

A proposed framework for establishing and evaluating hypotheses about the behaviour of extinct organisms

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Abstract

Reconstructing the possible behaviours of long extinct species, and especially those with no close living relatives, are naturally fraught with difficulty: data are often limited and hard to interpret. However, the field of palaeoethology has not been helped by a poor understanding of the range and plasticity of the behaviour of extant organisms, coupled with a tendency to generalize and over-interpret the limited information available. Here we attempt to construct a framework for the establishment of viable hypotheses about the behaviour of extinct organisms and the generation of support for, or testing of, these hypotheses. We advocate that it is preferable to under-interpret available data, than to suggest problematic hypotheses that may become accepted as correct.

Introduction

From the earliest days of palaeontology, hypotheses have been generated about the behaviour of extinct taxa: William Buckland in 1829, for example, suggested that the pterosaur *Pterodactylus* may have been insectivorous and lived in flocks. However, while palaeontology has developed enormously as a field in this time, the analysis and assessment of the behaviours of extinct animals have not continued apace with the development of ethology as a field. The latter culminated in the sharing of the 1973 Nobel Prize in Physiology or Medicine by K. Lorenz, N. Tinbergen and K. von Frisch. Tinbergen's 'four questions' approach to the study of behaviour (mechanism, development, survival value and evolution), together with the comparative method favoured by Lorenz, has provided a solid framework for interpretation of behaviour from the fossil record.

Meanwhile, the foundations of the field of sociobiology were laid in the 1960s by biologists with increasing emphasis being given to understanding how genetic influences may explain behaviour (e.g. Hamilton, 1964). In the intervening decades, our knowledge and understanding of behaviour in extant animals has increased markedly. Neurobiological processes can now be visualized *in vivo* by scanning techniques, and mechanisms teased apart at the molecular level. Molecular genetic techniques have totally revolutionized the field of behaviour at all levels. Genetic fingerprinting enables unambiguous assignment of parentage, mating system and the kin structure of groups, all of which are essential in understanding

and interpreting behaviour and testing the original hypotheses of Hamilton and others (Burke *et al.*, 1991; Ross, 2001). The new field of sociogenomics, underpinned by next generation sequencing technologies, seeks to utilize the growing numbers of whole genome datasets now available to find candidate genes associated with particular behaviours. As a result, the genetic basis of even complex mammalian behaviour is being revealed (Robinson, 2004; Robinson, Grozinger & Whitfield, 2005; Robinson, Fernald & Clayton, 2008).

Can any of these modern methodologies be brought to bear on the fossil record? In most cases, probably not directly, but they can certainly allow a more informed interpretation and offer the possibilities of reconstructing ancestral gene and protein sequences (e.g. Chang, Ugalde & Matz, 2005). Taking a likelihood-based phylogenetic approach, Chang *et al.* (2002) recreated the sequence and then synthesized and tested a functional ancestral archosaur visual pigment (for a node dated within the Early Triassic Period). From this, they were able to show that their hypothesized ancestral pigment had an absorption maximum that was shifted towards the red end of the electromagnetic spectrum in relation to mammals and fish, but at the higher end of the range of that reported for birds and reptiles. Although behavioural inferences are not drawn from this data, it is a good example of what is possible and could be applied to make functional predictions from genes known to affect behaviour.

Within the emerging field of ancient genomics, the latest technologies are being applied to sequence and analyze the tiny quantities of degraded DNA that may persist in some

sub-fossils (Lambert & Millar, 2006; Millar *et al.*, 2008). A good example of the use of this data to make inferences about behaviour is the Neanderthal genome project. Comparison of the Neanderthal, human and chimpanzee genomes has enabled regions subjected to positive selection and selective sweeps to be identified. Some of the loci that differ between humans and Neanderthals contain genes involved in cognition, and supports recent work by Pearce, Stringer & Dunbar (2013) suggesting Neanderthals had different cognitive abilities and behaved differently to contemporary early modern humans. This study used a comparative morphometric approach measuring orbital volume, and concluded that Neanderthals had larger visual systems and reduced endocranial capacities relative to body size. As a consequence of this different organization of the brain, it is hypothesized that Neanderthals compromised their social cognition and behaved differently to early modern humans. Similarly, a combination of genetic work and ancient human cave art (Bar-Oz & Lez-Yadun, 2012) has helped to infer the habitat preferences of ancient species of large mammal. These studies serve as a good example where very different techniques and lines of evidence support a hypothesis regarding the behaviour of an extinct organism. We strongly advocate that such holistic and integrative approaches should be brought to bear on the interpretation of behaviour from the fossil record wherever possible (see discussion below).

