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COMMENT

# Commentary: The ecological and evolutionary implications of allometry

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## Abstract

Allometry—the study of proportional growth of body parts, and the relationship of body size to an organism's morphology, physiology and behaviour—is a fundamental influencer of ecological and evolutionary diversity. Allometric studies can focus on scaling across an individual's development (ontogenetic allometry), among individuals at the same developmental stage (static allometry), and among species (evolutionary allometry). The key assumption in allometry is that an organism's body size is a critical factor in shaping its biology, so biological scaling underpins biological diversity. This commentary accompanies a special issue that collates original research papers on the wide-ranging ecological and evolutionary implications of biological scaling. We discuss the common themes uniting each contribution, such as how ontogenetic allometry facilitates evolutionary allometry, how size influences feeding performance and trophic niche, methodology in allometry and size estimation, and allometry in sexual selection. In doing so we highlight areas of particular need for future studies to better understand the role of allometry in evolutionary ecology.

**Keywords** Biological scaling · Allometry · Evolutionary ecology · Morphometrics

Body size is arguably the most obvious aspect of biological diversity, and size affects the magnitude of structures and rates of processes (Schmidt-Nielsen and Knut 1984; Peters and Peters 1986). The scientific study of scaling and relative growth, known as allometry, has a rich history embedded within ecology and evolution (Huxley and Teissier 1936; Cock 1966; Gould 1966): from establishing biological scaling laws (Snell 1892; Dubois 1897; Sholl 1947) to providing early insights on the genetic control of phenotypes (e.g., Robb 1929; Reeve 1950; Cock 1966; Leamy 1977) and the developmental processes underlying evolutionary diversity (e.g., Alberch et al. 1979; Raff and Wray 1989; Klingenberg and Spence 1993). Subsequent studies sought to understand ecological and evolutionary

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processes from allometric patterns, including the relevance of exaggerated traits in sexual selection (Kodric-Brown et al. 2006; Emlen 2008), the hormonal mechanisms underlying variation in exaggerated traits (Emlen and Nijhout 2000; Emlen et al. 2012), and whether allometric scaling acts as a line of least resistance for evolutionary diversity (Marroig and Cheverud 2005; Marcy et al. 2020). Allometric studies offer a robust quantitative framework for testing biological hypotheses.

Allometric research in evolution and ecology increased rapidly in the 1990s and remains a widely-studied phenomenon (Fig. 1). Allometric studies can focus on scaling at three hierarchical and related biological levels (Bertalanffy and Pirozynski 1952; Cock 1966; Cheverud 1982; Klingenberg 1996): across an individual's development (ontogenetic allometry), across individuals at the same developmental stage (static allometry), and across species (evolutionary allometry). Publications in this special issue span all three levels, use diverse methodological approaches, and include a range of animal taxa including insects, arachnids, fish, anurans and reptiles (Fig. 2). Below,

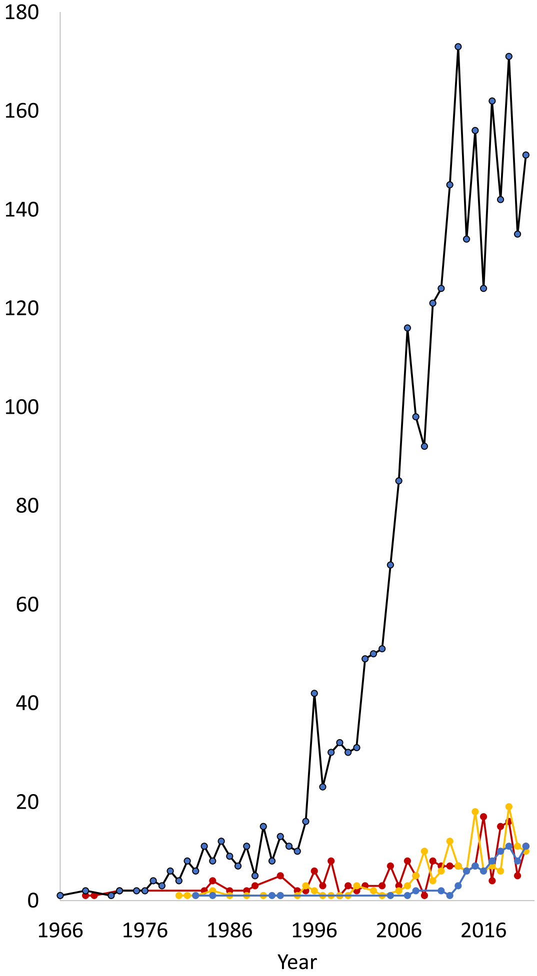

**Fig. 1** Publication history for papers on "allometry AND evolution OR ecology" (black), and specifically "ontogenetic allometry" (red), "static allometry" (yellow), "evolutionary allometry" (blue). Number of papers with search terms found in title, abstract or keywords. Data from Scopus accessed 31/05/2022

