

The integration of locomotion and prey capture in vertebrates: Morphology, behavior, and performance

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Synopsis For most vertebrates, locomotion is a fundamental component of prey capture. Despite this ubiquitous link, few studies have quantified the integration of these complex systems. Several variables related to locomotor performance, including maximum speed, acceleration, deceleration, maneuverability, accuracy, and approach stability, likely influence feeding performance in vertebrates. The relative importance of these measures of performance, however, depends on the ecology of the predator. While factors such as morphology and physiology likely define the limits of these variables, other factors such as motivation of the predator, prey type, and habitat structure can also influence performance. Understanding how these variables relate to feeding under a given suite of ecological conditions is central to understanding predator–prey interactions, and ultimately how locomotion and feeding have co-evolved. The goals of this article are to discuss several variables of locomotor performance related to prey capture, present new data on the relationship between locomotor and feeding morphology in fishes, discuss the evolution of prey capture in cichlid fishes, and outline some future directions for research. While suction feeding is a primary mechanism of prey capture in fishes, swimming is vital for accurately positioning the mouth relative to the prey item. Many fishes decelerate during prey capture using their body and fins, but the pectoral fins have a dominant role in maintaining approach stability. This suggests that fishes employing high-performance suction feeding (relatively small mouth) will have larger pectoral fins to facilitate accurate and stable feeding. I provide new data on the relationship between pectoral fin morphology and maximum gape in centrarchid fishes. For seven species, pectoral fin area was significantly, and negatively, correlated with maximum gape. This example illustrates that the demands from one complex system (feeding) can influence another complex system (locomotion). Future studies that examine the morphological, physiological, and functional evolution of locomotion involved in prey capture by aquatic and terrestrial vertebrates will provide insight into the origin and consequences of diversity.

Introduction

Locomotion is highly integrated with prey capture in vertebrates, including diverse groups such as fishes (e.g., Nyberg 1971; Wainwright et al. 2001; Higham et al. 2005a, 2005b, 2006a, 2007; Rice and Westneat 2005; Higham 2007), snakes (e.g., Alfaro 2003), turtles (e.g., Rivera et al. 2006), amphibians (e.g., Hoff et al. 1985; Dean 2003), lizards (e.g., Irschick and Losos 1998; Cooper Jr and Whiting 2000; Cooper Jr 2006), birds (e.g., Shiffman and Eilam 2004) and mammals (e.g., Altenbach 1989; Dunbar and Badam 2000; Domenici 2001). The idea that locomotion and feeding are linked has been considered for quite some time, although studies have focused primarily on the relationships between locomotor morphology and feeding ecology (Keast and Webb 1966) or foraging behavior (Webb 1984b; Webb and Gerstner 2000; Jastrebski and Robinson 2004; Parsons and

Robinson 2007). Although the function of each system has been studied extensively, and continues to garner interest from many disciplines including engineering, physiology, and functional morphology, few experimental studies have addressed how locomotor performance and morphology are related to feeding performance. With a large body of information in place, we can now start constructing predictions about how these complex systems are integrated, and propose new areas of research that may illuminate how these systems have co-evolved in vertebrates. We can then begin to identify common features of the locomotor system that aid in particular strategies of prey capture across diverse groups of vertebrates.

Successful prey capture is facilitated by several factors related to the locomotor system including, but not limited to, maximum locomotor speed, acceleration (Harper and Blake 1990, 1991), deceleration

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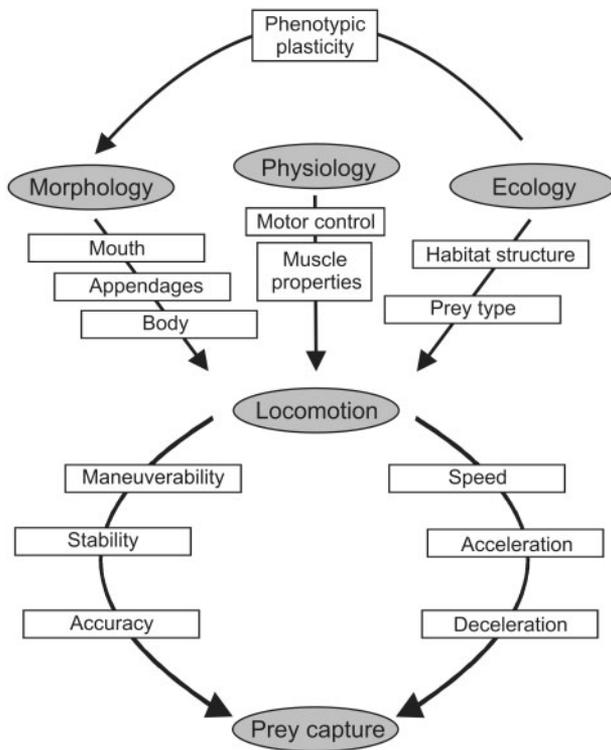


Fig. 1 A schematic highlighting the integration of locomotion and prey capture in vertebrates. Morphology, physiology, and ecology can all influence locomotor performance/behavior. A variety of locomotor structures can be involved in prey capture such as the body, fins and limbs. In addition, characteristics of other structures can also be integrated with the locomotor system. For example, an increase in mouth size in fishes is correlated with an increase in swimming speed during prey capture. Locomotor performance of the predator can be characterized in a number of ways, including speed, acceleration, deceleration, accuracy, stability, and maneuverability. However, the relative importance of these variables, and which combination of variables enhances prey capture, depends strongly on the ecology of the predator and prey. Many vertebrates exhibit flexibility in morphology depending on ecological characteristics (phenotypic plasticity).

