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Outrun or Outmaneuver: Predator-prey interactions as a model system for integrating biomechanical studies in a broader ecological and evolutionary context

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10 **Synopsis**—Behavioral studies performed in natural habitats provide a context for the
development of hypotheses and the design of experiments relevant both to biomechanics
and to evolution. In particular, predator-prey interactions are a model system for
integrative study because predation success or failure has a direct effect on fitness and
drives the evolution of specialized performance in both predator and prey. Although all
15 predators share the goal of capturing prey, and all prey share the goal of survival, the
behavior of predators and prey are diverse in nature. This paper presents studies of some
predator-prey interactions sharing common predation strategies that reveal general
principles governing predator and prey behaviors, even in distantly related taxa. Studies
of predator-prey interactions also reveal that maximal performance observed in a
20 laboratory setting is not necessarily the performance that determines fitness. Thus,
considering locomotion in the context of predation ecology can aid in evolutionarily
relevant experimental design. Classification by strategy reveals that displaying
unpredictable trajectories is a relevant anti-predator behavior in response to multiple
predation strategies. A predator's perception and pursuit of prey can be affected
25 indirectly by divergent locomotion of similar animals that share an ecosystem. Variation

in speed and direction of locomotion that directly increases the unpredictability of a prey's trajectory can be increased through genetic mutation that affects locomotor patterns, musculoskeletal changes that affect maneuverability, and physical interactions between an animal and the environment. By considering the interconnectedness of ecology, physical constraints, and evolutionary history of behavior, studies in biomechanics can be designed to inform each of these fields.

1 Behavioral studies direct evolutionarily relevant biomechanical inquiry

Behavioral studies of animals in their natural habitat provide a context for the integration of biomechanical and evolutionary analysis. Laboratory experiments often focus on determining maximal performance, such as peak velocity, which is important for understanding the capabilities derived from a certain morphology. However, maximal performance is only one of several determinants of fitness for an animal in its natural context. For example, cryptic stick-insects avoid predation by "rocking" their body in ways that closely resemble the gentle swaying of twigs in the wind, which is far from the maximal performance capabilities of stick-insect morphology observed in a laboratory environment (Robinson, 1969).

Many biomechanical studies are performed in laboratory settings, where the sensory and physical landscape can differ greatly from the natural habitat. In an outdoor carnival contest, frogs (*Rana catesbeiana*) jumped up to twice the maximum distance recorded in the laboratory (Astley et al., 2013). Similarly,

flights by fruit flies in an outdoor setting reach significantly higher peak velocities than those occurring within a laboratory ([Combes et al., 2012](#)). These studies suggest that experimentation in a laboratory may underestimate, and therefore
50 limit, the understanding of both the biomechanics and relevant ecological context of an animal operating in a model experimental system.

Behavioral studies can thus direct evolutionarily relevant biomechanical inquiry. For these types of integrative studies, it is important to focus on a behavior in which physical performance determines fitness. Specialized herbivorous feeding,
55 sexual selection on male-male competition, and predator-prey interactions are examples of behaviors in which biomechanical function determines fitness and drives the evolution of associated morphological features. Each of these behaviors can therefore serve as a model system for integrative studies ([Grant and Grant, 2014](#); [Emlen et al., 2007](#); [Lopez-Darias et al., 2012](#)). Predator-prey
60 interactions are especially interesting and potentially illuminating because they involve co-evolution between different species.

2 Predation is a model system for the integrative study of locomotion, behavior, and evolution.

Predator-prey interactions strongly influence the evolutionary fitness underlying
65 the locomotor performance both of predator and of prey. Successful predation

events sustain the predator's life and prevent the prey from further reproduction, making success or failure reliable proxies for fitness. Since successful hunting and escape often require specialized morphology, understanding the variation in relevant structures over time is critical to the study of adaptive evolution.

70 Predator-prey interactions represent an opportunity to connect biomechanical and evolutionary studies, given the underlying selective drive for highly co-adapted locomotion and morphology.

Behavioral studies of predator-prey interactions in the natural habitat are often analyzed in isolation or classified taxonomically (Domenici et al., 2011b). While
75 these investigations further the understanding of a particular species-pair in its ecosystem, it is difficult to determine whether the conclusions drawn from a particular study are applicable to other species. Alternatively, theoretical models of predator-prey interaction often are generalized with respect to a predator's strategy (Broom and Ruxton, 2005; Yuan, 1948). Sorting diverse predator-prey
80 interactions by studying predation strategy can reveal patterns of form-function principles shared by even distantly related taxa. This integrative approach makes it possible to test general hypotheses regarding the effect of differing strategies on the evolution of morphology and performance.

The behavioral and ecological factors that drive predator-prey interactions are essentially straightforward: in the presence of an acceptable prey item, the predator benefits by expending as little energy as possible to capture the prey, while successful escape by the prey enhances its survival and potential to reproduce (Lima and Dill, 1990). Relatively simple models can predict the ideal escape behavior in simple cases of predator-prey interaction, in which the predator and prey move in the same geometric plane and the prey must avoid capture by the predator (Broom and Ruxton, 2005; Ellard and Eller, 2009; Cooper and Frederick, 2009). However, such simple models fail to explain the diversity and complexity of escape behaviors observed in the natural world (Domenici et al., 2011a,b). Additionally, most animals act as predator or as prey in different biotic interactions throughout their lives. While creating a model for combined predator and prey strategy would inform an estimation of overall fitness throughout an animal's lifetime, an overarching model of this sort would be extremely complex and is beyond the scope of our paper.

