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Surveying death roll behavior across Crocodylia

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The “death roll” is an iconic crocodylian behaviour, and yet it is documented in only a small number of species, all of which exhibit a generalist feeding ecology and skull ecomorphology. This has led to the interpretation that only generalist crocodylians can death roll, a pattern which has been used to inform studies of functional morphology and behaviour in the fossil record, especially regarding slender-snouted crocodylians and other taxa sharing this semi-aquatic ambush predator body plan. In order to test this hypothesis, we surveyed death roll behaviour across animals representing all extant crocodylian species. Animals were prompted to death roll using two methods of stimulation: a feeding cue and an escape cue. The feeding cue involved presenting each animal with a bait item, to which resistance would be applied during a biting event. The second cue involved capturing each animal with a rope or catch pole, a standard technique for capturing crocodylians, but one that also often prompts an attempt to escape. All species tested, except *Paleosuchus palpebrosus*, exhibited the behaviour in response to at least one of the stimuli. This included the following slender-snouted species: *Gavialis gangeticus*, *Tomistoma schlegelii*, *Mecistops cataphractus*, *Mecistops leptorhynchus*, *Crocodylus johnstoni*, and *Crocodylus intermedius*. The patterns of death roll behavior observed in this survey suggest that this behaviour is not novel to any one crocodylian clade, morphotype, or dietary niche. Also, the prevalence of death rolling behaviour across Crocodylia in response to perceived threats indicates that it is not solely, or maybe even primarily, a feeding behaviour, but is also utilised during inter- and intra-specific conflict as a means to escape or injure an opponent. The results of this case study highlight the importance of using multiple modern analogues when attempting to correlate form and function across diverse clades, both living and extinct.

KEY WORDS: crocodile, alligator, caiman, gharial, axial rolling, rotational feeding, twist feeding.

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INTRODUCTION

Within Crocodylia, snout shape classifications are often used as shorthand to characterise feeding ecology and behaviour. In general, crocodylians with long, slender snouts are often thought to be largely piscivorous (e.g. Iordansky 1973; Langston 1973; Pooley 1989; Busbey 1995) or small-prey specialists (McHenry et al. 2006); those with shorter, boxy snouts are interpreted as durophagous (e.g. Carpenter & Lindsey 1980; Salas-Gismondi et al. 2015), and the ones which fall between, with longer, broader snouts, are seen as being dietary generalists (Brochu 2001). Initial classifications of snout morphotypes were qualitative (Busbey 1995; Brochu 2001), but these classifications have been largely supported in subsequent quantitative analyses exploring snout shape and modelling snout function (Pierce et al. 2008; Sadleir & Makovicky 2008; Wilberg 2017; D'Amore et al. 2019).

These snout morphotypes are well represented across the extant species of crocodylians (Brochu 2001), but ecological studies are not evenly distributed across these groups. Several species are threatened or endangered, some critically so, making surveys of wild populations challenging (e.g. Thorbjarnarson & Wang 2010; De Silva et al. 2011). The most heavily studied, living species are all large-bodied, numerous, valued by the skin and meat industries, and, incidentally, members of the “generalist” snout morphotype (Rowe et al. 1999; Tzika & Milinkovitch 2008): *Alligator mississippiensis* (Daudin 1801 [1802]), *Crocodylus niloticus* (Laurenti 1768), and *Crocodylus porosus* (Schneider 1801). The ecology of many members of other snout shape categories, especially the tube-snouted crocodylians, is significantly less well understood (Brochu 2001). When diet among these slender-snouted crocodylians is surveyed directly, it often exhibits more diversity, both in prey clade and size, than would be expected of true fish specialists (Thorbjarnarson 1990; Tucker et al. 1996; Webb & Manolis 2010; Selvaraj 2012).