(Higham 2007), maneuverability (Domenici 2001), accuracy (Higham et al. 2006a), and approach stability (Fig. 1). In addition, postural behavior is important for arboreal vertebrates including many primate species, for which the acquisition of food occurs primarily in complex three-dimensional habitats (Bergeson 1998). The most commonly examined measure of performance, and arguably most vital, is the ability of a predator to accelerate and attain a high velocity of locomotion during a predator–prey interaction (Webb 1976; Webb and Skadsen 1980; Rand and Lauder 1981; Webb 1984a, 1984b; Domenici and Blake 1997; Hale 1999; Webb and Gerstner 2000; Walker et al. 2005). This limits the time the prey has to escape, increasing

the chances of successful prey capture. Successful prey capture, however, is unlikely to occur if acceleration is maximized in the absence of other variables related to performance such as strike accuracy. The relative importance of the measures of performance outlined above, and which combination of variables will maximize the success of capture, depends largely on the ecology of the predator and prey (Webb and Gerstner 2000). For example, predators that capture highly evasive prey typically utilize high-performance acceleration to minimize the time the prey has to escape. Thus, those predators feeding on evasive prey likely exhibit adaptations for high-performance acceleration.

Identifying commonalities and constraints that persist across diverse groups of vertebrates that utilize their locomotor system during prey capture is fundamental to understanding the origins and consequences of morphological and behavioral diversity, and ultimately the evolution of predator–prey interactions. The goals of this study are to discuss measures of locomotor performance that are important for prey capture in most vertebrates, discuss the importance of prey movements during prey capture, and discuss the roles of morphological and behavioral diversity in prey capture. In addition, I will discuss the evolutionary relationships between locomotion and feeding, and present new data regarding the relationships between locomotor and feeding morphology in centrarchid fishes.

Locomotor performance and prey capture

Measures of locomotor performance are vital for understanding the link between feeding and locomotion. As with other measures of performance, it is important to understand the context of the behavior in order to interpret the level of performance (Irschick 2003). For example, maximum acceleration is likely different during an escape than during a predatory strike. In addition, measuring performance in the laboratory may give results that differ considerably from results in the animal's natural habitat. Maximum performance is often measured as an average of several trials, which will result in the inclusion of sub-maximal trials and will ultimately lead to a lower estimate of maximum performance. This is problematic given that maximum performance represents the maximum capacity to execute a certain behavior (Losos et al. 2002). Thus, using a single maximum value (or a very small number) as an indication of maximum performance is

recommended (e.g., Losos et al. 2002; DeVries and Wainwright 2006; Higham et al. 2006a). It is also important to conduct enough trials in order to accurately estimate maximum performance (Losos et al. 2002).

Measuring multiple variables related to locomotor performance is important for understanding how multiple behaviors are integrated, and might also highlight potential trade-offs between different behaviors. Swimming speed and accuracy have been identified as conflicting behaviors, but some variables likely work in concert as a passive result of morphology. For example, an increased ability to decelerate is likely accompanied by increased maneuverability in fishes due to the use of common structures (pectoral fins). Furthermore, some measures of performance in fishes can likely change independently of others given the many-to-one mapping of form to function (Alfaro et al. 2005; Wainwright et al. 2005). This redundancy potentially enables some fins to be optimized for one behavior while other fins are optimized for a different behavior.

Speed

The speed of a predator during prey capture will have many consequences for the outcome of a feeding event. For example, most felids and canids run at high speeds in order to overtake prey (Murray et al. 1995). Swimming (ram) speed in fishes is vital for overtaking evasive prey items, and can vary considerably among and within species (Norton 1991; Norton and Brainerd 1993; Wilga and Motta 1998; Motta and Wilga 2001; Wainwright et al. 2001; Waltzek and Wainwright 2003; Higham et al. 2006a, 2007). The forward movement during prey capture has the potential to influence several characteristics of the suction-generated flow. Higham et al. (2005a; 2006a) examined the interactions between swimming speed and suction generation in bluegill sunfish and largemouth bass. Interestingly, at relatively slow swimming speeds, bluegill do not suffer a decrement in suction performance. However, as attack speed increases the shape of the ingested volume of water is stretched in the plane of the long axis of the fish in both bluegill and largemouth bass. Fishes that feed on highly evasive prey seem to employ a different tactic than species relying on high-performance suction feeding. Fish that feed on evasive prey tend to have larger mouths (e.g. Norton 1991) and thus ingest a much larger volume of water during feeding (Higham et al. 2006a). This increased volume relieves the constraints imposed by accuracy

and allows these fish to swim at high speeds during prey capture, which is necessary for capturing evasive prey. This dichotomy in feeding modes likely results in different locomotor adaptations, and may be an important source of morphological diversity among fishes.