This review classifies the existing diversity in predator-prey behavior with respect to predation strategy to reveal common principles underlying predator-prey interactions in each classification. Ambush Predation (Fig 1A) involves a stereotyped behavior triggered by the presence of prey. No prediction of the prey's behavior or feedback is involved. Ballistic Interception (Fig. 1B) involves

the predator adjusting an attack trajectory to observed movements by the prey,
105 and commitment to that trajectory without the use of feedback. Pursuit Predation
(Fig. 1C) involves the predator adjusting their intercept-trajectories according to
updated sensory feedback on the prey's movements. Many forms of predation,
such as stalking by *Anolis sp.* or persistence-hunting by hominins, do not fit into
the strategies presented here (Moermund, 1981; Liebenberg, 2006). Similarly,
110 the effect of sociality and feeding-pressure are reviewed elsewhere (Lima and
Dill, 1990). Rather than providing a comprehensive list of all predator-prey
interactions, we focus on three strategies, Ambush Predation, Ballistic
Interception, and Pursuit Predation, which serve as preliminary examples of the
integration of biomechanics, behavior, and evolution in determining some general
115 principles underlying the evolution of locomotion.

2.1 Ambush Predation

The simplest predation strategy to model is that of a predator ambushing its prey
using one stereotypic motion, which is triggered by a key stimulus (namely, prey
entering the predator's proximity). Ambush predators typically have heightened
120 visual, chemical, or tactile senses they use in detecting prey. Examples of
ambush predators include angel sharks, trapdoor spiders, and frogs (Fouts and
Nelson, 1999; Bradley, 1996; Ewert et al., 2001). As "sit-and-wait" predators,

ambush predators often create a burrow to stay hidden, which constrains the target range of their stereotyped attack (Caraco and Gillespie, 1986). Rapid movement is key to a successful strike, as the predator does not need to predict the prey's movement if it can move quickly enough to prevent the prey from sensing and reacting to the oncoming attack (deVries et al., 2012). These circumstances have favored the evolution of ambush behavior as a fixed action pattern with little or no feedback in response to the prey's behavior. The simplicity of this system makes ambush predation an attractive model for studying pattern recognition and motor reflexes (Ewert et al., 2001).

Ambush predation is most effective when there is a high density of suitable prey near the hiding predator (Bradley, 1996). In systems with a lower density of prey, ambush predators create lures that attract prey to the predator's proximity (Hagman et al., 2008). The prey can only avoid predation if it has evolved either acute sensory organs that can detect the hidden predator, or quick reflexes that permit escape once the predator has revealed itself (Martin and Hammerschlag, 2012). Since predation is highly stereotypic and does not rely on feedback in response to movement by the prey, the prey can move away from the predator via a variety of headings, so long as it can move quickly enough. However, both predator and prey face a lower boundary to their co-evolutionary arms race; reaction time is limited by the sensory-motor neural processing

required before adjustments in the trajectory of movement can be initiated
(Jindrich and Full, 2002).

145 **2.2 Ballistic Interception**

Ballistic interception consists of an initial observation of movement by the prey,
prediction of the prey's future location, computation of an intercept course, feed-
forward neuromuscular control and commitment to that course, and a
subsequent discrete success or failure at the time and location of predicted
150 interception. The delay between the commitment to the course and the discrete
endpoint of success or failure is the window of opportunity for the prey to escape.
Ambush predation and ballistic interception exist on the same predation strategy
continuum, but it is useful to distinguish between the two when addressing
predator aiming. Ballistic interception at close distances still requires adjustment
155 of the predator's attack behavior in response to the behavior of the prey, while
ambush predators use a stereotyped motion to attack at the same target area
with respect to their own location. Predation of unmoving prey is a variant of
ballistic interception because the predator must aim and predict the future
location of the prey, even though the predator may strike when the prey is not
160 moving. The predator is predicting the future state of the prey as unmoving, and
fails when the prey moves during an attack. On the other hand, ambush

predation as defined above does not require any aiming or prediction of future locations of prey, and is simply a fixed strike pattern triggered by the presence of prey in the target range. Examples of ballistic predators include dragonflies, 165 chameleons, the colubrid snake *Elaphe quadrivirgata*, archerfish, and submarines launching torpedoes at boats during the First World War (Mischiati et al., 2014; Anderson et al., 2010; Nishiumi and Mori, 2014; Rossel et al., 2002; Scott-Samuel et al., 2011).

To determine whether dragonflies use ballistic interception to capture prey, head 170 and body orientation of the dragonfly, and heading and location of the prey were tracked during attempts at predation (Mischiati et al., 2014). Tracking dragonflies' eyes with respect to the location of the prey revealed that the eyes track the predicted path of the prey. Purely reactive tracking, such as Parallel Navigation (Yuan, 1948), were inconsistent with dragonflies' tracking behavior, indicating 175 that the predation strategy is predominantly predictive. In light of these findings, studies of the ability of dragonflies to track prey during flight, or of the mechanics of initiating sharp turns, may not be very informative for evaluating evolutionary or ecological hypotheses since these metrics are not necessary for successful predation. Instead, it is more generally useful to study how natural behavior of 180 the prey and environmental variation affect dragonflies' ability to predict the future location of prey. This can be assessed indirectly by recording the factors

associated with the initiation of predation, or lack thereof (Combes et al., 2012).

Recent work has shown that dragonflies do not initiate predation when the speed, size, or distance of the prey limits reliable prediction of its trajectory.

185 Indeed, failure of initiated predation attempts is correlated with highly variable flight trajectories of the prey, thereby limiting the relevance of predictive interception (Combes et al., 2013).