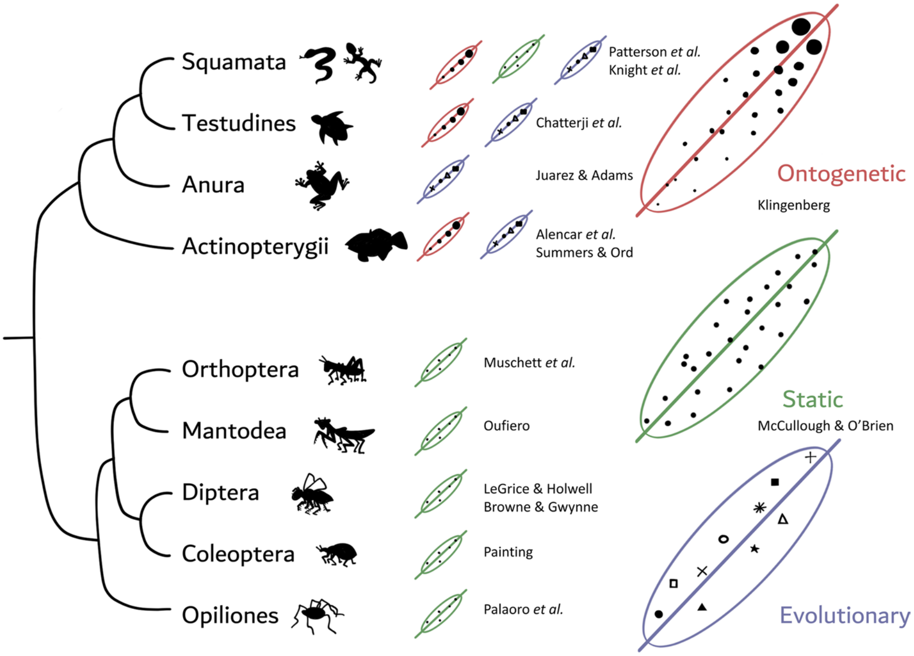

**Fig. 2** Summary of the taxonomic breadth and biological levels of allometry included in this special issue. Levels (right) are represented as a schematic scatterplot, where points represent specimens, line is the regression fit and ellipse is the 95% confidence interval of the data. Ontogenetic level points are scaled to size to represent growth; static level points are the same shape and size, representing individuals of the same age class; evolutionary level points are different shapes, representing different species

we consider the common themes of the 14 papers and indicate future directions where research is encouraged.

Two different viewpoints on allometry exist in the literature (reviewed by Klingenberg 2016). It is important for students of biology to appreciate that both viewpoints are valid, existing side by side because of historical differences in analytical frameworks and approaches to proportions among measurements. Here, Alencar et al. (2022) examines how body size is a complex trait evolving among bony fishes to produce the diversity in body form we observe today. In this manner, they exemplify the "Huxley-Jolicoeur" viewpoint, where allometry is the covariation among two or more traits in response to variation of size, and each trait contains its own size information (see Klingenberg 2022). The alternative, where size is a separate component from shape—known as the "Gould-Mosimann" viewpoint—is exemplified by several other studies in this issue (e.g., Patterson et al. 2022; Chatterji et al. 2022; Painting 2022; Juarez and Adams 2022).

Whether the research question aligns with the "Huxley-Jolicoeur" or "Gould-Mosimann" viewpoint will drive the analytical approaches used. In situations where multiple traits (dependent variables) need to be considered simultaneously (e.g., geometric morphometric shape analysis), the methods of multivariate allometry should be employed. There are many analytical approaches, but Klingenberg (2022) helps in choosing amongst them. Computer simulations demonstrate how different methods function under different scenarios (numbers of variables), and two biological examples are provided to illustrate why the approach taken matters in studies of ontogenetic allometry.

Allometric trait variation plays an important role in feeding performance and dietary specialisation during ontogeny. Here, Patterson et al. (2022) demonstrate that leveraging positive allometry in the upper and lower jaws of dugite snakes (*Pseudonaja affinis*) can facilitate the dietary shift from reptilian prey as juveniles to predominantly mammalian prey as adults. Chatterji et al. (2022) reveals that varying timing of growth changes allometric trajectories among species of sea turtles (Chelonioidea), facilitating access to different dietary niches as adults. Oufiero (2022) demonstrates that prey capture is not easy for juvenile ghost praying mantises (*Phyllocrania paradoxa*), but through negative allometry they grow into high performance adults. These studies suggest that allometric scaling may be a fundamental mechanism in trophic adaptation.