Acceleration

Accelerating is a vital component of prey capture for many predatory species of vertebrates, especially those feeding on evasive prey. Webb and Skadsen (1980) noted that piscivorous fishes should employ maximal acceleration during prey capture, which will minimize both prey movement away from the strike path and the time for the predator to reach the prey. In addition, larger prey items (apparent rather than actual size) elicit increased acceleration performance in fishes (Harper and Blake 1991), which is likely associated with the fact that larger prey items tend to have a greater ability to accelerate. The kinematics of predatory accelerations of fishes during prey capture has received considerable attention, revealing that fishes typically assume an S-shape (Hoogland et al. 1956; Webb and Skadsen 1980; Rand and Lauder 1981; Harper and Blake 1990, 1991; Domenici and Blake 1997; Schriefer and Hale 2004), but can also assume a C-shape (Wöhl and Schuster 2007), which is common during escape maneuvers. S-starts have been subdivided depending on how long the S-shape is maintained (Webb and Skadsen 1980), the acceleration profile of the movement and the number of tail strokes following the S-shape prior to prey capture (Harper and Blake 1991). Interestingly, the S-shape can also be assumed during a startle response (Schriefer and Hale 2004). Understanding how predators accelerate towards a prey item is necessary for understanding predator-prey interactions.

Factors limiting acceleration during a predator-prey encounter could be the ability to stop (Higham et al. 2005b) and the need for accuracy. An increased acceleration will require an increased deceleration if the distance between the predator and prey is relatively short. Not stopping in time could result in a collision and potentially injury. In addition, maximal acceleration might preclude an accurate strike by limiting the time the predator has to adjust its position relative to the prey item. Ultimately, a balance must be struck between getting to the prey before it can escape and accurately striking at the prey. Given these constraints, the maximum acceleration performance of an animal, which typically occurs when escaping from a predator, does not

necessarily reflect the magnitude of acceleration that an animal might employ during prey capture. An exception is the archer fish, which exhibits comparable magnitudes of acceleration when escaping from a predator and when capturing prey (Wöhl and Schuster 2007). The archer fish is able to maximize acceleration during prey capture because the ultimate trajectory of the prey item can be determined by the predator prior to the strike. Studies that measure an animal's maximum capacity to accelerate, and then measure acceleration during a predatory strike, such as in Wöhl and Schuster (2007), will enable one to determine under what ecological conditions an animal exhibits maximum performance.

Deceleration

Braking is important for a number of vertebrate behaviors including intermittent locomotion (Higham et al. 2001), avoiding obstacles in an environment, arriving predictably at a given location (Higham et al. 2005b), and during prey capture (Webb 1984a; Higham et al. 2005b; Higham 2007). To brake, fishes commonly protract and extend their pectoral, caudal and median fins in order to increase drag (Harris 1937; Geerlink 1987; Jayne et al. 1996; Drucker and Lauder 2002, 2003, Higham et al. 2005b; Rice and Westneat 2005; Higham 2007). For example, fishes protract and abduct their pectoral fins in order to brake during prey capture (Drucker and Lauder 2002; Higham et al. 2005b; Rice and Westneat 2005; Higham 2007). Acanthomorph fishes, such as bluegill sunfish, have pectoral fins that are located close to the fish's center of mass, suggesting they are more effective for maintaining stability during braking (Drucker and Lauder 2002). Furthermore, the pectoral fins act as a pair and thus reduce the likelihood of slip and yaw (Drucker and Lauder 2000; Webb 2006). Given the importance of braking for fishes that must capture prey very accurately, there may be a significant selective pressure for large pectoral fins that maximize stability and drag. However, few studies have examined the relationships between fin morphology and feeding behavior (Higham 2007).

For other aquatic vertebrates, such as amphibians, limb protraction can increase the frontal area of the body and help the animal decelerate (Hoff et al. 1985; Dean 2003). For example, Dean (2003) found that pipid frogs (*Hymenochirus boettgeri*) first protracted their forelimbs during prey capture, and then protracted their hind limbs. The coordination of fins and limbs during prey capture is not fully understood, and future work will enable us

to better understand how animals decelerate and maintain stability during prey capture.

Maneuverability

Turning maneuvers can be extremely important during predator-prey interactions in order to chase evasive prey (Domenici 2001; Rossel et al. 2002; Wöhl and Schuster 2006, 2007). Because maneuvering locomotion is relatively difficult to quantify, we are only starting to understand the mechanisms of turning. Aquatic turtles, for example, execute forward turns during prey capture by holding the forelimb on the inside of the turn stationary in a protracted position to increase drag (Rivera et al. 2006). To turn, fishes employ asymmetrical fin movements and forces that differ considerably from that during steady swimming (Gerstner 1999; Budick and O'Malley 2000; Walker 2000; Drucker and Lauder 2001; Lauder and Drucker 2004). It is expected that turning maneuvers during prey capture would be executed in a similar fashion. This mechanism of generating a yawing movement is in contrast with terrestrial vertebrates that must impart a force on the ground in order to turn. In a complex arboreal habitat that has discontinuous substrate, animals often incorporate jumping into a turn (Higham et al. 2001), which might also be employed during a predator-prey encounter. The prevalence, and role, of these behaviors during prey capture, however, has not been thoroughly explored.

