Ontogeny of Performance in Vertebrates*

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ABSTRACT

When competing for food or other resources, or when confronted with predators, young animals may be at a disadvantage relative to adults because of their smaller size. Additionally, the ongoing differentiation and growth of tissues and the development of sensory-motor integration during early ontogeny may constrain performance. Because ectothermic vertebrates show different growth regimes and energetic requirements when compared to endothermic vertebrates, differences in the ontogenetic trajectories of performance traits in these two groups might be expected. However, both groups of vertebrates show similar patterns of changes in performance with ontogeny. Evidence for compensation, resulting in relatively high levels of performance in juveniles relative to adults, appears common for traits related to locomotor and defensive behaviors. However, there is little evidence for compensation in traits associated with feeding and foraging. We suggest that this difference may be due to different selective regimes operating on locomotor versus feeding traits. As a result, relatively high levels of locomotor performance in juveniles and relatively high levels of feeding performance in adults are observed across a wide range of vertebrate groups.

Introduction

Young animals often move and forage in the same environment as adults. Consequently, juveniles and adults are faced with the same predators and compete for the same resources (e.g., microhabitats, food, etc.). However, when competing for food or other resources, young animals are likely at a performance and competitive disadvantage because of their smaller absolute size (Hill 1950; Schmidt-Nielsen 1984; Werner and Gilliam 1984; La Barbera 1989). Moreover, the ongoing differentiation of tissues and the development of sensory-motor integration during the early life-history stages may set absolute limits to musculoskeletal performance in juveniles (Ricklefs 1979; Carrier 1996). In addition, because of their small size, young animals are vulnerable to a wider range of predators than adults. Thus, selection on juvenile performance is likely strong (Carrier 1996). To cope with this strong selection pressure, some juvenile mammals have modified the growth trajectories of muscles and bones, allowing them to perform at levels similar to adults (Carrier 1983, 1995; Trillmich et al. 2003). Moreover, the growth trajectories of body parts that must function at birth or hatching differ significantly from those of systems that become functional later in ontogeny (Carrier and Leon 1990). Yet several recent studies examining performance of locomotor and feeding function in juvenile ectotherms did not demonstrate disproportionately rapid growth or relatively high levels of performance at the earliest life-history stages (see, e.g., Irschick 2000; Meyers et al. 2002).

Despite several recent reviews of locomotor and feeding systems in vertebrates (Schwenk 2000; Biewener 2002; Irschick and Garland 2001), the effects of ontogeny on performance have been generally ignored. Yet the rapid growth observed during early ontogeny, and/or discrete ontogenetic transitions as observed in organisms with larval life-history stages (e.g., fish and amphibians), may affect an animal's ability to carry out ecologically relevant functions such as feeding and locomotion. Thus, selection on these early life-history stages may be crucial in determining the adult phenotype (Carrier 1996). In this review, we explore whether different ontogenetic trajectories are present among different vertebrate groups and/or in different functional systems and, if different trajectories are present, why this might be the case. Moreover, we attempt to demonstrate that studies investigating the ontogeny of performance are critical to our understanding of the evolution of functional traits. To this end, we review the available literature and compare performance in ecto- and endothermic verte-

brates, as well as in different functional systems that must operate throughout ontogeny (i.e., locomotor and feeding systems).

We hope that this review and the accompanying articles demonstrate that the study of ontogenetic changes in performance and the underlying growth of morphological structures may offer novel insights into the origins of diversity in functional systems in vertebrates. Moreover, we hope that this collection of articles will stimulate future researchers to assess critically the ideas presented here.

Ontogeny of Locomotor Performance

Studies of locomotor performance provide some of the best examples of compensation at juvenile life-history stages (see Carrier 1996). For example, juvenile jackrabbits are able to generate similar takeoff velocities and higher takeoff accelerations when compared to much larger adults (Carrier 1995, 1996). At first glance this appears unsurprising, as muscle shortening velocity generally decreases with increasing body dimensions in both mammals (Rome et al. 1990) and ectotherms such as sharks, fish, and frogs (Curtin and Woledge 1988; Altringham et al. 1996; James et al. 1998). However, as juveniles are small in absolute terms, and as performance is likely constrained by the rapid differentiation of tissues during early ontogeny and the maturation of sensory-motor systems, lower absolute levels of performance are expected. Interestingly, an analysis of the growth patterns of the musculoskeletal system in jackrabbits demonstrated distinct growth allometries in key functional traits (e.g., moment arms) that allow juveniles to perform at levels comparable to adults even in absolute terms (Carrier 1983; Carrier and Leon 1990). This appears to be a general trend in mammals (Carrier 1996; Trillmich et al. 2003).