A common application of allometric models is their use in estimating body size, for example in fossil taxa. Knight et al. (2022) performed a comprehensive analysis on a suite of variables across a large sample of extant *Phrynosoma* lizards to test the effectiveness of this approach. While body size can be effectively estimated among closely related species, greater error margins exist with phylogenetic distance. This is because similarity in estimated allometric trajectories decreases as you proceed up the phylogenetic tree. This highlights the need for more multi-level studies to understand why ontogenetic and static allometry do not necessarily scale up to evolutionary allometry.

Because sexually-selected traits often scale disproportionately with body size (Kodric-Brown et al. 2006; Shingleton and Frankino 2013), allometric studies have garnered significant attention from sexual selection researchers, including in this issue. McCullough and O'Brien (2022) compare the allometric slopes of intra-sexually-selected structures (i.e., armaments) and find that the slopes are steeper for structures that are primarily used as aggressive signals and shallower for structures that are primarily used as weapon. Variation in allometric slopes can thus be used to glean information about the function of armaments. Palaoro et al. (2022) similarly find that function correctly predicted the allometric slope of contest-related traits in tusked harvestmen (*Phareicranaus manauara*), with threat devices exhibiting hyper-allometry and tactile structures exhibiting hypo-allometry.

Allometric studies of sexually-selected traits almost always focus on traits that are exaggerated in males, with female traits either missing entirely from the study or used as a baseline for comparison (Simmons and Tomkins 1996; Baker and Wilkinson 2001). The study by Browne and Gwynne (2022) on long-tailed dance flies (*Rhamphomyia longicauda*) therefore provides a rare examination of static allometry in female-specific traits. They find that female ornaments show strong positive allometry, which suggests that they are honest indicators of female quality and serve a similar function to traditional male ornaments, exaggerating differences in female condition and informing male mating decisions. Intriguingly, they find that homologous traits in males also showed positive allometry (despite not being used for mate choice), which supports the recommendation by Palaoro et al. (2022) that homologous traits in the opposite sex often may not be appropriate controls.

Painting's (2022) investigation of the shield-like heads of male weevils (*Hoherius meinertzhageni*) offers an intriguing example of how sexually-selected traits can diverge in shape as well as size, both between the sexes and among male morphs. In this study, male head size and shape was dimorphic, had higher levels of shape variation and showed steeper allometric trajectories in shape space than females. In another study addressing male-male competition, Muschett et al. (2022) provide a comparison of the fighting behaviour, sexual dimorphism and trait allometry among four species of skyhopper grasshoppers (*Kosciuscola*), a group not normally known for their aggressive behaviour. Their study highlights the power of combining behavioural experiments with morphometrics in a comparative framework to test predictions on how aggressive behaviour and functional constraint can influence the allometric signatures of traits used during contests and foraging.

In an elegant study evoking memory of the classic Andersson (1982) widowbird tail experiments, Summers and Ord (2022) manipulated the head crest size of land-dwelling blenny fish (*Alticus* sp. *cf. simplicirrus*) to test whether female choice for male ornaments can provide a mechanism for how positive allometry evolves. They found that females showed a preference for males with 'supersized' head crests, providing rare experimental evidence that mate choice can drive the positive allometry of male ornaments. We encourage future studies to use this experimental approach to unravel how mate choice or competition shapes allometry. However, compared to male weapons and ornaments, studies examining coercive traits used to overcome female resistance to mating within an allometric context are rare. LeGrice and Holwell (2022) address this gap in their study of two kelp flies species (*Coelopella curvipes*, *Chaetocoelopa littoralis*), finding sexual dimorphism and positive allometry in the tibia length of both species, suggesting selection on traits relevant to coercive mating systems.

Finally, Juarez and Adams (2022) remind us that sexual dimorphism is not limited to morphological traits. By examining male and female frog jumping performance in an allometric framework, they suggest that natural selection on jumping behaviour is driving these patterns of sexual dimorphism in morphology. Thus, by suggesting that jumping behaviour evolved prior to morphological specialisation, they provide evidence to support the theory that behaviour precludes morphological adaptation (West-Eberhard 1989).

In summary, this special issue aims to draw attention to the importance of allometry in evolutionary ecology and highlights how methodological advances have deepened our understand of the biological mechanisms that underpin the scientific study of scaling and relative growth. We encourage future research to expand our understanding of how and why allometries evolve. Insights on the "how" will come from studies that examine the congruence between the three levels of scaling. More studies across the tree of life and from diverse ecologies will shed light on the "why".

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## Declarations

**Conflict of interest** The authors declare no conflict of interest.

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