It is clear that the locomotor system can strongly influence feeding performance, but in some cases the feeding system can influence locomotor performance. For example, an increase in the depth of the body of fishes increases maneuverability (Walker 2004; Collar and Wainwright 2006). Suction feeding involves a rapid expansion of the mouth cavity, which is driven in part by the recruitment of the epaxial muscle mass (Carroll and Wainwright 2006). Increased suction feeding performance is associated with an increased moment arm and cross-sectional area of the epaxial muscle mass (Carroll et al. 2004), which ultimately leads to an increase in body depth. Thus, an increase in suction feeding performance may be associated with an increase in maneuverability. Future studies that elucidate ways that feeding morphology can influence locomotion will enhance our understanding of interactions between these complex systems.

Accuracy and approach stability

Strike accuracy is an often overlooked aspect of feeding performance, and this attribute is strongly

influenced by the locomotor system. For example, an increase in swimming speed in fishes results in a decrease in strike accuracy (Webb and Skadsen 1980; Higham et al. 2006a). This decrease in accuracy can likely be attributed to predator error rather than prey movements (Nyberg 1971; Webb and Skadsen 1980). However, prey movements can also alter the success rate of prey capture (Norton 1991; Shiffman and Eilam 2004). Accuracy of vertebrate strikes can be defined as the number of successful feeding attempts relative to the number of unsuccessful attempts (Nyberg 1971; Webb and Skadsen 1980; Drost 1987; Norton 1991; McLaughlin et al. 2000; Shiffman and Eilam 2004), but accuracy can also be measured among successful strikes by relating the location of the prey to the location of the predator's mouth (Drost 1987; Coughlin 1991; Higham et al. 2006a).

A stable animal is one that resists forces that tend to result in a change of motion. I am calling a stable approach one that resists changes in the overall trajectory of the predator during a feeding event. In this case, the posture of the predator need not be constant, only the overall trajectory of the body. This differs considerably from the stability required when an arboreal predator, such as a primate, maintains a certain posture during prey capture by clinging to a branch or tree trunk. In this case, it is the posture of the animal that is of the utmost importance. For animals that slow down during a strike, such as centrarchid fishes (Drucker and Lauder 2002; Higham et al. 2005b; Higham 2007), the pectoral fins can act as brakes and they also prevent yawing movements (Higham 2007), ultimately helping to maintain approach stability. Fishes can alleviate the need to maintain a stable approach by ingesting a relatively large volume of water during a strike. This is likely important for a fish that swims fast during prey capture because the predator will have less time to accurately position its body relative to the prey.

Morphological and behavioral plasticity

Vertebrates commonly exhibit a plastic phenotypic response to ecological parameters, thus optimizing fitness for a given suite of conditions (e.g., Bronmark and Miner 1992; Robinson and Wilson 1996; Robinson and Parsons 2002; Jastrebski and Robinson 2004; Langerhans et al. 2004; Parsons and Robinson 2007). For example, pumpkinseed sunfish raised on different diets will exhibit divergent body forms that improve feeding performance for a particular prey type (Parsons and Robinson 2007).

Mouth size was larger in sunfish raised on a littoral diet (amphipods) compared with sunfish raised on a pelagic-like diet (daphnia). In addition to the plasticity in mouth and body form, the shape of the paired fins can also exhibit a plastic response to varying ecological conditions (e.g., Lavin and McPhail 1986; Robinson et al. 1993; Robinson and Wilson 1995; Proulx and Magnan 2004). Given the relationship found between pectoral fin area and mouth size in centrarchids (see subsequent text), it is expected that pectoral fin morphology will vary in parallel with mouth size. Terrestrial vertebrates can also exhibit morphological plasticity depending on ecological conditions. For example, *Anolis* lizards raised in terraria with only broad surfaces exhibited longer limbs than those raised with only narrow surfaces (Losos et al. 2000). Given this plasticity, other ecological factors, such as prey type, could influence the morphology of the locomotor system in these lizards. Continuing efforts to elucidate the plasticity in locomotor and feeding morphology with changes in ecological conditions will provide important information regarding the demands of prey capture.

The motivation of a predator has a strong influence on locomotor performance during prey capture. For example, fishes exhibit much higher swimming speeds when feeding on relatively evasive prey compared with nonevasive prey (Nemeth 1997; Wainwright et al. 2001). This increased swimming speed will decrease the overall closing time between the predator and prey, which will ultimately decrease the time that the prey has to escape. Snakes also modulate their behavior during prey capture depending on the type of prey (e.g., Mehta 2003). For example, *Elaphe quadrivirgata* captured smaller frogs by seizing and swallowing them, whereas larger frogs were first constricted and then consumed (Mori 1991). In another study, *E. helena* captured smaller prey by simply seizing them, whereas larger prey were captured using pinion and constriction behaviors (Mehta 2003). These examples of plasticity in behavior highlight how the predator can match its energy expenditure with the type, size, or behavior of the prey. Are some species more plastic than others? One possibility is that species that exhibit a greater diversity in diet will have an increased flexibility with regards to prey capture behavior. For example, within the family Centrarchidae, fish species from the genus *Lepomis* eat a greater diversity of prey items than species from the genus *Micropterus* (Collar et al. 2005). Whether this greater diversity exhibited by *Lepomis* species is accompanied

by a greater flexibility in locomotor behavior during prey capture requires further investigation.