One iconic crocodylian feeding behaviour, the “death roll,” provides a window into the need for broader ecological surveys when using modern groups to explore behaviour in extinct species. A death roll involves the animal grasping part of an item in its mouth and then spinning around the long axis of its body in order to drag larger prey animals off of their feet, to reduce prey into sections that are small enough to swallow (Fish et al. 2007), or to injure or escape a rival during inter- or intra-specific competition (e.g. Webb et al. 1983). The behaviour is well documented in several living crocodylians which exhibit the generalist snout morphology (e.g. McIlhenny 1935; Fish et al. 2007; Blanco et al. 2014). Twisting and rolling behaviours are common in non-crocodylians as well. When associated with food acquisition, the terms rotational or twist feeding sometimes are used, as in amphisbaeneans, eels, and whales (e.g. Pivorunas 1979; Helfman & Clark 1986; Goldbogen et al. 2006; Measey & Herrel 2006). Twisting has also been employed during such disparate behaviours as grooming (e.g. Kenyon 1969) and mating avoidance (e.g. Payne 1995; Marsh 2002).

Death rolling previously has not been reported among slender snouted crocodylians. The interpretation that members of this morphotype cannot perform this behaviour has been further bolstered by biomechanical analyses, specifically finite element analyses, which demonstrate that slender snouted crania experience higher stress than other crocodylian snout morphotypes under different loading regimes, including simulated torsion (Pierce et al. 2008, 2009; McCurry et al. 2017). These lines of evidence, partnered with discussions of diet, have been used to argue that tube snouted crocodylians, both living and extinct, could not death roll (Cleurens & De

Vree 1999; Blanco et al. 2014). However, is this pattern driven by true functional constraints, or is it an artifact of the limited number of studies of these species' feeding ecology?

Here we report incidents of death rolling in extant members of Crocodylia, through direct observations of the behaviour in captive animals spanning 25 species, and all available morphotypes, within extant members of the clade. Ensuing patterns are used to explore the potential for fossil crocodylians, as well as more distantly related groups that share a similar body plan, to perform this behaviour.

MATERIALS AND METHODS

The animals observed during this study are held at the St. Augustine Alligator Farm Zoological Park (SAAF) in St. Augustine, Florida, USA. Crocodylians are a widespread group, found throughout tropical to temperate regions of the globe (Markwick 1998), but several lineages are also threatened or endangered. This can make large-scale surveys across wild members of the crown group challenging to perform. Fortunately, many of these species also survive and breed well in captivity, providing researchers with access to animals that would otherwise be difficult to impossible to observe (Drumheller et al. 2016).

However, captive animals can also exhibit behaviours and morphologies that diverge from their wild counterparts. Among crocodylians, differences in snout shape (Sadleir 2009; Drumheller et al. 2016) and bite force (Erickson et al. 2004) have been noted, although the intensity of these differences can vary depending on the conditions of captivity and the general health of the animals involved (Drumheller et al. 2016). Captive crocodylians often also exhibit larger fat deposits, most likely related to their more sedentary lifestyle (Erickson et al. 2004). Therefore, the potential effects of captivity need to be addressed in research utilising these animals.

The SAAF animals have a variety of backgrounds, ranging from recently captured nuisance animals, to individuals that were hatched and raised at the facility, to specimens that were transferred from other institutions. As such, these animals exhibit a range of modifications, reflecting the differences in the conditions of their captivity. For example, some of the slender-snouted individuals exhibit dorsal bending of the rostrum, a trait often seen in captives of this morphotype, while others have the straighter snouts of their wild counterparts. These animals all share a more sedentary lifestyle than their wild relatives, with regular feedings replacing active hunting, although predation within the enclosures and competition between animals has been observed (e.g. Dinets et al. 2013). As such, these animals are probably less likely than their wild counterparts to perform death rolls, lacking the same experience, physical conditioning, and opportunities to exercise this behaviour than those animals that must regularly catch and subdue living prey. The individual animals used in this study, as well as associated veterinary metadata, are presented in Table 1 and the Supplementary Material, available online.