Even with these techniques and sources of data, work on the behaviour of animals from the fossil record has understandably lagged that of traditional ethology. It is clearly difficult to attempt to reconstruct the behaviour of an extinct animal (Benton, 2010). Many details cannot possibly be reconstructed as no trace of them could be preserved or determined with any degree of accuracy. For example the exact nature of a courtship ritual, whether or not monogamous species indulged in extra pair copulations (which even today can only be determined unambiguously through genetic analysis of parentage), or whether or not a species was territorial will likely never be determined for any truly ancient species. However, many fundamental issues can potentially be inferred such as whether or not a species was social or asocial, or was herbivorous or carnivorous, though not always without controversy.

New and innovative research has produced new insights into the behaviour of fossils animals (e.g. Finite-element analysis, Rayfield *et al.*, 2007 or computed tomography work to reveal the brain structure of birds, Walsh *et al.*, 2009), and this has been supported by more traditional functional analyses (e.g. Snively & Russell, 2001) and the discovery of exceptional fossils that show evidence of behaviour [e.g. dinosaurs that show unequivocal evidence for brooding on a nest (Norell *et al.*, 1995) or scavenging (Hone & Watabe, 2010)].

Unfortunately, despite this new wealth of data, many hypotheses have been proposed to explain the behaviour of fossil animals (from individual specimens through to entire clades) that are based on little evidence, equivocal data or that rely on huge extrapolation, or misunderstandings of, behaviour. The incredible adaptability of animals to their environments and the complexities of interactions between and within



Figure 1 Life restoration of a spinosaurid theropod dinosaur in the act of killing a large ornithocheirid pterosaur. An exceptional fossil of a series of ornithocheirid pterosaur cervical vertebrae penetrated by an *in situ* spinosaur tooth (Buffetaut, Martill & Escullí, 2004) from Brazil demonstrates that at least one spinosaur once fed upon a pterosaur. But is this a near unique event or part of a more general pattern of behaviour? Image by Mark Witton and used with kind permission.

species (Faulkes & Bennett, 2013; Kappeler *et al.*, 2013), combined with the limited evidence from the fossil record perhaps makes this inevitable (Fig. 1). There are not even that many good correlations between many behaviours or types of behaviour and the kinds of anatomical features that readily preserve in the fossil record (or ichnological traces that can be correctly tied to a given species).

Here we document some of the pitfalls that have beset previous statements about the behaviour of extinct animals. We attempt to layout a framework for the future establishment of viable hypotheses and how evidence could be accumulated for these. While the issues documented here are applicable across extinct animals, our research interests mean that examples are primarily drawn from the dinosaurian and mammalian literature.

Discussion

Problems and errors

The fossil record provides only a limited amount of certain kinds of evidence (primarily hard tissues such as skeletons and shells, and ichnites such as tracks), limiting the power of interpretations of behaviour. Palaeontologists have only a tiny amount of the data that would be available to an ethologist studying an extant organism. Some kinds of palaeontological data are readily available, but costly or time consuming to acquire or may damage the specimens (e.g. histological thin sections of bone, or synchrotron scanning of fossils). Furthermore, all fossils specimens are subject to the filter of taphonomy that can potentially profoundly alter the available data, presenting misleading pictures of the evidence (e.g. lamellibranch shells having suffered drilling from predators transport further than do intact ones, Lever *et al.*, 1961).