Locomotor behavior during prey capture is intimately associated with the structure of the habitat (e.g., Robinson and Holmes 1982; Savino and Stein 1982, 1989; Anderson 1984; Priyadarshana et al. 2001). For example, the planktivorous fish, *Pseudorasbora parva*, exhibits slower swimming speeds during feeding in complex habitats compared with open water feeding (Priyadarshana et al. 2001). Prey capture kinematics in fishes can also vary depending on whether the fishes are feeding in open water or from substrate (Nyberg 1971; Rand and Lauder 1981). For example, largemouth bass, *Micropterus salmoides*, exhibit a reduction in approach speed when capturing prey from substrate compared with capturing prey in open water (Nyberg 1971). The locomotor behavior of birds during prey capture is also constrained by the structure of the habitat (Robinson and Holmes 1982; Whelan 2001). Passerine birds that forage in highly-structured habitats exhibit a reduced number of searching modes compared with species foraging in more open habitats (Robinson and Holmes 1982). In addition, insectivorous birds exhibit different strike behaviors when feeding in different species of trees and different locations within a tree (Whelan 2001). Ultimately, behavioral plasticity can arise from several factors, which highlights the importance of incorporating ecological variables when assessing the performance capacity of a predator during feeding.

In addition to phenotypic plasticity, there are strong differences in locomotor morphology among incipient species, such as three-spined sticklebacks from Paxton Lake, British Columbia, Canada (Law and Blake 1996; Blake et al. 2005). These two species occupy different regions of the lake, including one that occupies the benthic region and one that occupies the limnetic region. The former feeds primarily on insect larvae whereas the latter feeds primarily on zooplankton. Although morphologically different, both species exhibited comparable levels of acceleration performance (Law and Blake 1996). However, this is during an escape rather than during prey capture. Future studies that examine the prey capture behavior in these two closely-related species may provide insight into the differences in morphology.

Morphological structures involved in prey capture

A variety of morphological structures can be important during prey capture, including the mouth, body

and limbs. Most aquatic and aerial vertebrates utilize their mouth to capture prey (e.g., Yanega and Rubega 2004; Higham 2007). For vertebrates that fly or swim during prey capture, several situations are enhanced by a larger mouth, such as ram feeding (e.g., Higham et al. 2006a). Terrestrial and aerial vertebrates, on the other hand, commonly use structures in addition to their mouths including their body and/or limbs (Gonyea and Ashworth 1975). Bats and birds can use their feet to capture prey during flying (Altenbach 1989). With the exception of the cheetah (Russell and Bryant 2001), most large felids utilize their forepaws for capturing prey (Gonyea and Ashworth 1975). Many primates, such as lorises (Nekaris 2005) and galagos (Bishop 1962), use their forelimbs to capture prey in arboreal environments by thrusting their hands out to capture insects. Snakes, on the other hand, typically capture prey first using their mouths and then their body to constrict or manipulate prey (Greenwald 1978; Jayne et al. 2002; Jackson et al. 2004). The use of the body may be common among elongate vertebrates, such as snakes and eels (Miller 1989). Ultimately, the structures employed during prey capture will be an important factor in determining the relationships between locomotor morphology and feeding. Perhaps those animals that use multiple body parts to capture prey will be less constrained in terms of morphology given the redundancy. However, it is also clear that selection for one functional system can influence another system. For example, cheetahs are adapted for cursorial locomotion, and this has likely precluded the use of retractable claws for capturing prey (Russell and Bryant 2001). Future studies that examine common features among different vertebrate groups that utilize the same body parts for prey capture will provide insight into convergent traits that facilitate prey capture.

A large amount of research has been devoted to postural behavior during feeding in the Order Primates (e.g., Bergeson 1998; Nekaris and Rasmussen 2003; Nekaris 2005), and these studies often identify the appendage that is attached to the substrate during prey capture. In addition to the hands and feet, the prehensile tail of many species provides a strong point of attachment while capturing prey (German 1982; Meldrum 1998; Garber and Rehg 1999; Dunbar and Badam 2000).