Species previously known to death roll, particularly *Alligator mississippiensis* (McIlhenny 1935; Harding & Wolf 2006; Fish et al. 2007; Langley 2010; Drumheller & Brochu 2014), were used to refine the following protocols in concert with SAAF animal curators and staff. In order to prompt death roll behaviour from these animals, two methods were used: a feeding cue (Fig. 1) and an escape cue (Fig. 2). During the feeding cue, a bait item secured on a rope or catch pole, was introduced to the animal. The bait used came from partially butchered portions of domestic cow limbs, but the specifics varied according to the size of the animal. For example, the smallest animals were offered cut pieces of soft tissue (usually tendon, or other tough portions of meat and connective tissue). The largest animals were presented with partially fleshed-out long bones, cut in half transversely along the midshaft. Mid-range animals were offered cut sections of long-bone shaft (roughly 5 cm in length, although this dimension could vary by roughly ± 2 cm). These bone samples were more heavily defleshed than the others, and so some animals were presented with the bare bone while others received a sample that was encased in leather, in order to give

Table 1.

Specimens organised by species and animal identification number (indicated with a #) or, when numbers were unavailable, animals enclosure identifiers (which lack a #). Cue types (Feeding cue and Escape cue) are followed by descriptors of each test (Bait type and Restraint type).

| Species | Identification number | Feeding cue | Bait type | Escape cue | Restraint type |
|-----------------------------------|-----------------------|-------------|------------------------|------------|------------------------------|
| <i>Alligator mississippiensis</i> | Ed Pool | ROLL | bone | | |
| | Ed Pool | ROLL | bone | | |
| | Ed Pool | ROLL | bone | | |
| | CH10 | ROLL | tendon | ROLL | became ensnared in bait rope |
| | A15209 | ROLL | bone | | |
| <i>Alligator sinensis</i> | A07012 | NO ROLL | bone | | |
| | A09027 | ROLL | bone w/leather, tendon | | |
| | A09012 | NO ROLL | bone w/leather | | |
| | A10012 | | | ROLL | catch pole catch pole |
| <i>Caiman crocodilus</i> | 96054 | NO ROLL | tendon | | |
| | A08004 | NO ROLL | tendon | | |
| | A02019 | NO ROLL | tendon | | |
| | Gray | NO ROLL | bone w/leather | | |
| | Ed Pool | NO ROLL | bone w/leather | | |
| | Ed Pool | | | ROLL | catch pole |
| <i>Caiman latirostris</i> | #86012 | NO ROLL | bone w/leather, tendon | | |
| | #A14088 | NO ROLL | tendon | | |
| | #A15170 | NO ROLL | tendon | | |
| | #95117 | NO ROLL | bone w/leather | | |

| | | | | | |
|-----------------------------|----------------------|---------|---------------------------|---------|------------|
| | #14088/ #A15170 | ROLL | soft tissue | | |
| | #95117 | | | ROLL | catch pole |
| <i>Caiman yacare</i> | #89037/#89038/#89039 | NO ROLL | bone w/leather | | |
| | #89037/#89038/#89040 | ROLL | tendon | | |
| <i>Paleosuchus</i> | S2 | NO ROLL | tendon | NO ROLL | jaw rope |
| <i>palpebrosus</i> | S2 male | NO ROLL | tendon | | |
| | #A10071 | NO ROLL | soft tissue | | |
| | #85029 | NO ROLL | bone w/leather | | |
| | #A04031 | NO ROLL | bone w/leather | | |
| | CH2 | | | NO ROLL | jaw rope |
| | CH2 | | | NO ROLL | catch pole |
| | CH2 | | | NO ROLL | catch pole |
| | CH2 | | | NO ROLL | catch pole |
| | CH2 | | | NO ROLL | catch pole |
| <i>Paleosuchus</i> | #85029/#A04031 | NO ROLL | bone | | |
| <i>trigonatus</i> | #87028 | NO ROLL | tendon | ROLL | catch pole |
| <i>Melanosuchus niger</i> | #92041 | NO ROLL | bone w/leather, half bone | ROLL | catch pole |
| <i>Crocodylus</i> | #91278 | ROLL | bone, bone w/leather | | |
| <i>intermedius</i> | #A09027 | | | ROLL | catch pole |
| <i>Crocodylus johnstoni</i> | #97016 | NO ROLL | tendon, bone w/leather | | |
| | #A10029 | NO ROLL | bone w/leather | ROLL | catch pole |
| <i>Crocodylus</i> | #A03033 | NO ROLL | tendon, bone w/leather | ROLL | catch pole |
| <i>mindorensis</i> | #A03032 | NO ROLL | tendon | | |