Detailed studies or exceptional specimens can potentially reveal much information (e.g. the potential to separate out at what time various tracks were laid down relative to one another – Milner, 2005, evidence for transport of material – Voorhies, 1969, and to distinguish between trample marks or bite marks – Fiorillo, 1984) and support for a conjecture. However, these must be put in the context of the specimens, a correct understanding and appreciation of behaviour, and framed as a specific hypothesis. They must also be formulated in an appropriate manner that does not immediately lead to a false premise being created. Given the limitations of palaeontological data, we would advocate that formulated hypotheses need not be testable in the present based on the then available data, but at least have the capacity to be tested on the basis of future finds or analyses.

Here we outline some previous problems affecting hypotheses about palaeobehaviours. We do not intend to overtly criticize the studies cited as examples, but rather draw attention to potential pitfalls that may have been previously overlooked. Note that not all of these examples may ultimately be incorrect; however, they are not supported by the data as suggested:

(1) False dichotomy or premise. Mutually exclusive hypotheses are useful as they allow the evidence for only a single concept to be used to infer the state of another. However, such relationships must truly be antagonistic, or a false dichotomy is created and evidence for one hypothesis incorrectly used as evidence against another. For example, Taylor *et al.* (2010) showed that Senter's (2007) claim of a dichotomy between sexual selection and feeding envelope increase in sauropod dinosaur necks was false. Thus Senter's arguments in favour of sexual selection did not rule out a functional role.

(2) Incorrect claims about behaviour. Extant organisms provide analogies to apply to extinct taxa, and also data for the extant phylogenetic bracket approach (Bryant & Russell, 1992; Witmer, 1995). However, data drawn from extant animals needs to be correct. For example, in their analysis of putative pack hunting in non-avian dinosaurs, Roach & Brinkman (2007) suggest that apparent cooperative hunting in extant archosaurs is both different to, and more limited than,

that seen in modern mammals, thus by inference, limiting the capacity of social hunting in the dinosaurs. However, at least some birds show complex social hunting behaviours (FitzSimmons, 1962) as potentially do some crocodylians (Yamashita, 1991), so it is incorrect that social hunting may be beyond the behavioural repertoire of birds at least.

(3) Over extrapolation or conflation. Data available for a single species may be assumed to be present in many or all related forms when this need not be the case, and data that may only point in a limited way to one interpretation may be extrapolated to a more narrow behavioural range. For example, numerous trackways are known for dinosaurs, which appear to show many individuals of a single ichnotaxon moving in a subparallel direction. This has been inferred as evidence for sociality (e.g. Lockley, 1991) but this relies on heavy extrapolation – conspecifics during migration or trying to reach important locations (e.g. breeding sites, water holes) may well travel in large numbers in a single direction, but this does not mean they are necessarily a social species that habitually lived in groups. Similarly, there is some association between body size and degrees of sociality in African mole-rats, and this has led to speculation that some fossil forms may have had a solitary lifestyle based on their larger body size (Jarvis & Bennett, 1991), but some social species are now also known to attain larger body sizes (e.g. the Zambian mole-rat *Fukomys mechowii*) than other mole-rats. More recently, Matthews, Denys & Parkington (2006) suggested that the abundance of specimens of the fossil dune mole rat *Bathyergus hendeyi* raises the possibility that the species may have been a social animal, despite that all extant *Bathyergus* are strictly solitary. This seems tenuous as extant solitary bathyergids (e.g. *B. suillus*) may often be present in high densities where food is plentiful (Bray *et al.*, 2012).

(4) Ideas not supported by, or contradicted by, the presented data. Hypotheses have been proposed based on a single line of evidence that are illogical or incorrect. Wilkinson & Ruxton (2012), for example, suggested that the long necks of azhdarchid pterosaurs might have evolved to assist reaching into the carcasses of sauropod dinosaurs. However, not only do modern scavengers clearly not require necks capable of reaching into the largest bodies available (the necks of African vultures are short compared to the depths of the ribcages of elephants and rhinos), but the jaws of the largest azhdarchids were as much as 3 m in length (Buffetaut, Grigorescu & Csiki, 2002). At this size, they alone would be big enough to reach into the deepest bodied sauropod known (at around 2 m Lü *et al.*, 2007) making an elongate neck redundant in the context of this hypothesis.

