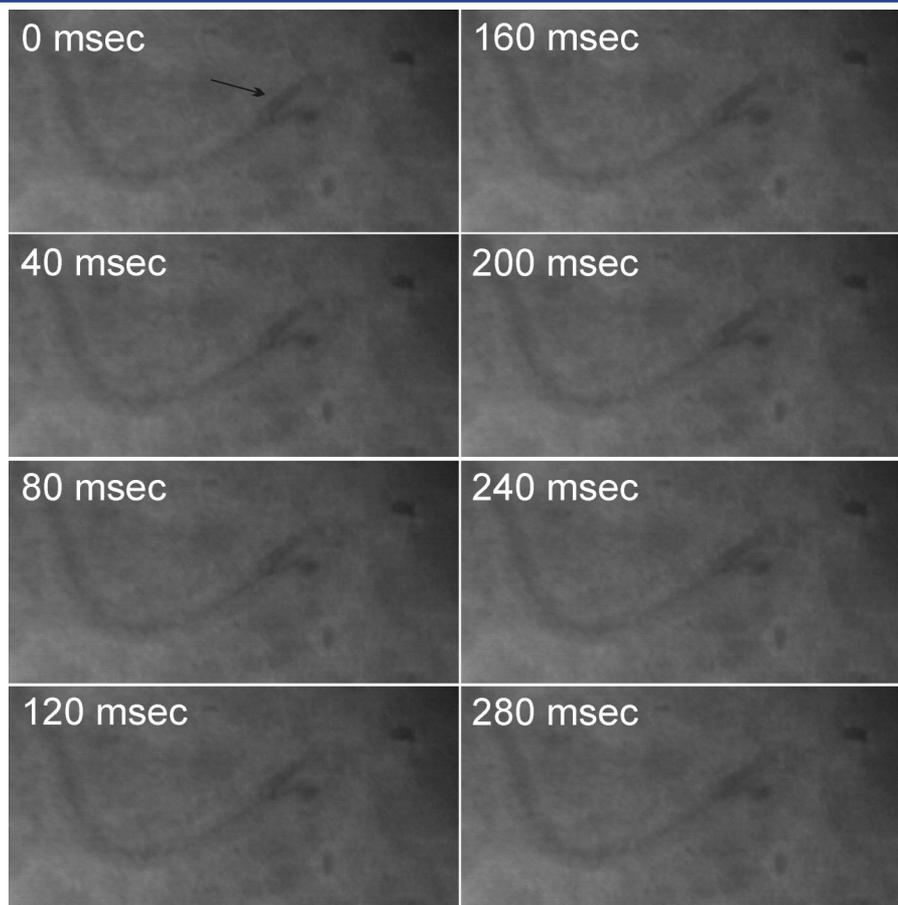


Figure 2. Representative image sequence of a *Boulengerula taitana* feeding on a cricket recording using X-ray video. The arrow depicts the head of the caecilian. Note that the jaws are open in the first frame illustrated (0 msec) and nearly closed at the last frame (280 msec).

Table 2. Summary kinematics of feeding behavior in two species of caecilian.

	<i>B. taitana</i> (N = 2)	<i>B. taitana</i> ^a	<i>S. thomense</i> (N = 1)
Gape angle (°)	64.8 ± 18.0	69.41	58.1
Gape distance (mm)	5.1 ± 1.5	4.02	5.77
Head angle (°)	34.2 ± 11.1		
V _{open} (m msec ⁻¹)	9.3 ± 9.6	63.6	10.4
V _{close} (m msec ⁻¹)	12.6 ± 8.4	77.3	9.7
V _{lunge} (m msec ⁻¹)	71.2 ± 18.0		
Slow open duration (sec)	0.36 ± 0.23	0.03	1.29
Fast open duration (sec)	0.28 ± 0.12	0.03	0.23
Fast close duration (sec)	0.24 ± 0.11	0.04	0.20
Slow close duration (sec)	0.19 ± 0.11	0.02	0.43
Total cycle duration (sec)	0.67 ± 0.29	0.12	2.15

^aSequence where the animal snaps its jaws closed in an attempt to capture a food item, but misses. N, number of individuals for which sequences in lateral view were obtained for analysis; V_{close}, average peak jaw closing speed; V_{lunge}, average peak lunge speed; V_{open}, average peak jaw opening speed.