Escape by prey depends on multiple factors, including the prey's intrinsic ability to move, conspecific behavior linked to the predator-prey interaction, and

190 features of the local habitat. The frog *Pelophylax nigromaculatus* escaping from a ballistic strike from the snake *Elaphe quadrivirgata* presents an escape strategy contingent on these factors. In response to the presence of a snake, the frog adopts the behavioral strategy of waiting and letting the snake approach slowly (Nishiimi and Mori, 2014). By freezing while the snake approaches, the frog

195 allows for the possibility that another prey item will distract the snake during the approach. Next, the "Close-Quarters Effect" works to the frog's advantage: if the frog jumps while the snake is far away, the angular adjustment in the direction of the snake's attack is relatively minor. Since biomechanical studies show that terrestrial frogs are not capable of repeated jumps (Peters et al., 1996), it is

200 unlikely that the frog would be able to immediately perform another maneuver to escape the re-adjusted snake strike. The closer the snake is to the frog before

the frog jumps, the greater the angular adjustment the snake must make, thereby decreasing the likelihood of a successful strike. Finally, the frog often waits until after the snake initiates a strike to begin its jump. Since the snake is committed
205 to a specific trajectory (Nishiumi, *pers. observ.*), it cannot adjust to strike at the frog's new position. Thus, even prey that are only capable of intermittent locomotion may successfully escape due to the feed-forward sensory-motor planning of the ballistic interception strategy.

2.3 Pursuit Predation

210 Pursuit predation involves high-speed locomotion of both the predator and the prey. In the absence of the prey turning or exploiting features of the landscape inaccessible to predators, the predator must simply maintain a speed greater than the prey for a sufficient time to successfully catch the prey. In this simplest case of a linear rundown, sensory-motor and musculoskeletal adaptations for
215 faster speed and acceleration can improve the fitness of both the predator and the prey. Visual and auditory camouflage is favored, potentially allowing predators to get as close as possible to the prey before the pursuit begins, and permitting prey to avoid the pursuit altogether (Lima and Dill, 1990).

When prey turn during an attempted escape, the pursuit strategy must become
220 reactive for successful predation, involving ongoing sensory-motor feedback to

execute new intercept-trajectories during the pursuit. A simple model for the neural control of predators adopting the pursuit strategy in a two-dimensional plane is the Parallel Navigation Principle, the strategy used by bats hunting mantises (Ghose et al., 2009). According to this model, the predating bat holds
225 the mantis at a fixed angle to its own heading while reducing the distance to the mantis. A fixed angle of approach minimizes the mantis's relative perception of the bat's movement. If the mantis changes heading, the bat compensates by establishing a new intercept course, again keeping the mantis at a fixed angle while decreasing the distance between the two. The Parallel Navigation Principle
230 strategy of pursuit naturally evolved in bats and goshawks (Kane et al., 2015), and humans convergently derived the strategy to control target-seeking devices (Yuan, 1948). Pursuit predation is a useful model system for determining effective morphologies and strategies for tracking while the tracker is moving. Animals acting as predator or prey in pursuit predation interactions are well
235 suited to biomechanical examination because their locomotor structures often exhibit morphologies that confer high maneuverability.

A well-known strategy for evasion of a predator by prey in the context of pursuit predation is the Turning Gambit (Howland, 1974), in which predator and prey are assumed to be moving in the same two-dimensional plane. As described above,
240 the predator maintains a higher speed than the prey. However, there is a tradeoff

between speed and maneuverability for most forms of locomotion

([Biewener, 2003](#); [Jindrich and Qiao, 2012](#)). Because predators are typically

larger than their prey, most predators are unable to make turns as sharply or as quickly as the prey, so the prey can escape even if they move more slowly.

245 Studies of encounters can reveal whether predator and prey are successful by outrunning or outmaneuvering each other. A recent study integrating structural ecology, behavioral interactions, and biomechanical performance showed that in response to prey that take many sharp turns, cheetahs run at sub-maximal speeds to improve their turning ability to successfully capture prey ([Wilson et](#)
250 [al., 2013](#)).

3 Insights from an integrative perspective

3.1 Understanding how locomotor ecology affects predator-prey interactions aids experimental design

Careful consideration of the locomotor ecology of predator-prey interactions,

255 including the sensory and physical landscape, enables studies of animals in similar motivational states, as well as co-option of natural triggers of locomotion for optimal experimental design. Sensory cues affect locomotion by allowing predators to detect prey or by alerting prey to attempts at predation (see [Stevens and Merilaita \[2009\]](#) for a comprehensive review). For instance, comparing the

260 activity of burrowing rodents between sites without considering the phases of the moon may introduce error to an experiment, since as prey animals, nocturnal rodents decrease their activity owing to increased visibility to predators during full moon (Diete, et al.; Clarke, 1983; Griffin et al., 2005; Daly et al., 1992). In addition to inhibiting locomotion, sensory cues can also elicit locomotion.

265 Heteromyid rodents with inflated auditory bullae have evolved a stereotypical vertical jump in response to vibrations at the frequency produced by predators' locomotion (Webster and Webster, 1971). Similarly, a change in the flow of fluid produced by movement in water or air can trigger an escape response in prey animals (Stewart et al., 2013; Domenici et al., 2008). Experimenters can vary the

270 natural sensory cues for predation or evasion in their study system to reliably elicit a desired behavior.

In certain cases there is selection for maximal performance, but other behaviors also contribute to fitness. For example, some prey modify behavior in ways that hide them from potential predators. Mice have few locomotor specializations and

275 exhibit high open field anxiety, preferring the safety of cover (Bourin and Hascoe, 2003). Similarly, aquatic prey may choose to "hide" in areas of low flow, thereby reducing the likelihood that a predator will pick up their chemical cues (Hay, 2009). Many biomechanical experiments requiring locomotion in exposed areas may be confounded by an animal's open field anxiety, but the natural

280 preferences of prey can also aid in experimental design. Lizards preferring shelter can be motivated to locomote by providing shelter at the opposite end of a racetrack (Libby et al., 2012). By affecting the prey's ability to avoid predation, the physical environment can thus have an effect on an animal's motivation to locomote.