Case study: Pectoral fin area and mouth size in centrarchid fishes

As mentioned above, the pectoral fins of acanthomorph fishes are optimal brakes during prey capture given that the reaction force goes through the center

of mass of the fish (Drucker and Lauder 2002), limiting unstable body movements. Given the importance of braking for fishes that must capture prey accurately, there may be a significant selection pressure for large pectoral fins that maximize stability and drag. To test the hypothesis that species of fishes with smaller mouths (increased suction generating capacity) have larger pectoral fins (Fig. 2), I quantified pectoral fin area and maximum vertical gape in seven species of centrarchid fishes, including four different genera (*Lepomis*, *Micropterus*, *Eneacanthus*, and *Centrarchus*). From freshly euthanized specimens, I extracted the pectoral fin from one side of the fish and pinned it to a Styrofoam block as in Higham (2007). Each fin was brushed with formalin for preservation. With a ruler in the field of view, pictures were taken of each pectoral fin using a Kodak EasyShare CX7430 digital camera (1728 × 2304 pixels). The digital images were then imported into ImageJ version 1.33 (NIH, Washington, DC, USA) and the area of each fin was calculated. I also measured body mass and maximum vertical gape distance of each specimen. To account for differences in body size, I first log transformed body mass, pectoral fin area, and maximum gape. I then calculated the residuals of fin area and body mass, and gape and body mass,

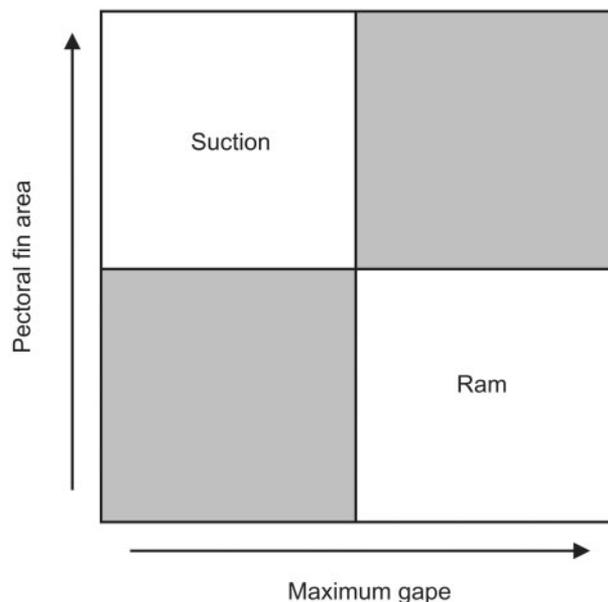


Fig. 2 A schematic showing the hypothesized relationship between pectoral fin area and maximum gape in fishes. High-performance suction feeders are expected to have small mouths and large pectoral fins. In contrast, ram feeding fishes are expected to have large mouths and small pectoral fins. See text for a discussion.

using a least squares regression. I then used a reduced major axis (RMA) regression to determine the relationship between the residuals.

Fish with smaller mouths exhibit significantly larger pectoral fins ($r^2=0.46$; $P=0.006$). This is most pronounced for largemouth bass (Fig. 3) on one end (large mouth and small fins) and bluegill on the other end (small mouth and large fins), with the other species of centrarchids falling in between. Interestingly, bluegill are able to generate the greatest suction pressures among centrarchids (Carroll et al. 2004; Higham et al. 2006b), which is related to the ability to generate a suction induced flow. It is important to note that these results do not include all of the species of centrarchids, and a more complete analysis controlling for phylogenetic non-independence is required. Nonetheless, this relationship may be widespread among fishes and indicates that there might be a strong selection pressure for having large pectoral fins that could stabilize the body during suction feeding. Species that swim fast during prey capture, and have a larger mouth, might benefit from having smaller fins due to the reduced need for muscle force for fin protraction (Higham 2007). Thus, efficiency could be maximized for suction- and ram-feeders. If pectoral fin area does indeed enhance accuracy in high-performance

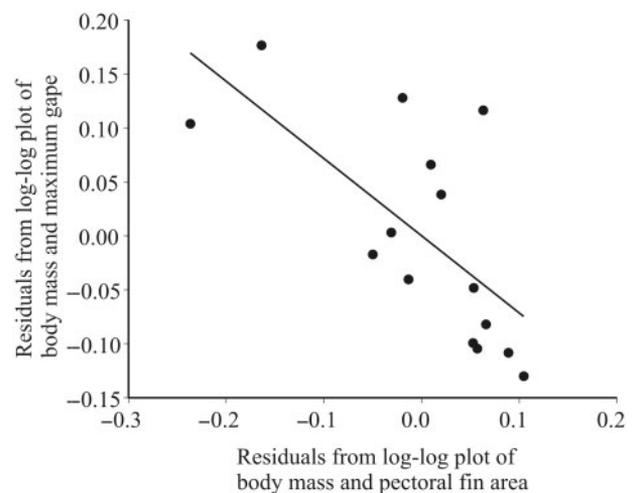


Fig. 3 The relationship between maximum gape and pectoral fin area for seven species of centrarchid fishes. An increase in maximum gape resulted in a significant decrease in pectoral fin area ($r^2=0.46$; $P=0.006$). Note that the effects of body size (mass) were removed from each variable by using the residuals of a least squares regression performed on the log-transformed variable and mass, which was also log-transformed. The species shown in the graph include *Centrarchus macrochirus* ($n=2$), *Eneacanthus chaetodon* ($n=2$), *Lepomis macrochirus* ($n=3$), *Lepomis gulosus* ($n=2$), *Lepomis marginatus* ($n=2$), *Lepomis cyanellus* ($n=2$), and *Micropterus salmoides* ($n=2$).

suction feeders, then a reduction in fin area should result in a decrement in capture success. Future studies that quantify strike accuracy before and after reducing pectoral fin area would determine whether larger pectoral fins are an adaptation for suction feeding. The strong relationship between the morphology of the locomotor and feeding systems in centrarchid fishes is a specific example, but this relationship is likely common among vertebrate groups. For example, terrestrial vertebrates may exhibit strong relationships between limb and mouth morphology, depending on the ecology of the predator. Future studies that examine the relationships between locomotor and feeding morphology will help illuminate the extent to which feeding and locomotion are integrated.