(Continued)

Table 1.
(Continued)

| Species | Identification number | Feeding cue | Bait type | Escape cue | Restraint type |
|--------------------------------|-----------------------|-------------|---------------------------|------------|----------------|
| <i>Crocodylus moreletii</i> | #A05004 | NO ROLL | tendon, bone w/leather | ROLL | catch pole |
| <i>Crocodylus niloticus</i> | #A13073 | ROLL | bone w/leather | | |
| | #A13073 | | | ROLL | catch pole |
| <i>Crocodylus novaeguineae</i> | #A05013 | NO ROLL | bone w/leather, half bone | | |
| | #A05012 | NO ROLL | bone w/leather | ROLL | catch pole |
| <i>Crocodylus palustris</i> | Nursery | NO ROLL | soft tissue | | |
| | WT5 | NO ROLL | soft tissue | ROLL | jaw rope |
| | Nursery | NO ROLL | soft tissue | | |
| <i>Crocodylus porosus</i> | WT7 | ROLL | soft tissue | | |
| | #A16051/#A16052 | | | ROLL | catch pole |
| <i>Crocodylus rhombifer</i> | #86057 | NO ROLL | bone w/leather | | |
| | #A07018 | ROLL | bone w/leather | | |
| <i>Crocodylus siamensis</i> | Ed Pool | NO ROLL | bone, bone w/leather | ROLL | catch pole |
| | Ed Pool | NO ROLL | bone | | |
| | Ed Pool | NO ROLL | bone, bone w/leather | | |
| | Ed Pool | NO ROLL | bone | | |
| | #A14008 | NO ROLL | tendon | | |
| <i>Crocodylus suchus</i> | #A11022 | NO ROLL | bone w/leather, half bone | ROLL | catch pole |
| <i>Mecistops</i> | #96015 | NO ROLL | bone w/leather | | |
| <i>cataphractus</i> | #A10035 | ROLL* | bone w/leather | | |
| | #A10035 | | | ROLL | catch pole |

| | | | | |
|-----------------------------|---------|---------|------------------------|----------|
| <i>Osteolaemus</i> | #A13015 | NO ROLL | bone | |
| <i>tetraspis</i> | #A13014 | NO ROLL | bone | |
| | #A11026 | NO ROLL | bone w/leather, tendon | |
| | Nursery | NO ROLL | soft tissue | |
| <i>Tomistoma schlegelii</i> | #A08085 | ROLL | tendon | |
| | #A09038 | ROLL | | jaw rope |



Fig. 1. — Examples of death roll behaviours observed during the feeding stimulus experiments. Clockwise from upper left: *Crocodylus niloticus*, *Caiman latirostris*, *Alligator mississippiensis*, and *Crocodylus intermedius*.

them better purchase and a softer surface to bite. All bait types were recorded, and are presented in Table 1 and the Supplementary Material.

If the bait was taken, animal handlers would apply pressure on the rope securing the bone or meat. This resistance was meant to prompt the animals to exhibit natural behaviours used by crocodylians to subdue and dismember prey (Fig. 1). The method was loosely based on the technique presented by Fish et al. (2007), but the majority of the animals observed in this study were significantly larger, thus necessitating the use of larger bait and rope, rather than hand-held forceps. Behaviour exhibited in response to resistance applied to the bait was recorded, and is presented in Figs 1, 3; Table 1; and the Supplementary Material.

Death rolling is most often described as a feeding behaviour, but it also has been observed during inter- and intra-specific competition as both an attack and an escape behaviour (e.g. Webb et al. 1983). Within the context of captive animals, individuals are also known to attempt death rolls during capture as a means to attempt escape (S.K. Drumheller, J. Darlington, K.A. Vliet personal observations). In order to explore patterns of this type of death rolling, a second escape cue was used as well (Fig. 2). Study animals were captured using either a loop of rope (for the smaller individuals) or a catch pole (for larger individuals). Catch poles are standard equipment for catching crocodylians in this manner, and consist of long sturdy tubes with loops of fabric rope or metal cable on one end, allowing more distance between the handler and the snared animal. When possible, incidental observations of this stimulus were made during captures related to normal management of the animals. Behaviour exhibited during capture was recorded, and is presented in Figs 2, 3; Table 1; and the Supplementary Material.