285 Importantly, the locomotor matrix (i.e. water, substrate, air, or perches) spatially constrains the locomotion of both predator and prey. Transformation of forest into agricultural fields has caused documented vicariance in the native range of animals dependent on suitable perches for locomotion (Essner, 2007; Mattingly and Jayne, 2004; Anderson et al., 2007). Predators attuned to the spatial

290 limitations of their prey can hunt accordingly, such as the dolphins that cooperate to beach fish on the shore, where the fish lie immobile and unable to escape the elongate jaws of these predators (Sargeant et al., 2005). Studies of terrestrial locomotion often assume that movement in the horizontal plane is most relevant, but examination of trajectories measured in two dimensions can present

295 misleading results when the experimental subjects are capable of significant excursions outside of that plane. In a study comparing the escape behavior of sympatric quadrupedal and bipedal rodents, analysis of locomotion limited to the horizontal plane did not show significantly different performance between the quadrupedal versus bipedal species (Djawdan and Garland, 1988), despite

300 significant evidence that bipedal rodents evade predators more frequently
(Longland and Price, 1991). Incorporating the considerable excursions of the
bipedal *Dipodomys sp.* in the vertical plane of motion would likely reveal
differences in escape behavior important for successful escape and maintaining
fitness. Indeed the escape behavior of kangaroo rats (*D. spectabilis*) in response
305 to the sound of an approaching predator is to jump vertically and to hop
erratically away (Webster and Webster, 1971), consistent with studies of maximal
jump performance in this species (Biewener and Blickhan, 1988). Although the
locomotor matrix often predisposes animals to move in a specific plane, animals
capable of significant out-of-plane excursions demand consideration in three
310 dimensions for ecologically and evolutionarily relevant analysis.

3.2 Indirectly or directly limiting the predator's ability to predict prey locomotion discourages predation

For successful Pursuit Predation and especially Ballistic Interception strategies
the predator must predict the future location of the prey. To decrease the
315 predator's ability to build a reliable model of the prey's trajectories, and thus plot
a successful intercept course, prey can produce unpredictable trajectories, also
called "Protean Behavior" (Chance and Russell, 1959). Studies show that prey
adopting a trajectory that is difficult for the predator to predict or perceive
decreases the likelihood that predation will be attempted (Combes et al., 2013).

320 Unpredictability of trajectories can be increased indirectly, by comparison to the locomotion of other prey species, or by directly modifying trajectories.

To increase the perceived unpredictability of trajectories, prey can inhabit an ecosystem with similar organisms performing an alternative form of locomotion. A predator observing an uncommon animal's trajectory would likely predict its
325 future position incorrectly based on the trajectories of the more common species. This effect is enhanced if the species with differing trajectories exhibit similar cues to the predator. Human fighters illustrate this effect with the hypothesis for maintenance of left-handedness at low frequency in human populations. Since left-handed humans are less common, it is less likely that a given fighter will have
330 experience fighting a left-handed opponent, giving the left-handed opponent an advantage over the more common (and thus, predictable) right-handed opponents. Studies of cave paintings indicate that the frequency of left-handedness has been relatively constant over time, but slight increases have been noted in indigenous societies with higher rates of violence (Faurie and
335 Raymond, 2005). If patterns of movement have equal intrinsic predictability, the fitness of the less common animal is highly frequency-dependent, and is therefore maintained at low frequency.

Directly decreasing predictability of locomotion requires maneuverability: the physical ability to change the speed or direction of motion. Maneuverability can be quantified by determining how quickly and sharply an animal can perform a turn (Norberg, 1994; Webb, 1983). However, the ability to move in many directions does not, on its own, affect unpredictability. By choosing to move with more equal probability in multiple directions, prey increase the unpredictability of their movements (Fig. 2) The majority of studies of escape trajectories concerned with Protean Behavior have quantified variance as a proxy for unpredictability (see Domenici et al. [2011a,b] for a comprehensive review). However, although unpredictability requires variability (made possible by maneuverability), not all variability contributes equally to unpredictability (Shannon, 1948). Indeed, natural systems of predator and prey show a difference in fitness between variability and unpredictability in escape behavior. For example, tentacled snakes can successfully catch fish that suddenly change in speed and direction, called a C-start. The escape behavior results in trajectories with variable direction, but the initiation of the behavior is so stereotyped that it is predictable (Catania, 2009).

Diversity in behavior has been classically catalogued by ethograms - histograms of how often distinct behaviors are exhibited. Ethograms are used in the analysis of different escape strategies of prey, e.g. to determine whether the prey uses only the optimal escape trajectory or a variety of sub-optimal escape trajectories

([Domenici et al., 2011a](#)). Currently ethograms are rarely used because they depend strongly on the coordinate system used and the method for distinguishing behaviors ([MacNulty et al., 2007](#)). Some behaviors even exhibit continuous variation and are impossible to discretize. Building on the history of ethogram analysis to determine the fitness of different escape behaviors, novel methods are currently being developed to characterize continuous variation in the locomotion of prey explicitly in the context of unpredictability using information theory ([Moore et al., 2014](#)). These methods enable characterization of non-steady state locomotion in ways that relate more directly to prey fitness in the context of Ballistic Interception and Pursuit Predation.