(5) Overuse of generalities that make it hard to ascertain what exactly is being suggested (e.g. 'social', 'parental care'). Strong assertions relating to the nature and degree of sociality are especially problematic in relation to fossil-based data, as disagreement continues among sociobiologists about the best way to define social systems. Indeed, even intensive behavioural study of extant species still provokes debate as to whether a species is 'eusocial' (for which a specific definition does exist) or a 'cooperative breeder' (see Faulkes & Bennett, 2007, 2009 for further discussion).

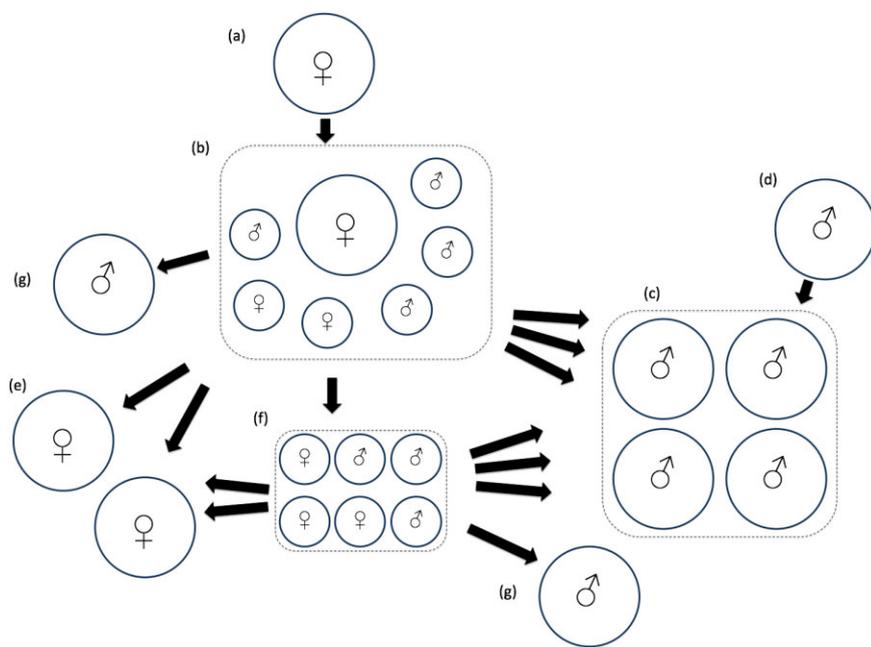


Figure 2 Schematic diagram illustrating the plasticity in cheetah social organization: (a) adult and pregnant females are solitary with large home ranges overlapping male territories, with females and males only interacting briefly for mating (males not shown); (b) a group composed of a female with her cubs may persist for months before either (c) male sibs form adult groups (lasting years), sometimes being joined by lone males (d), while females disperse singly (e) or (f) temporary adolescent sib groups form (duration can be months) before male groups form (c) and female dispersal (e); (g) lone male dispersing from either natal group (b) or adolescent sib group (f) (Caro, 1994).

Proposed line of evidence

In addition to the above noted issues to avoid, we also propose a series of fundamental lines of evidence that can be used to establish whether or not an idea can be supported enough to generate a formal hypothesis about the behaviour of a species or clade based on the available data. Many will not be applicable to a given taxon or specimen given the limitations of preservation, but ideally as many as possible should be used to build up an accurate representation of the inferred behaviours.

(1) Make it clear that a specific hypothesis is being established about the taxon/specimen in question. Quantify and qualify the data and evidence as far as possible, and in particular provide tight and detailed definitions of the behaviour in question (e.g. does ‘parental care’ only include post-hatching care, or is this limited to brooding of eggs etc.). These definitions may be different to those currently in the literature, but should be specific and consistent. Do not over-extend these across whole clades because of evidence in a single species, unless there are strong correlates between them (e.g. a similar functional structure such as antlers).

(2) Be specific about the terminology or extent of a behaviour. Is this behaviour considered obligatory, or likely common, or only an occasional part of a possible range of behaviours? Many animals may be piscivorous in that they will catch and consume fish, but such a label does not apply equally to a dedicated piscivore, an animal that will hunt fish on occasion, and one that will do so only very occasionally or could, but generally does not.