While this study focuses specifically on animals held at the St. Augustine Alligator Farm Zoological Park, our observations were supplemented by observations made during regular animal care and interaction by the following individuals: Miroslav Procházka, (Crocodile ZOO Protivín,



Fig. 2. — Examples of death roll behaviours observed during the escape stimulus experiments. Clockwise from upper left: *Gavialis gangeticus* (image courtesy of Miroslav Procházka and Crocodile ZOO Protivín), *Mecistops cataphractus*, *Crocodylus johnstoni*, and *Alligator sinensis*.

Protivín, Czech Republic) shared observations and images of *Gavialis gangeticus* (Gmelin 1789) death roll behaviour, Joe Wasilewski (Jadora LLC) shared further information on death rolling among members of *Crocodylus acutus* (Cuvier 1807) from Florida (but see Milián-García et al. 2018 for notes on potential diversity across this clade), and Matthew Shirley shared observations of death rolling by members of the newly resurrected species *Mecistops leptorhynchus* (Bennet 1835; sensu Shirley et al. 2018). These observations are included in the Results section.

RESULTS

Prior to this study, death roll behaviour had been recorded in seven species of broad-snouted, generalist crocodylians (Fig. 3). Here, we report incidents of this behaviour in 24 of 25 living taxa, including several slender-snouted forms (Fig. 3; Table 1; Supplementary Material). Observations are organised by whether members of each species exhibited death rolling behaviour in response to both types of cues, only the feeding cue, only the escape cue, or neither cue. It is important to note that while a positive result (i.e. a death roll) should be viewed as a true positive (i.e. members of this species can perform this behaviour), a negative result (i.e. no death roll) might not indicate a true negative (i.e. while these individuals did not death roll under these specific circumstances, other members of the species might still be capable of performing this behaviour).