3.3 Mechanisms determining locomotor variability at multiple levels of biological complexity may confer anti-predator advantages

The fitness advantage conferred by musculoskeletal sources of variability in locomotion is demonstrated in certain cases by biomechanical studies of ecologically relevant behaviors. However, the sources of variability have been identified at other levels of complexity, ranging from whole-body shape to single gene mutations. Integrative approaches used to study the musculoskeletal system can lead to insights regarding the adaptive significance of these additional sources of variability.

At the musculoskeletal level, the relatively stiff tendons of kangaroo rats, *Dipodomys spectabilis*, transmit large forces and changes in length with little mechanical delay for rapid and powerful movements, as in jumping (Biewener and Blickhan, 1988). Such a design favors successful escape in response to sound emitted by approaching predatory owls and rattlesnakes at frequencies to which the animal's auditory system is highly sensitive (Webster and Webster, 1971). Since these animals are natural predators of kangaroo rats, the rats' jumping, and the associated morphologies, are considered adaptations that enable them to evade predators.

The shape or general body plan of an animal also affects how it interacts with its physical environment during locomotion. For example, the location of sea lions' flippers dampen roll rotation and translational motion, but cannot significantly dampen rotations in the yaw and pitch axes, thereby enhancing turning performance in these axes during swimming (Fish et al., 2003). While animals with bilateral symmetry favor locomotion in one direction, animals with radial symmetry, like brittle stars, can quickly change direction without turning by choosing to lead with a different limb (Astley, 2012). It is difficult to test the selective advantage these body shapes have on the locomotion of either predator or prey because they do not vary greatly in nature. However, it is possible to vary shape by modifying robot models (Briod et al., 2014; Peterson et

al., 2011). If the variation in locomotion associated with each shape is correlated with a predator 's preference (see the experimental design of Ioannou et al. [2012]), it may be possible to determine whether body shape can be adapted
400 to enhance evasive locomotion.

Genetic mutations may also affect motor control and thereby generate variability in gait and in patterns of the activation of muscles. For example, a premature stop-codon mutation in the DMRT3 gene is associated with the ability to perform pace and tölt gaits in horses, in addition to walks, trots, canters, and gallops
405 (Andersson et al., 2012). Knockouts of the same DMRT3 gene correspond to uncoordinated locomotion in a mouse model, demonstrating a causal effect between this gene and variability in locomotion. The locomotor effect of mutations in many genes has recently been studied in *Caenorhabditis elegans*. Each unique mutant displays distinct utilization of locomotor motifs, or
410 "eigenworms" (Brown et al., 2013). By comparing locomotion in mutant and wild-type *C. elegans*, it is possible to determine the effect of individual mutations on locomotor variability. If the behavioral consequences of mutations are understood, population-wide variability can be estimated by measuring the frequency of certain alleles in that population. Although these studies do not
415 specifically address predator-prey interactions, investigation of genetic sources of variation in locomotion in a natural context would enable the use of population

genetics to make predictions regarding how the locomotion both of predator and of prey may evolve through time.

4 Future Directions

420 The field of biomechanics currently benefits from an integrative approach that incorporates biology, physics, and engineering concepts. Similarly, applying an integrative approach that unites the fields of biomechanics, behavior, and evolution has the potential to contribute form-function insights to the evolution of biomechanical performance through time. Predator-prey interactions, in
425 particular, can serve as a model system for integrative inquiry due to their strong effect on fitness and their dependence on locomotor performance.

Uniting diverse studies of predator-prey interactions from distinct fields is possible when classified by the strategies of predators and prey. Each of the strategies presented above have characteristic behavioral and sensory-motor
430 patterns that favor distinct forms of locomotion both for predation and escape. Identifying underlying mechanisms that mediate such interactions enables comparison of even taxonomically distant animals that share a common strategy to reveal common co-evolutionary patterns between predator and prey. Thus, predator-prey interactions represent a model experimental study system for

435 incorporating locomotor ecology into biomechanical inquiry, which increases the applicability of biomechanical results to evolutionary hypotheses.

Indeed, by espousing this integrative approach, it may be possible to determine whether predation strategies favor certain evolutionary patterns. For example escape from predation is often cited as a potential driver of the expansion or contraction of niches (Colwell and Fuentes, 1975; Sexton et al., 2009). The evolutionary transitions from water to land and from land to air involve expansion of the locomotor niche, and it has been suggested that evasion of predators drives the expansion of niches in these cases (Davenport, 1994; Dudley, 2000; Dial, 2003). Certain strategies, such as those that are reliant on discontinuity of locomotor matrix (Baylis, 1982), may be associated with niche expansion in prey. If there is an association between certain strategies for predator evasion and the expansion of prey niches, biomechanical and behavioral studies have the potential to make even more informative contributions towards the understanding of evolutionary patterns, such as adaptive radiations following invasion of a novel locomotor matrix.

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References

Anderson, J, Rowcliffe, J M, Cowlishaw, G. "Does the matrix matter? A forest primate in a complex agricultural landscape." *Biol Cons* (2007) 135:212-222.