The large body of literature on fast escape performance in fish (e.g., James and Johnston 1998; Hale 1999; Wakeling et al. 1999; Wesp and Gibb 2003; also reviewed in Domenici and Blake 1997) and aquatic salamanders (e.g., D'Août and Aerts 1999; Azizi and Landberg 2002) generally shows that near maximal performance levels are reached early in ontogeny, as has been observed for mammals (see also Gibb et al. 2006, in this issue). Although absolute levels of performance, such as peak velocity, continue to increase with body size as these animals grow, relative levels of performance (e.g., expressed in body lengths s^{-1}) are often highest in juveniles (James and Johnston 1998; D'Août and Aerts 1999). The formation of adult locomotor morphology during ontogeny ensures a rapid increase in performance early in the life history of aquatic vertebrates, after which relative performance levels decrease with size (Hale 1999; Gibb et al. 2006). However, acceleration performance, potentially the most relevant performance parameter in a predator-prey context, is often independent of body dimensions in fish (Webb 1976; Domenici and Blake 1993; Hale 1999; but see Wakeling et al. 1999; Wesp and Gibb 2003; Gibb et al. 2006).

For terrestrial ectotherms, patterns of change in locomotor performance throughout ontogeny appear less uniform. Whereas compensation has never been demonstrated for some performance traits, such as endurance (Garland 1984; Jayne and Bennett 1990), for other traits, such as sprint speed or acceleration capacity, juveniles show full compensation or rapid increases to near-adult levels of performance at small sizes (Garland 1985; Marsh 1988; Toro et al. 2003). However, in some species of lizard, juveniles still demonstrate markedly lower levels of sprint performance when compared to adults (Irschick 2000; Irschick et al. 2000). Interestingly, data on sprint speeds collected under natural conditions show that in these circumstances juveniles typically run more closely to their maximal levels than do adults, which suggests a form of behavioral compensation for their lower absolute levels of performance (Irschick 2000). Thus, lower absolute levels of performance might lead to alternative behavioral strategies when adults and juveniles confront predators (Irschick 2000) or compete for resources (Irschick and Lailvaux 2006, in this issue).

However, sprint speed may not be the most relevant performance trait to examine. For example, data on both frog and lizard jumping elegantly demonstrate that although acceleration capacity was generally invariant with body dimensions (Emerson 1978; Toro et al. 2003), jump distance was typically greater in larger individuals (Emerson 1978; Toro et al. 2003; but see Wilson et al. 2000). Because removing yourself from the immediate vicinity of the predator is likely more important than how far you can jump, this suggests that the aspects of locomotor performance most directly acted on by selection may be size invariant (see also Emerson 1978). Studies that have examined the morphological basis for the observed differences in performance have shown allometric changes in limb dimensions and muscle physiology that allow young individuals to reach comparable levels of performance to adults (see Marsh 1988 for a nice example). These allometric changes are similar to those observed for mammals (Carrier 1983, 1996). In general, it appears that the ontogeny of locomotor performance is under strong selection for high levels of juvenile performance, with systems apparently tuned to the ecological demands imposed on them (see also Main and Biewener 2006, in this issue).

Future studies investigating multiple performance traits (e.g., sprint speed, endurance, acceleration capacity) in both laboratory and field settings may shed further light on the apparent lack of physiological compensation in juveniles of some groups, such as lizards. Although behavioral and ecological compensation may be valid alternative strategies for these groups, this idea must be investigated further. Despite the apparent generality of the patterns discussed above, it should be noted that the actual number of studies investigating performance traits throughout ontogeny is still quite small. The majority of groups are vastly underrepresented, and few performance traits have been examined. Studies examining the ontogeny of complex performance traits, such as maneuverability, may be especially

insightful because this trait is likely constrained by the maturation of sensory-motor systems and their integration during ontogeny. Thus, compensation for some traits may be impossible and will likely lead to behavioral compensation instead.

Ontogeny of Feeding Performance

Although relatively few studies have examined the ontogeny of locomotor performance in ectotherms, even fewer have examined the ontogeny of feeding performance. Only one area of feeding performance has received much attention to date: there are many studies examining the ontogeny of bite force, and data are available for a wide range of taxa (see, e.g., Hernandez and Motta 1997; Herrel et al. 1999, 2005; Binder and Van Valkenburg 2000; Meyers et al. 2002; Erickson et al. 2003; Thompson et al. 2003; Herrel and O'Reilly 2006, in this issue). Bite forces have been demonstrated to be ecologically relevant (because they correlate with diet and handling time; see Hernandez and Motta 1997; Verwaijen et al. 2002; Van der Meij 2004), making them a good model to examine the ontogeny of performance in vertebrates. Unexpectedly, all data available at present, including data for mammals (Binder and Van Valkenburg 2000; Thompson et al. 2003), lizards (Herrel et al. 1999; Meyers et al. 2002), alligators (Erickson et al. 2003), turtles (Herrel and O'Reilly 2006), birds (Herrel et al. 2005), and fish (Hernandez and Motta 1997) show a similar pattern of significant positive allometry of bite force relative to body and head dimensions. This suggests that juveniles do not (or cannot) compensate for their lower absolute levels of performance but, rather to the contrary, that relative performance levels are highest in larger individuals (but see Herrel and O'Reilly 2006 for a possible exception). Moreover, data on muscle masses suggest that a distinct hypertrophy of the jaw muscles (i.e., positive allometry) occurs during ontogeny; this could, at least in part, explain observed changes in bite force (Anapol and Herring 1989; Grubich 2003).