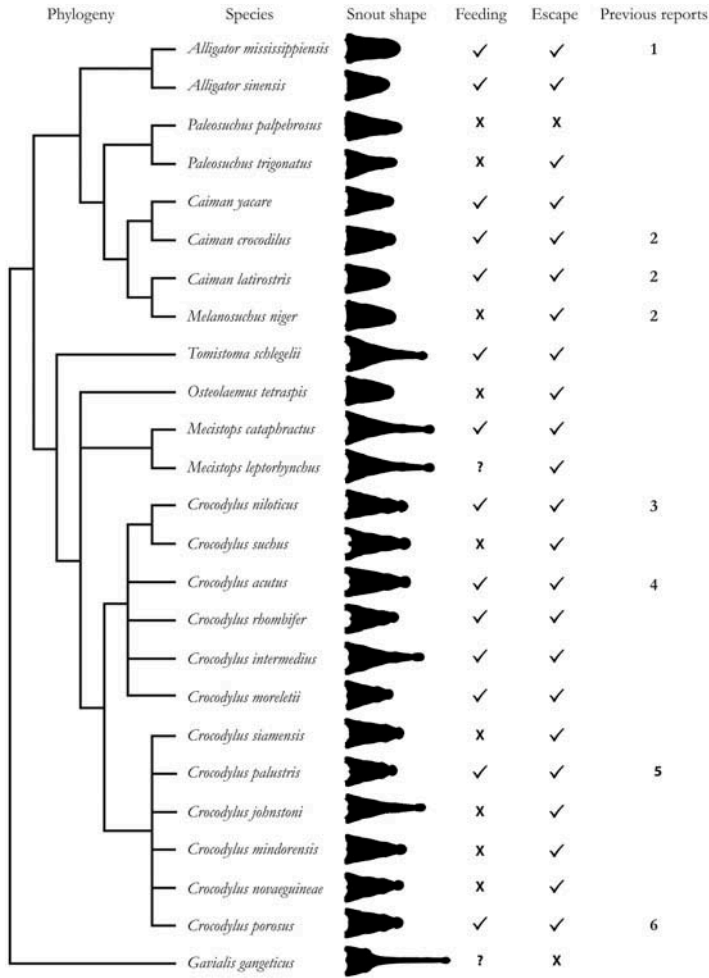


Fig. 3. — Death roll behaviour across extant Crocodylia, in phylogenetic and ecomorphological context. Phylogeny adapted from Drumheller and Brochu (2016). Skull silhouettes based on adult exemplars of each species. Feeding and escape cue results, supplemented with previous reports: ✓ = observed death roll behavior, X = no observed death roll behaviour, ? = behaviour was not tested in this study or published in other studies. Previous reports: 1 = McIlhenny (1935); Harding and Wolf (2006); Fish (2007); Langley (2010); Drumheller and Brochu (2014), 2 = Blanco et al. (2014), 3 = Guggisberg (1972); Pooley and Gans (1976); Helfman and Clark (1986); Njau and Blumenschine (2006), 4 = Álvarez Del Toro (1974); Mendieta and Duarte (2009); Cupal-Magaña et al. (2010), 5 = Bhattarai (2015), 6 = Loveridge (1946); Allen (1974); Pooley et al. (1989); Davidson and Solomon (1990); Caldicott et al. (2005); Wood (2008); Chattopadhyay et al. (2013).

Feeding and escape

As one of the most heavily studied species (Rowe et al. 1999) as well as one of the most common held at the SAAF, *Alligator mississippiensis* was used to test and develop feeding and escape cue methodologies. This species was already known to exhibit death

roll behaviour (Fig. 3), and we observed several individuals performing death rolls in response to both feeding and escape cues (Table 1, Supplementary Material). *Caiman latirostris* (Daudin 1801 [1802]; Blanco et al. 2014), *Crocodylus acutus* (Álvarez Del Toro 1974; Mendieta & Duarte 2009; Cupal-Magaña et al. 2010), *Crocodylus niloticus* (Guggisberg 1972; Pooley & Gans 1976; Helfman & Clark 1986; Njau & Blumenschine 2006), and *Crocodylus porosus* (Loveridge 1946; Allen 1974; Pooley et al. 1989; Davidson & Solomon 1990; Caldicott et al. 2005; Wood 2008; Chattopadhyay et al. 2013) previously have been documented death rolling, and these species also exhibited this behaviour in response to both cues in our trials as well.

Several other species exhibited death roll behaviour in response to both cues, including the following slender-snouted forms: *Crocodylus intermedius* (Graves 1819), *Mecistops cataphractus* (Cuvier 1825), and *Tomistoma schlegelii* (Müller 1838). *Alligator sinensis* (Fauvel 1879), *Caiman yacare* (Daudin 1801 [1802]), *Crocodylus moreletii* (Duméril & Bibron 1851), *Crocodylus rhombifer* (Cuvier 1807), which all have the more generalist snout morphology, also exhibited this behaviour. This represents the first record of death roll behaviour in these species.

Crocodylus palustris (Lesson 1831) and *Caiman crocodilus* (Linnaeus 1758) were previously observed utilising death roll behaviour during feeding events (Blanco et al. 2014; Bhattarai 2015), but were only observed exhibiting the behaviour during the escape cue portion of this study. Taken together though, these separate sets of observations indicate that these species are capable of performing this behaviour under both sets of circumstances, which is reflected in the difference in our raw observational data (Table 1; Supplementary Material) and the results presented in Fig. 3.

Feeding only

No species exhibited death roll behaviour in response to the feeding cue, but not the escape cue.

Escape only

Melanosuchus niger (Spix 1825), which previously has been recorded death rolling (Blanco et al. 2014), exhibited this behaviour in response to the escape cue, but not the feeding cue. In addition to this species, the following taxa previously have not been documented death rolling: *Paleosuchus trigonatus* (Schneider 1801), *Crocodylus johnstoni* (Kreffft 1873), *Crocodylus mindorensis* (Schmidt 1935), *Crocodylus novaeguineae* (Schmidt 1928), *Crocodylus siamensis* (Schneider 1801), *Crocodylus suchus* (Geoffroy Saint-Hilaire 1807), and *Osteolaemus tetraspis* (Cope 1861) (Fig. 3). Of these, *Crocodylus johnstoni* exhibits the tube snouted morphotype.