465 doi:10.1016/j.biocon.2006.10.022

Anderson, C V, Deban, S M. "Ballistic tongue projection in chameleons maintains high performance at low temperature." *Proc Natl Acad Sci USA* (2010) 107(12):5495-5499. doi:10.1073/pnas.0910778107

- Andersson, L S, Larhammar, M, Memic, F, et al. "Mutations in DMRT3 affect locomotion in horses and spinal circuit function in mice." *Nature* (2012) 470 488(7413):642-6. doi:10.1038/nature11399
- Astley, H C. "Getting around when you're round: quantitative analysis of the locomotion of the blunt-spined brittle star, *Ophiocoma echinata*." *J Exp Biol* (2012) 215:1923-1929. doi:10.1242/jeb.068460
- 475 Astley, H C, Abbott, E M, Azizi, E, Marsh, R L, Roberts, T J. "Chasing maximal performance: a cautionary tale from the celebrated jumping frogs of Calaveras County." *J Exp Biol* (2013) 216:3947-53. doi:10.1242/jeb.090357
- Baylis, J R. "Unusual escape response by two cyprinodontiform fishes, and a bluegill predator's counter-strategy." *Copeia* (1982) 1982(2):455-457.
- 480 Biewener, A A, Blickhan, R. "Kangaroo rat locomotion: design for elastic energy storage or acceleration?" *J Exp Biol* (1988) 140:243-55.
- Biewener, A A. *Animal Locomotion* (2003) Oxford Animal Biology Series, Oxford University Press.
- Bourin, M, Hascoe, M. The mouse light / dark box test." *Eur J Pharmacol* (2003) 485 463:55-65. doi:10.1016/S0014-2999(03)01274-3

Bradley, R A. "Foraging Activity and Burrow Distribution in the Sydney Brown Trapdoor Spider (*Misgolas rapax* Karsch: Idiopidae)." *J Arachnol* (1996) 25(1):5867.

490 Briod, A, Kornatowski, P, Zufferey, J C, Floreano, D. "A Collision-Resilient Flying Robot." *J Field Robot* (2014) 31(4):496-509. doi:10.1002/rob.21495

Broom, M, Ruxton, G D. "You can run - Or you can hide: Optimal strategies for cryptic prey against pursuit predators." *Behav Ecol* (2005) 16:534-540. doi:10.1093/beheco/ari024

495 Brown, A E X, Yemini, E I, Grundy, L J, Jucikas, T, Schafer, W R. "A dictionary of behavioral motifs reveals clusters of genes affecting *Caenorhabditis elegans* locomotion." *Proc Natl Acad Sci USA* (2013) 110(2):791-6. doi:10.1073/pnas.1211447110

Caraco, T, Gillespie, R C. "Risk-Sensitivity: Foraging Mode in an Ambush Predator." *Ecology* (1986) 67(5):1180-1185

500 Catania, K. "Tentacled snakes turn C-starts to their advantage and predict future prey behavior." *Proc Natl Acad Sci USA* (2009) 106:11183-11187.

Chance, M, Russell, W. "Protean displays: a form of allaesthetic behavior." *P Zool Soc Lond* (1959) 132:65-70.

Clarke, J A. "Moonlight's influence on predator/prey interactions between short-
505 eared owls (*Asio flammeus*) and deermice (*Peromyscus maniculatus*)." *Behav
Ecol Sociobiol* (1983) 13:205-209.

Colwell, R K, Fuentes, E R. "Experimental Studies of the Niche." *Annual Review
of Ecology and Systematics* (1975) 6:281-310.

doi:10.1146/annurev.es.06.110175.001433

510 Combes, S A, Crall, J D, Mukherjee, S. "Dynamics of animal movement in an
ecological context: dragonfly wing damage reduces flight performance and
predation success." *Biol Lett* (2010) 6:426-429. doi:10.1098/rsbl.2009.0915

Combes, S A, Rundle, D E, Iwasaki, J M, Crall, J D. "Linking biomechanics and
ecology through predator-prey interactions: flight performance of dragonflies and
515 their prey." *J Exp Biol* (2012) 215:903-913. doi:10.1242/jeb.059394

Combes, S A, Salcedo, M K, Pandit, M M, Iwasaki, J M. "Capture success and
efficiency of dragonflies pursuing different types of prey." *Integr Comp Biol* (2013)
53(5):787-798. doi:10.1093/icb/ict072

Cooper, W E, Frederick, W G. "Predator lethality, optimal escape behavior, and
520 autotomy." *Behav Ecol* (2009), 21:91-96. doi:10.1093/beheco/arp151

Daly, M, Behrends, P R, Wilson, M I, Jacobs, L F. "Behavioural modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*." *Anim Behav* (1992) 44:1-9.

doi:10.1016/S0003-3472(05)80748-1

525 Davenport, J. "How and why do flying fish fly?" *Rev Fish Biol Fisher* (1994) 4:184-214. doi:10.1007/BF00044128

deVries, M S, Murphy, E A K, Patek, S N. "Strike mechanics of an ambush predator: the spearing mantis shrimp." *J Exp Biol* (2012) 215:4374-84.

doi:10.1242/jeb.075317

530 Dial, K P. "Wing-assisted incline running and the evolution of flight." *Science* (2003) 299:402-404. doi:10.1126/science.1078237

Diete, R L, Meek, P D, Dickman, C R, Leung, L K-P. "Burrowing behaviour of the northern hopping-mouse (*Notomys aquilo*): field observation." *Aust Mammal*

(2015) 36:242-246. doi:http://dx.doi.org/10.1071/AM13039

535 Djawdan, M, Garland, T J. "Maximal Running Speeds of Bipedal and Quadrupedal Rodents." *J Mamm* (1988) 69:763-772.

Domenici P, Blagburn JM, Bacon JP. "Animal escapology I: theoretical issues and emerging trends in escape trajectories." *J Exp Biol* (2011a) 214:2463-2473.

540 Domenici P, Blagburn JM, Bacon JP. "Animal escapology II: escape trajectory case studies." *J Exp Biol* (2011b) 214:2474-2494.

Domenici, P, Booth, D, Blagburn, J M, Bacon, J P. "Cockroaches Keep Predators Guessing by Using Preferred Escape Trajectories." *Curr Biol* (2008) 18(22):1792-1796. doi:10.1016/j.cub.2008.09.062

545 Dudley, R. "The Evolutionary Physiology of Animal Flight: Paleobiological and Present Perspectives." *Annu Rev Physiol* (2000) 62:135-55.