However, bite force is only one of a suite of potentially relevant performance traits associated with the feeding system. Although data on other performance traits are rare and often restricted to single groups of organisms (e.g., suction performance), they generally suggest a similar pattern to that observed for bite forces. Jaw opening and closing velocities, for example, tend to increase with size in both fish (Richard and Wainwright 1995; Hernandez 2000) and lizards (Meyers et al. 2002), indicating that larger individuals open and close their jaws faster, which implies that larger individuals are better at capturing more mobile or elusive prey than are juveniles. For aquatic organisms more specifically, suction generation ability also tends to increase with increasing size in both sharks (Tanaka 1973; Robinson and Motta 2002) and catfish (Van Wassenbergh et al. 2006, in this issue). These ontogenetic changes in suction performance may in turn result in ontogenetic changes in diet (Hjelm et al. 2000, 2003; Svanbäck and Eklöv 2002). Also, in many terrestrial systems, ontogenetic changes in diet occur that appear to correlate with distinct changes in performance across ontogeny (Ballinger et al. 1977; Capel-Williams and Pratten 1978; De Marco et al. 1985; Paulissen 1987; see Werner and Gilliam 1984 for an overview of changes in prey size throughout ontogeny). However, more data on a variety of different aspects of feeding performance, such as handling times, energetic costs, and prey capture success, are necessary to assess the ecological relevance of ontogenetic changes in performance traits such as bite force and jaw velocity.

Other Performance Traits

Although data for traits other than those related to locomotor or feeding systems are scarce, the article by Moon and Tullis (2006) included in this issue provides unique insights into the ontogeny of the physiological capacity of an antipredatory system: the rattlesnake rattle. The pattern that emerges from their data is similar to that observed for the ontogeny of locomotor performance: physiological capacity in the smallest individuals rapidly increases to adult levels and then remains largely constant, or even decreases slightly, despite a further fivefold increase in body mass. Presumably, strong selection on the ability to produce sound effectively to deter potential predators has resulted in this rapid initial increase in performance during the earliest ontogenetic stages.

Conclusions

Whereas ectothermic and endothermic vertebrates show similar patterns of changes in performance throughout ontogeny despite their different growth regimes and energetic requirements, very different patterns apparently emerge when locomotor and feeding systems are compared. Whereas evidence for compensation resulting in high levels of performance in juveniles relative to adults is prominent for traits related to locomotor and defensive behaviors, little support for compensation is found when examining traits associated with feeding and foraging behavior. For locomotor systems, it appears that juveniles compensate for those traits most directly relevant to their escape ability. For example, when considering acceleration capacity (i.e., the ability of an individual to get away from a predator quickly), juveniles generally show levels of performance similar to those of adults. Strong selection on the ability of an individual to survive to a reproductive age is likely present and may be responsible for the observed performance compensation. As this often goes hand in hand with modification of growth trajectories, selection on the juvenile life-history stage will also affect the adult phenotype. Thus, when examining the evolution of adult phenotypes, it is important to keep in mind that selection may have operated strongly on juvenile life-history stages as well. Consequently, the adult morphology may potentially not reflect current selection regime but rather may be a reflection of the ghost of "selection past." Although this

has been stated repeatedly in literature (e.g., Ricklefs 1979; Werner and Gilliam 1984; Carrier 1996), it is often ignored in comparative evolutionary studies.

Why don't most vertebrates demonstrate compensation for traits related to feeding performance? A priori theoretical arguments suggest that an increase in performance traits, such as bite force or jaw closing velocity, would enable juveniles to access a larger proportion of the available prey spectrum. For example, as handling times increase exponentially with prey size and/or hardness (Paulissen 1987; DeMarco et al. 1985; Pough et al. 1997; Verwaijen et al. 2002), an increase in bite force would make larger or harder prey energetically interesting for smaller lizards. However, when examining literature data on prey availability, it becomes clear that small prey are disproportionately abundant in the environment (see, e.g., Schoener 1968; Lister 1981; Paulissen 1987; A. Herrel, personal observation). Large prey are thus relatively rare in the environment but profitable for adults because small prey are expensive to obtain and process and result in a lower net energy gain for large animals (Hoyle and Keast 1987). Thus, both selection and scaling favor better performance in large individuals (adults) rather than smaller individuals (juveniles).

Further studies investigating the ontogeny of performance from ecological, behavioral, and functional perspectives are badly needed to understand better the selection regime imposed on juvenile life-history stages. Additionally, quantifying performance levels for systems with discrete ontogenetic stages (e.g., fish, amphibians) or for complex performance traits such as maneuverability are likely to bring novel insights into the role of differentiation and growth of tissues and the maturation of sensory-motor systems on performance. We hope that this review and the other articles in this special collection will be a first step toward a better understanding of the role of juvenile life-history stages in the evolution of adult phenotypes.

Acknowledgments

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