One specimen of *Gavialis gangeticus* was subjected to only the escape cue, during which it did exhibit death roll behaviour. Whether they might death roll in response to a feeding cue remains untested, but this species does exhibit the strongest specialisation for piscivory among the tube-snouted groups (Thorbjarnarson 1990), and observations of regular feeding by SAAF *Gavialis* resulted in some twisting behaviour, but nothing resembling full-blown death rolls. These results are further supported by similar observations of *G. gangeticus* at Crocodile ZOO Protivín. Additionally, specimens of *Mecistops leptorhynchus* were observed death rolling during capture as part of

the recent redescription and resurrection of this species (Shirley et al. 2018; M.H. Shirley personal observation). Therefore, these species are tentatively placed within this category, but further research is required.

No death rolling behavior

Of the tested animals, only one species did not perform at least one death roll in response to either stimulus type: *Paleosuchus palpebrosus* (Cuvier 1807) (Fig. 3). Six individuals were prompted using both cues multiple times with no positive results (Table 1; Supplementary Material). Initially, it was considered that members of *Paleosuchus*, being more terrestrial in their behaviour and possessing of a deeper snout than many of their counterparts (Brochu 2001; Gignac & O'Brien 2016), might not death roll. However, *P. palpebrosus*' close relative, *Paleosuchus trigonatus* performed the behaviour in one of the final trials, potentially negating that line of reasoning. Bearing in mind that every other observed species performed this behaviour, it is important to remember that this result is not necessarily a blanket negative for the taxon, and other individuals may still death roll under different conditions. Note the discussion of our *Crocodylus palustris* and *Caiman crocodilus* results above for examples of this potential limitation. More research is required.

DISCUSSION

In the light of this study's results, a better question to ask might not be "Can slender-snouted crocodylians death roll?" but instead "Why might a slender-snouted crocodylian death roll?". Functional studies have demonstrated that these animals are better suited to be small-prey specialists (e.g. Cleurens & De Vree 1999; McHenry et al. 2006), but several ecological surveys of the diet among these crocodylians have proven to include a variety of prey items beyond just fish (e.g. Tucker et al. 1996; Webb & Manolis 2010; Selvaraj 2012). The idea that tube-snouted crocodylians are strict fish-eaters has become so well entrenched that broad similarities to this morphotype have been used to justify interpretations of piscivory in very distantly related archosaurs, such as phytosaurs and spinosaurid dinosaurs, even though bite mark evidence provides potential interpretations to the contrary (Buffetaut et al. 2004; Drumheller et al. 2014). While members of this morphotype often focus on physically smaller prey, the kind that do not typically need to be subdued or dismembered through rotational feeding (Cleurens & De Vree 1999; Blanco et al. 2014), documented incidents of scavenging on larger-bodied prey suggest incidences in which the behaviour may still be needed in a feeding context (e.g. fossil *Tomistoma* scavenging a gomphothere in Antunes 2017 and extant *Gavialis* scavenging human remains in Pooley et al. 1989).

This is not the first study to determine that some crocodylian species seem to over-shoot the apparent requirements of their niche (Gignac & Erickson 2016; Gignac & O'Brien 2016). Extensive surveys have demonstrated that there is a close linear relationship between bite force and body mass in crocodylians (Erickson et al. 2003, 2012, 2014). This pattern holds up within ontogenetic series of single crocodylian species as well as across all extant Crocodylia, with the possible

exception of *Gavialis gangeticus*, the perennial odd man out within the clade. In other words, tube snouted crocodylians do not typically exhibit reduced bite force even though they shift to more compliant prey, and species which exhibit durophagy or specialise in larger prey animals do not gain a commensurately higher bite force to accommodate their diet either. The bigger the crocodylian, the higher its bite force, no matter the shape of its snout (Erickson et al. 2003, 2012, 2014; Gignac & Erickson 2016; Gignac & O'Brien 2016).