Ellard, C G, Eller, M C. "Spatial cognition in the gerbil: Computing optimal escape routes from visual threats." *Anim Cogn* (2009) 12:333-345. doi:10.1007/s10071-008-0193-9

550 Emlen, D J, Corley Lavine, L, Ewen-Campen, B. "On the origin and evolutionary diversification of beetle horns." *Proc Natl Acad Sci USA* (2007) 104:8661-8. doi:10.1073/pnas.0701209104

Essner, R L. "Morphology, locomotor behaviour and microhabitat use in North American squirrels." *J Zool* (2007) 272:101109. doi:10.1111/j.1469-7998.2006.00247.x

555 Ewert, J P, Buxbaum-Conradi, H, Dreisvogt, F, et al. "Neural modulation of visuomotor functions underlying prey-catching behaviour in anurans: Perception,

attention, motor performance, learning.” *Comp Biochem Physiol A Mol Integr Physiol* (2001) 128:4170461. doi:10.1016/S1095-6433(00)00333-0

560 Faurie, C, Raymond, M. “Handedness, homicide and negative frequency - dependent selection.” *Proc R Soc B* (2005) 272:25-28.
doi:10.1098/rspb.2004.2926

Fish, F E, Hurley, J, Costa, D P. “Maneuverability by the sea lion *Zalophus californianus*: turning performance of an unstable body design.” *J Exp Biol* (2003) 206:667-674. doi:10.1242/jeb.00144

565 Fouts, W R, Nelson, D R. “Prey capture by the Pacific angel shark, *Squatina californica*: Visually mediated strikes and ambush-site characteristics.” *Copeia* (1999) 1999(2):304-312.

Ghose, K, Triplehorn, J D, Bohn, K, Yager, D D, Moss, C F. “Behavioral responses of big brown bats to dives by praying mantises.” *J Exp Biol* (2009) 212:693-703. doi:10.1242/jeb.019380

570 Grant, P R, Grant, B R. *40 Years of Evolution: Darwin’s Finches on Daphne Major Island* (2014) Princeton: Princeton University Press.

Griffin, P C, Griffin, S C, Waroquiers, C, Mills, L S. "Mortality by moonlight: Predation risk and the snowshoe hare." *Behav Ecol* (2005) 16:938-944.

575 doi:10.1093/beheco/ari074

Hay, M E. "Marine Chemical Ecology: Chemical Signals and Cues Structure Marine Populations, Communities, and Ecosystems." *Ann Rev Mar Sci* (2009) 1:193-212. doi:10.1016/j.biotechadv.2011.08.021.Secreted

580 Hagman, M, Phillips, B L, Shine, R. "Tails of enticement: Caudal luring by an ambush-foraging snake (*Acanthophis praelongus*, Elapidae)." *Funct Ecol* (2008) 22:1134-1139. doi:10.1111/j.1365-2435.2008.01466.x

Howland, H C. "Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability." *J Theor Biol* (1974) 47:333-350. doi:10.1016/0022-5193(74)90202-1

585 Ioannou, C C, Guttal, V, Couzin, I D. "Predatory Fish Select for Coordinated Collective Motion in Virtual Prey." *Science* (2012) 337(3):1212-1215. doi:10.1126/science.1218919

Jindrich, D L, Full, R J. "Dynamic stabilization of rapid hexapedal locomotion." *J Exp Biol* (2002) 205:2803-23.

- 590 Jindrich, D L, Qiao, M. "Maneuvers during legged locomotion." *Chaos* (2012) 19(026105):1-14. doi:10.1063/1.3143031
- Kane, S A, Fulton, A H, Rosenthal, L J. "When hawks attack: animal-borne video studies of goshawk pursuit and prey-evasion strategies." *J Exp Biol* (2015) 218:212-222
- 595 Liebenberg, L. "Persistence Hunting by Modern Hunter - Gatherers." *Curr Anthropol* (2006) 47(6):1017-1026.
- Libby, T, Moore, T Y, Chang-Siu, E, Li, D, Cohen, D J, Jusufi, A, Full, R J. "Tail - assisted pitch control in lizards, robots and dinosaurs." *Nature* (2012) 481(7380):181-184.
- 600 Lima, S L, Dill, L M. "Behavioral decisions made under the risk of predation: a review and prospectus." *Can J Zool* (1990) 68:619-640. doi:10.1139/z90-092
- Longland, W S, Price, M V. "Direct Observations of Owls and Heteromyid Rodents: Can Predation Risk Explain Microhabitat Use?" *Ecology* (1991) 72(6):2261-2273.
- 605 Lopez-Darias, M, Schoener, T W, Spiller, D A, Losos, J B. "Predators determine how weather affects the spatial niche of lizard prey: Exploring niche dynamics at a fine scale." *Ecology* (2012) 93(12):2512-2518. doi:10.1890/12-0483.1

- MacNulty, D R, Mech, L D, Smith, D W. "A Proposed Ethogram of Large-Carnivore Predatory Behavior, Exemplified by the Wolf." *J Mamm* (2007) 88(3):595-605. doi:10.1644/06-MAMM-A-119R1.1
- 610
- Martin, R A, Hammerschlag, N. "Marine predator-prey contests: Ambush and speed versus vigilance and agility." *Mar Biol Res* (2012) 8:90-94. doi:10.1080/17451000.2011.614255
- Mattingly, W B, Jayne, B C. "Resource Use in Arboreal Habitats: Structure Affects Locomotion of Four Ecomorphs of *Anolis* Lizards." *Ecology* (2004) 85(4):1111-1124.
- 615
- Mischiati, M, Lin, H-T, Herold, P, Imler, E, Olberg, R, Leonardo, A. "Internal models direct dragonfly interception steering." *Nature* (2014) 517(7534), 333-338. doi:10.1038/nature14045
- 620
- Moermond, T C. "Prey-attack behavior of *Anolis* lizards." *Z Tierpsychol* (1981) 56:128-136
- Moore, T Y, Vasudevan, R, Biewener, A A. "Measuring locomotor entropy to compare predator evasion ability in sympatric desert rodents." *Int Comp Biol* (2014) 54:E143-E143.