(3) It must be remembered that behaviour can be extraordinarily plastic even for single populations of species. For example, cheetahs (*Acionyx jubatus*) are both group and solitary hunters (Fig. 2), and puma (*Puma concolor*) range over a

huge variety of ecosystems (Currier, 1983). What is normal for an Alaskan puma is probably not true of one on the Argentine pampas or a Peruvian rainforest. Specializations can be a matter of behaviour and not morphology (e.g. prey choice may be limited by habitat or availability). In short, recognize that even with very convincing evidence for a given behaviour of a specimen, this may not be universal for the population, let alone the species or clade. For example, although morphologically similar subterranean rodents, African mole-rats (Bathyergidae) range in sociality from strictly solitary dwelling to highly social among species within a single family, and even within a species plasticity in behaviour may be observed (Faulkes & Bennett, 2013). Note that in addition to intra- and interspecific flexibility of behavioural traits, these may not be phylogenetically conservative and thus implications based on even near relatives may be uncertain (Kamilar & Cooper, 2013).

(4) Functional morphology can provide strong evidence for a given behaviour. Where possible, multiple correlates from different body parts should be used, and these should ideally also be present in a wide range of extant taxa. For example, robust and strongly curved claws are indicative of digging or burrowing behaviour (Hildebrand, 1985). However, such behaviour is also associated with robust phalanges, a large olecranon process and deltopectoral crest, broad ribs and a large sacrum (Hildebrand, 1985), providing evidence from across the skeleton. Functional analyses can also be used to rule out certain behaviours eliminating them from consideration as noted for example by Humphries *et al.* (2007) demonstrating not only the mechanical implausibility of surface skimming in pterosaurs, but also the lack of specialized anatomical features that would support this behaviour (e.g. a greatly elongated rhamphotheca).