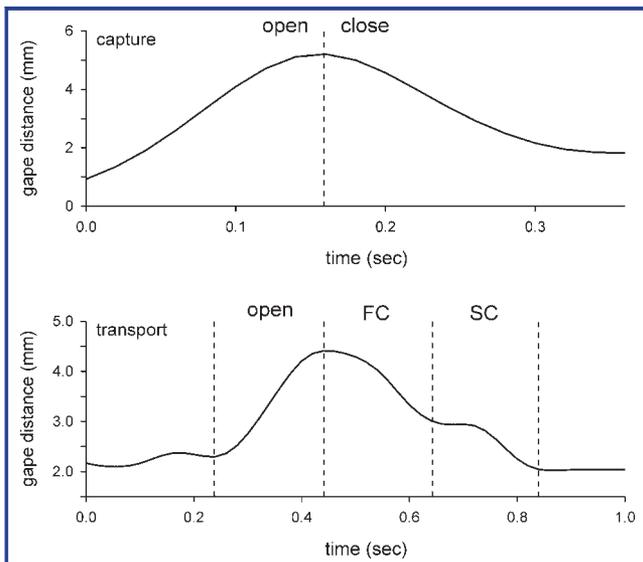


Figure 3. Kinematic profiles depicting the changes in gape distance over time during the capture (top) and a transport cycle (bottom) of a *Boulengerula taitana* eating an earthworm. Recordings based on high-speed videos recorded at 125 frames sec^{-1} . Indicated are the different kinematic phases discernible on the profiles. FC, fast close; SC, slow close.

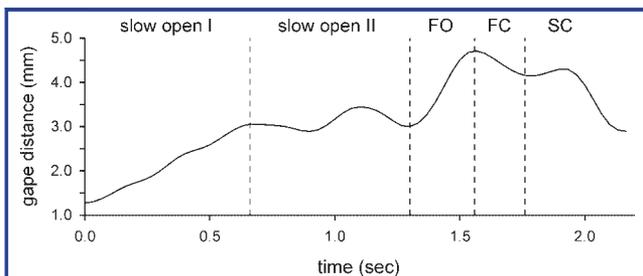


Figure 4. Kinematic profile depicting the changes in gape distance over time during a transport cycle in a *Schistometopum thomense* eating an earthworm. Based on X-ray videos recorded at 50 frames sec^{-1} . FC, fast close; FO, fast open; SC, slow close.

also be fast and attain similar speeds (Table 2). The discrepancy between the observations in previous studies (suggesting that caecilians approach and apprehend prey slowly) and our data is likely the result of the fact that previous studies made observations of animals feeding on the surface rather than in tunnels. Moreover, the animals used by Bemis et al. ('83) were still partially anesthetized when being recorded. When in tunnels, animals may need to move fast to capture their prey in some cases. Indeed,

although both species of caecilians studied here mostly eat slow prey such as earthworms and termites (Gaborieau and Measey, 2004; Delêtre and Measey, 2004), being able to move fast may be beneficial when feeding on ants and centipedes, which also form part of the natural diet in these species. In the laboratory, animals mainly showed fast lunges when trying to capture crickets (see also O'Reilly, 2000), although lunges towards earthworms were also observed.