Snout shape also is not a good indicator of phylogenetic relationships within Crocodylia, and different ecomorphs appear across the crocodylian evolutionary tree (Brochu 2001). It has been suggested that some variations in feeding strategy within living brevirostrine species could be explained as relict behaviours, passed down from an ancestor of one snout morphotype to descendants with differing morphologies (Drumheller & Brochu 2014). Many longirostrine groups are nested within more brevirostrine clades (Brochu 2001), so this line of reasoning might provide an alternate explanation for the near-ubiquity of death rolling across this clade.

However, the distribution of death rolling behaviour may have nothing to do with feeding strategy at all. An assumption sometimes made in interpretations of feeding strategies and behaviour is that the only time one animal might bite another is during a predation attempt. However, among living crocodylians, intraspecific competition often includes powerful bites to an opponent's head, limbs, and base of the tail (e.g. Webb et al. 1983). Possible evidence of this behaviour has been identified in several fossil taxa as well (Williamson 1996; Avilla et al. 2004; Mackness et al. 2010; Vasconcellos & Carvalho 2010) including slender-snouted forms such as the tomistomine *Toyotamaphimeia machikanensis* (Katsura 2004) and the dyrosaurid *Tilemsisuchus lavocati* (Buffetaut 1983).

Interspecific conflict with large-bodied animals is also documented among the slender-snouted crocodylians. One of the most comprehensive sources of data to discuss this is the Worldwide Crocodylian Attack Database (CrocBITE 2013), which records attacks by crocodylians on human beings in order to track patterns of these incidents and identify methods for mitigating them in the future through education and wildlife management. As of 5 December 2018, the CrocBITE database recorded the following number of attacks by slender-snouted crocodylians: *Gavialis gangeticus* = 1, *Tomistoma schlegelii* = 32, *Crocodylus intermedius* = 1, and *Crocodylus johnstoni* = 20. While these numbers are significantly smaller than those attributed to large-bodied, brevirostrine species, such as *Crocodylus niloticus* (967 recorded incidents) and *Crocodylus porosus* (1369 recorded incidents), they still demonstrate that the tube-snouted species will attack animals that are significantly larger than their usual prey under certain circumstances.

Within this study, some of the observed animals were clearly interested in the feeding cue as a potential food source (even eating the items if the opportunity arose). However, this was not always the case. Reactions from individual animals ranged widely, as would be expected among a clade whose mouths are one of their main instruments for interacting with and exploring their surroundings (Brochu 2001). Added to which are the results of the escape cue survey, in which no potential food item was presented to these animals, and the utility of this behaviour outside of feeding alone becomes clear. Perhaps then, the importance of inter- and intra-specific conflict, rather than feeding strategy, can explain the broad distribution of this behaviour across the clade.

CONCLUSIONS

The results of this survey suggest two things about crocodylian death roll behaviour. First, it is not restricted to any one snout morphotype, and is instead performed by species across the clade (Fig. 3). As such, it seems likely that the behaviour was equally widespread across members of Crocodyliformes that filled the role of semi-aquatic ambush predator, as well as other, more distantly related taxa that exhibited similar body plans (e.g. phytosaurs, choristoderes). Secondly, while crocodylians do death roll during predation and other feeding events, they also exhibit this behaviour under circumstances unrelated to feeding. When attempting to determine why certain crocodylian groups might death roll, both feeding ecology and inter- or intraspecific conflict should be addressed.

More broadly, this study highlights how surveys of modern groups can limit downstream interpretations of extinct clades. Within Crocodylia, the most studied species, and therefore the *de facto* model organisms for the clade, are all large-bodied generalists: *Alligator mississippiensis*, *Crocodylus niloticus*, and *Crocodylus porosus* (Rowe et al. 1999; Tzika & Milinkovitch 2008). The focus on these groups and morphologically similar species (Fig. 3), and the lack of baseline data addressing the presence or absence of death roll behaviour within other snout-shape classes, created a false impression that only generalist or brevirostrine species are able to perform this behaviour while specialised, longirostrine groups are not. More foundational research is required on crocodylian taxa outside of the perceived norm – physically smaller species like *Alligator sinensis*, slender-snouted species like *Tomistoma schlegelii*, more terrestrial species like *Paleosuchus palpebrosus* – before we can comfortably extend our behavioural assumptions into fossil groups.

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