Evolutionary relationships between locomotion and feeding in fishes

With the large number of well-defined phylogenies for different vertebrate groups, it is possible to start examining the evolutionary relationships between locomotion and feeding, both from morphological and behavioral perspectives (e.g., McElroy and Reilly 2005; Higham et al. 2007). Higham et al. (2007) examined the relationships between locomotion and feeding behavior in 18 species of Neotropical cichlids. With a phylogeny based on sequences from the cytochrome *b* gene and S7 intron, phylogenetic independent contrasts were used to determine the relationship between swimming (ram) speed and maximum gape. The expectation, that species that swim fast will exhibit a larger mouth (Fig. 4), was confirmed (Higham et al. 2007). They suggest two reasons for the increased speed. First, species that swim fast during prey capture are typically feeding on evasive prey such as fish, and these prey items are typically larger than nonevasive prey. Second, a predator with a smaller mouth must be more accurate in order to successfully capture prey, and increased ram speeds reduce strike accuracy (Nyberg 1971; Higham et al. 2006a). Future studies that quantify attack speed and strike accuracy, while manipulating prey size, prey evasiveness and energy content of the prey, will help determine the causal relationships between prey and predator behavior.

Prey movements during prey capture

Most studies of prey capture present immobile prey to the predator (e.g., Rice and Westneat 2005; Higham 2007). While these studies do represent an ecologically relevant situation, and provide important information regarding prey capture, prey movements

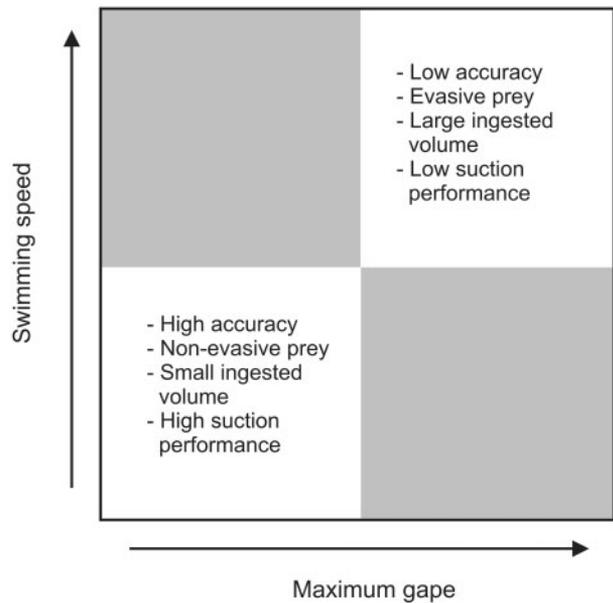


Fig. 4 A schematic showing the relationship between maximum gape and swimming speed in fishes. Higham et al. (2007) confirmed this relationship for 18 species of Neotropical cichlids. A larger gape offsets the decrease in accuracy associated with increased swimming speed.

are likely very important in determining the outcome of predator–prey interactions (Webb 1976; Webb and Skadsen 1980; Walker et al. 2005; Meager et al. 2006). For example, barn owls (*Tyto alba*) exhibit a much higher success rate when capturing a stationary prey compared with a mobile prey (Shifferman and Eilam 2004). In addition, certain movements of the prey are likely more effective at eluding a predator than others. Barn owls are less successful when a prey item moves sideways compared with movements along the axis of flight (Shifferman and Eilam 2004). The specific escape tactic of a prey item will depend on the relative performance of the predator and the morphological characteristics of the prey (Hedenstrom and Rosen 2001). For example, a climbing flight escape in birds is best performed by small individuals that have long wings and high wingbeat frequency, such as found in the swifts (Hedenstrom and Rosen 2001). Sensing a prey's movement in an aquatic environment can occur visually, but also via hydrodynamic trails left by the prey. The lateral line and visual system both play important roles in detecting prey and in determining strike behavior in fishes (Hanke et al. 2000; New et al. 2001).