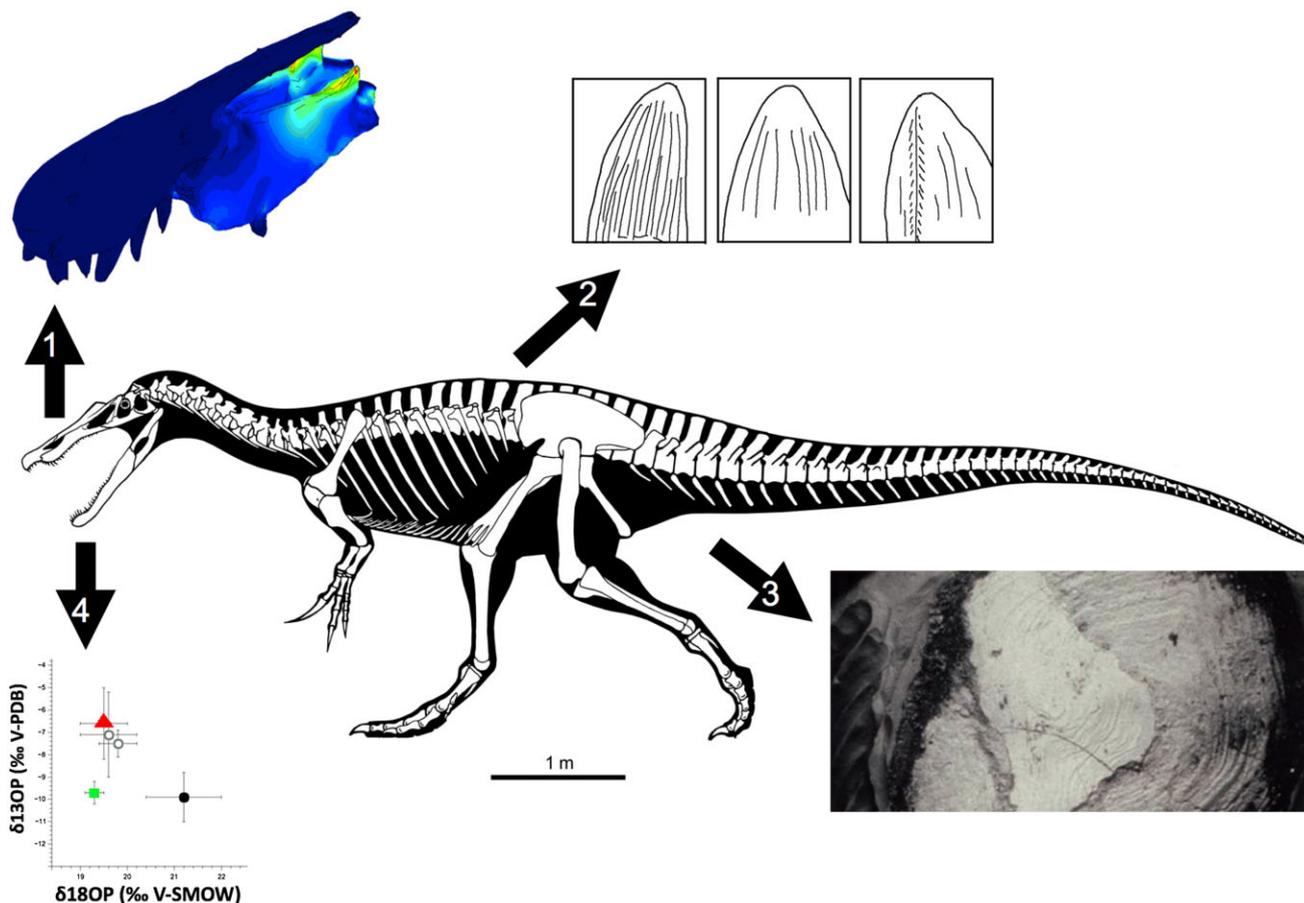


Figure 3 Multiple lines of evidence to support a single hypothesis, here the likely diet of spinosaurid theropod dinosaurs. Central image: skeletal reconstruction of the British taxon *Baryonyx walkeri* (image copyright Scott Hartman). (1) Finite element analysis of the rostrum of *Baryonyx* by Rayfield *et al.* 2007 showing the resistance of the jaws to torsion. (2) Similarity in form of the upper crown of a *Spinosaurus* tooth to that of other aquatic or semi-aquatic piscivorous reptiles L-R: *Spinosaurus* (tip restored), the fossil crocodile *Brachychampsa* and the marine reptile *Mosasaurus* (redrawn from Hasegawa *et al.*, 2010). (3) Stomach contents of *Baryonyx*: fish scales showing acid etching from Charig & Milner (1997) (image copyright to the Natural History Museum, London). (4) Isotope analysis of spinosaurid teeth (Amiot *et al.*, 2010) showing that spinosaurs (triangle) are closer to crocodiles (square) and fish (open circles) than other theropod dinosaurs (closed circle) and thus prefer aquatic environments to terrestrial ones.

(5) As far as possible, the hypothesised behaviour should be shown to be present in an extant taxon (or taxa) that can provide an appropriate analogue. There is a bewildering variety of animal life and behaviours, so while it is not impossible that the fossil taxon is engaging in something never previously seen, it is far from likely. For example, ‘species recognition’ has been advocated as an explanation for all the various crests and horns seen in many non-avian dinosaurs (Padian & Horner, 2010), despite that this effectively unknown in extant taxa (Kneel & Sampson, 2011). Others are universal or close to it – animals that have high food requirements are generalist feeders and tend to have large ranges, those that are highly specialized and limited to patchy resources tend to be territorial.

(6) Extant examples should be as close to the taxon in question as possible either phylogenetically or in terms of being

an ecological/functional analogue. It is much more convincing if the same behaviour posited for a sauropod dinosaur is found in birds (extant relatives) or elephants (multi-ton, terrestrial, quadrupedal herbivores). If possible pick multiple examples from multiple groups that can support the inference for different reasons, showing that the inferred behaviour is strongly convergent across multiple taxa. For example, ant-eating and digging specializations seen in profusion in parvicursorine theropod dinosaurs (Senter, 2005; Xu *et al.*, 2010) and these known to have originated in multiple independent mammalian lineages and similar adaptations are also seen in other tetrapod groups that dig or burrow (Hildebrand, 1985).