Our data suggest that feeding kinematics are similar to those previously reported (Bemis et al., '83; O'Reilly, 2000), including a pronounced neck bending of similar magnitude ($34.2 \pm 11.1^\circ$ in *B. taitana* vs. $34.2 \pm 4.9^\circ$ based on an analysis of images published in Bemis et al., '83; O'Reilly, 2000) characteristic of above-ground feeding. This may be surprising as in tunnels there may not always be enough space to bend the neck at these relatively high angles. Yet, it should be noted that the substrate was relatively loose in our experimental set-up, allowing the animals to bend their heads. In tunnels in hard, compacted soil this may not always be the case, however. Our data also show that gape profiles are variable and often lack distinct slow and fast opening and closing phases (SO being present in only 30% of all cycles; SC in 50% of all cycles). Moreover, multiple small adjustments of the gape during opening and closing are often present, as observed in other studies (compare Fig. 4 to Fig. 6.5 in O'Reilly, 2000). Although it is still unclear as to why these animals continuously adjust gape, they may be simply modulating gape to match prey size and thus preventing the prey from escaping (see O'Reilly, 2000).

Although gape cycles are often rather slow, rapid jaw closure is observed during prey capture (Fig. 3), with cycle times and jaw movement velocities similar to those observed in other terrestrial tetrapods (see Schwenk, 2000). The one fast capture cycle recorded in which an animal missed its prey was with 120 msec in duration, as fast as capture cycles recorded for many frogs and salamanders (O'Reilly, 2000). The longer cycle duration observed for *S. thomense* may be an artifact of the fact that only a single sequence could be analyzed for this species. However, this is mainly due to the long slow opening phase, the duration of the other phases being similar to those in *B. taitana*. Moreover, other studies have reported similarly long cycle times for terrestrial caecilians (e.g., about 2 sec for *Dermophis mexicanus*; 1.3 sec for *Hypogeophis rostratus*; and 1.8 sec for *Ichthyophis kohtaoensis*; see Bemis et al., '83; O'Reilly, 2000). Our data for *B. taitana*, with cycle times of 0.67 sec on average (similar to those observed for the aquatic *Typhlonectes natans*), suggest that this is a faster caecilian, but still slower than most other terrestrial amphibians on average.

Finally, our data show that gape angles are often large ($64.8 \pm 18^\circ$), in contrast to data reported for *D. mexicanus* by Bemis et al. ('83) with gape angles of only $30\text{--}40^\circ$. Yet, data in O'Reilly (2000) indicate that some species such as *T. natans* and *H. rostratus* may feed at large gape angles (over 70°). Moreover,

O'Reilly (2000) suggested that the gape angle should be dependent on the morphology of the retroarticular process. In species with recurved retroarticular processes bite force generation is suggested to be optimized at lower gape angles due to the change in the mechanical advantage of the m. interhyoideus posterior with gape (O'Reilly, 2000). If so, these species should select low gape angles during feeding. As both *B. taitana* and *S. thomense* have a recurved retroarticular process (Summers and Wake, 2005), this would imply that these species should feed at low gape angles, which is not the case. A more recent analysis of the mechanics of biting suggested, however, that the jaw system in caecilians may be optimized for producing relatively high bite forces independent of gape angle due to the complementary action of both the jaw adductors and the m. interhyoideus posterior (Kleinteich et al., 2008b), in which case gape angle should be independent of the morphology of the retroarticular process. Consequently, the observed differences in gape angle may be due to other factors such as the relative prey size fed to the animals. As the *D. mexicanus* used by Bemis et al. ('83) were large animals (over 250 mm) the earthworms fed to them may have been small relative to their head size. If so, this would suggest that caecilians modulate their prey capture behavior as a function of the size of the prey. However, this suggestion remains speculative at present and should be tested by feeding caecilians a range of prey items varying in size.

In summary, our data show that although feeding underground may impose constraints on feeding, it also offers unique opportunities to underground predators. Our data show that caecilians may be faster than previously thought, which may allow them to pursue and capture the more elusive prey that form part of their natural diet. Although these data provide novel insights in the kinematics of feeding in these enigmatic animals, they remain limited in sample size, the types of food offered, and the taxonomic and phenotypic diversity of the taxa studied. Future studies using similar methods to gain insights in naturalistic feeding in caecilians are much needed to better understand the evolution of the feeding system in these animals. As only 20% of all recorded sequences involved feeding events with caecilians in direct lateral view this suggests that 3D X-ray methods (Brainerd et al., 2010) might be better suited to study feeding in burrowing vertebrates.

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