Prey acceleration is an important factor determining the outcome of a predator–prey interaction (Walker et al. 2005). As prey, fishes typically employ a fast-start to evade a predator (Eaton et al. 1977;

Webb and Skadsen 1980). During a C-start, the path of the center of mass of the fish is typically normal to the original long-axis of the fish (Webb 1975; Eaton et al. 1977; Domenici et al. 2004; Wöhl and Schuster 2007). Thus, the optimal strategy for a predator is to attack the prey from the side (Webb and Skadsen 1980). It is important to note that Domenici and Blake (1991) found turning angle to be more variable, and Domenici (2001) suggests that attacking a prey item from the side will confer other advantages such as maximizing the area of the prey at which to aim. It is commonly thought that the likelihood of successful escape from a predator is related to acceleration performance of the prey (Webb 1986). In a recent study, guppies (*Poecilia reticulata*) that exhibited an increased fast-start performance also exhibited an increased probability of evading a predator (Walker et al. 2005). In addition to the C-start of the prey, a recent study by Wöhl and Schuster (2007) found that archer fish (*Toxotes jaculatrix*) employ C-starts to capture prey. Future studies that detail locomotor movements relative to prey movements may provide insight into the coordination of locomotor and feeding systems, and the coordination between predator and prey.

Minimizing predator locomotion during prey capture

While most predators utilize locomotion during prey capture, some species have adaptations that limit the need for the locomotor system. Two examples include tongue protrusion in amphibians and reptiles (Wainwright et al. 1991; Deban and Nishikawa 1992; Nishikawa et al. 1999; Deban et al. 2001; Meyers and Herrel 2005; Lappin et al. 2006), and jaw protrusion in fishes (Motta 1984; Wilga et al. 2001; Waltzek and Wainwright 2003). However, it is important to note that the presence of extreme jaw protrusion in fishes does not imply a lack of swimming during prey capture (e.g., Lauder and Liem 1981). Several reasons could explain the selection for minimizing locomotion during prey capture including increased stability, greater accuracy, surprising prey, and/or compensating for poor locomotor performance. Increased stability is likely important for animals moving in relatively complex habitats such as the three-dimensional network of perches found in arboreal habitats. Falling from a branch or tree trunk, while pursuing prey, could result in injury or death, so adaptations for minimizing locomotion would be beneficial. Surprising a prey item could be facilitated by jaw protrusion in fishes. Rather than

the entire body moving towards a prey item, having only the mouth move might minimize the likelihood of being detected by the prey. In addition, a bow wave, which is a wave of water generated by the body of a swimming fish that could push the prey item away from the predator, might be generated by some fishes during swimming, ultimately leading to a decrease in the success of prey capture (Ferry-Graham et al. 2003). This bow wave could be avoided by keeping the body stationary while moving only the mouth.

Poor locomotor performance is another reason why minimizing locomotion during prey capture might be beneficial. Chameleons, for example, exhibit maximum locomotor speeds that are much slower than other lizards (Peterson 1984; Higham and Jayne 2004a, 2004b). They also employ tongue protrusion in order to catch prey (Wainwright et al. 1991; Wainwright and Bennett 1992). Thus, the fast tongue projection makes up for the lack of sprinting speed. Future studies that examine the evolution of adaptations to reduce locomotion during feeding in relation to habitat structure would provide insight into this subject.

The structure of the habitat is another factor that can constrain movements of the predator. Arboreal primates, for example, commonly grip the substrate with one or more appendages while reaching out to capture prey (e.g., Bergeson 1998; Dunbar and Badam 2000; Nekaris and Rasmussen 2003; Nekaris 2005). Many prosimians (e.g., lorises, pottos, and gallagos) rapidly thrust an arm towards a prey item, such as a dragonfly or cicada, while maintaining a stable posture (Bishop 1962; Nekaris 2005). Thus, many arboreal primates rely on the locomotor structures for maintaining postural stability during feeding.

Future directions

Broad comparisons of locomotor and feeding morphology, using a phylogenetic framework, will provide considerable insight into morphological diversity within and between vertebrate groups. Detailed studies of aquatic locomotion during feeding have focused primarily on fishes. However, marine mammals, such as cetaceans, also swim during prey capture (Bloodworth and Marshall 2005; Goldbogen et al. 2006; Werth 2006). In addition, there is a paucity of studies examining the quantitative relationships (e.g., locomotor speed and acceleration) between locomotion and prey capture in terrestrial vertebrates. For example, there have been many studies examining the foraging

behavior of carnivorous mammals, but the actual prey capture event has received less attention. By incorporating various taxa that live in different habitats, our understanding of what constrains and facilitates locomotion during prey capture will be enhanced. For example, do all vertebrates exhibit locomotor behavior that is dependent on prey type and/or behavior? Do all vertebrates exhibit similar behaviors with changes in habitat structure and ecology? Ultimately, studying species that live in both aquatic and terrestrial habitats might provide insight into the constraints imposed by each environment. Work on amphibious snakes has revealed differences in the kinematics of feeding strikes depending on the environment (Vincent et al. 2005). Are these differences found in strictly aquatic and terrestrial species?

This article presents new information regarding the relationships between locomotor and feeding morphology in fishes. Other aspects of locomotor morphology not examined, such as body shape, are also connected to feeding biology and morphology (e.g., Webb 1984a; Parsons and Robinson 2007). However, we still lack information regarding the connections between locomotor and feeding performance. For example, do species that capture evasive prey exhibit a greater capacity for maneuvering? Future studies that examine the hydrodynamics, aerodynamics, morphology, behavior, and performance of locomotion during prey capture in a variety of taxa will provide insight into the evolution of locomotion involved in prey capture.

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