(7) Analogues should be chosen carefully because of the unusual behaviour of some, and many taxa engage in behaviour that few people realize. For examples giant pandas

(*Ailuropoda melanoleuca*) while more herbivorous than other members of Carnivora or even Ursidae, are not strictly vegetarian (Chorn & Hoffman, 1978). Evidence must therefore be used consistently and clear exceptions should not be ignored. Reversals or counter-examples can be useful to attempt to account for phylogenetic inertia (e.g. nighthawks and diurnal owls could provide alternates when examining nocturnal versus diurnal patterns in raptorial birds).

(8) Phylogenetic associations must be strongly supported. Almost every extant bird of thousands of species exhibit some form of parental care of eggs and/or hatchlings, so assuming other extinct birds did is reasonable. That some extant carnivorans are group hunters is not good evidence on its own that any other given example was a pack hunter given the variation seen (Fig. 2) and phylogenetic inconsistency.

(9) Traits may be multifunctional (e.g. the trunks of extant elephants may be used for combat, finding food, drinking, bathing, communication and olfaction among others; Shoshani & Eisenberg, 1982) and very different functions can result in convergent morphology (e.g. claws specialized for grasping prey and those for perching have similar shape and curvature, Birn-Jeffery *et al.*, 2012) though this problem can be offset by the use of multiple traits. Features may be under very strong selective pressure even if used only very occasionally – males may only mate once every few years, but obviously, there would be a strong pressure to maintain large genitals and a baculum if this increased reproductive success. (10) Taphonomy and sampling biases must be taken into account as far as possible and in particular, consistency across multiple specimens should be sought. For example, Witton & Naish (2008) showed that most azhdarchid pterosaur specimens are known from terrestrial deposits. Those from marine systems were with associated with terrestrial input (e.g. land plants) or were known only from isolated elements, suggesting considerable transport. Thus, despite a notable amount of specimens from marine systems, there remains strong support for the contention that these animals were primarily inhabiting terrestrial environments.

(11) Search for additional lines of evidence to support the hypothesis. For example, the spinosaurid dinosaurs are considered to have been primarily piscivorous or at least foraging in aquatic habitats. This is supported by analogy with modern crocodiles through functional analyses of the skull (Rayfield *et al.*, 2007), and gut content data (Charig & Milner, 1997). However, isotope analysis also supports the idea that these animals spent extended periods in the water (Amiot *et al.*, 2010) adding further weight to this (Fig. 3).

Collectively, the field of palaeobehaviour has suffered from a lack of rigour and problematic overstatements of support for some ideas, coupled with a lack of recognition of the plasticity and variations of the behaviour of many extant species and clades. While we hope that the ideas outlined here will help bring clarity to arguments, perhaps the most simple summary would be that it is better to under-interpret than over-interpret the available data. New data can always be recovered, and new analyses and techniques will be developed, but the creation of a false or unsupported

hypothesis can rapidly become established in the literature as a stock answer (e.g. see Hone & Naish, 2013 on species recognition).

However, new developments continue apace and new methods (or refinements of older techniques) bring new power to the analyses of palaeobehaviour. Further data is likely to be available from the application of existing techniques and integration of multiple methods. For example, we would suggest that it may be possible to determine whether or not some species had fixed breeding seasons. Dinosaur growth, maturity and egg laying can be determined from growth lines and the presence of medullary bone (Erickson *et al.*, 2007), which might be aligned in multiple specimens to show breeding occurred in conjunction with a certain age or in a certain part of the year, while analyses of sediments may show strong seasonality of the environment at the time.

Collectively, therefore, we contend that a more robust and rigorous, and in particular cross-disciplinary, approach is to be preferred for future analyses on the palaeobehaviour and palaeoecology of ancient animals. Collaborations between specialists from different fields will maximize the potential of the limited data. Given the information limits of palaeontological data over that of extant taxa, under-interpretation is to be favoured to over-extrapolation and the risk of the creation of hypotheses based on incorrect assumptions.

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