- 625 Mountcastle, A M, Combes, S A. "Biomechanical strategies for mitigating collision damage in insect wings: structural design versus embedded elastic materials." *J Exp Biol* (2014) 217:1108-1115. doi:10.1242/jeb.092916
- Nishiumi, N, Mori, A. "Distance - dependent switching of anti - predator behavior of frogs from immobility to fleeing." *J Ethol* (2014) doi:10.1007/s10164-014-0419-
630 z
- Norberg, R A. (1994). "Swallow Tail Streamer is a Mechanical Device for Self Deflection of Tail Leading Edge, Enhancing Aerodynamic Efficiency and Flight Manoeuvrability." *Proc Royal Soc B: Biol Scien* (1994) 257(1350):227-233. doi:10.1098/rspb.1994.0119
- 635 Peters, S E, Kamel, L T, Bashor, D P. "Hopping and Swimming in the Leopard Frog, *Rana pipiens*: I. Step Cycles and Kinematics." *J Morphol* (1996) 230:1-16.
- Peterson, K, Birkmeyer, P, Dudley, R, Fearing, R S. "A wing-assisted running robot and implications for avian flight evolution." *Bioinspir Biomim* (2011) 6(4):046008
- 640 Robinson, M H. "The defensive behaviour of some orthopteroid insects from Panama." *Trans R Entomol Soc Lond* (1969) 121(7):281-303.

Rossel, S, Corlija, J, Schuster, S. "Predicting three-dimensional target motion: how archer fish determine where to catch their dislodged prey." *J Exp Biol* (2002) 205:3321-3326.

645 Sargeant, B L, Mann, J, Berggren, P, Krützen, M. "Specialization and development of beach hunting, a rare foraging behavior, by wild bottlenose dolphins (*Tursiops* sp.)." *Can J Zool* (2005) 83:1400-1410. doi:10.1139/z05-136

Sexton, J P, McIntyre, P J, Angert, A L, Rice, K J. "Evolution and Ecology of Species Range Limits." *Annual Review of Ecology, Evolution, and Systematics* (2009) 40:415-436. doi:10.1146/annurev.ecolsys.110308.120317

Scott-Samuel, N E, Baddeley, R, Palmer, C E, Cuthill, I C. "Dazzle camouflage affects speed perception." *PLoS ONE* (2011) 6(6):2-6.
doi:10.1371/journal.pone.0020233

Shannon, C E. "A Mathematical Theory of Communication." *Bell Syst Tech J* (1948) 27(3):379-423.

Stevens, M, Merilaita, S. "Animal camouflage: current issues and new perspectives." *Philos T R Soc B* (2009) 364:423-427. doi:10.1098/rstb.2008.0217

Stewart, W J, Cardenas, G S, McHenry, M J. "Zebrafish larvae evade predators by sensing water flow." *J Exp Biol* (2013) 216:388-98. doi:10.1242/jeb.072751

660 Webb, P W. "Speed, acceleration and manoeuvrability of two teleost fishes." *J Exp Biol* (1983) 102:115-122.

Webster, D B, Webster, M. "Adaptive Value of Hearing and Vision in Kangaroo Rat Predator Avoidance." *Brain Behav Evol* (1971) 4:310-322.

Wilson, A M, Lowe, J C, Roskilly, K, Hudson, P E, Golabek, K A, Mcnutt, J W.
665 "Locomotion dynamics of hunting in wild cheetahs." *Nature* (2013)
498(7453):185-189. doi:10.1038/nature12295

Yuan, L C-L. "Homing and Navigational Courses of Automatic Target - Seeking Devices." *J Appl Phys* (1948) 19:1122-1128. doi:10.1063/1.1715028

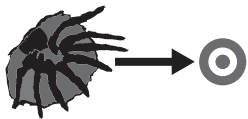
670 **Fig. 1** Schematic showing the predation strategies discussed in this paper. Black arrows indicate predator movement, gray arrows indicate the movements of prey
Solid lines indicate the velocity of currents, dashed lines indicate future trajectories predicted by the predators. A) Ambush Predation is represented by the trapdoor spider, *Misgolas rapax* (Bradley, 1996). B) Ballistic Interception is
675 represented by the dragonfly, *Plathemis lydia* (Mischiati et al., 2014). C) Pursuit Predation is represented by the big brown bat, *Eptesicus fuscus* (Ghose et al., 2009).

Fig. 2 Schematic showing how increases in maneuverability and variability contribute to greater entropy, or unpredictability. Dashed lines indicate directions in which the animal is capable of moving, and the length of the dashed line indicates the speed with which the animal is capable of moving in that direction. Solid lines indicate theoretically observed trajectories. Entropy, or unpredictability, is maximized when the number of possible trajectories increases and each of the possible trajectories are used with equal probability (quadrant B).

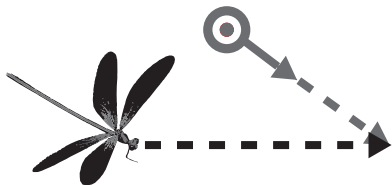
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Table 1 Studies in various fields, and in various model systems that share a common predation strategy. See References for full citations.

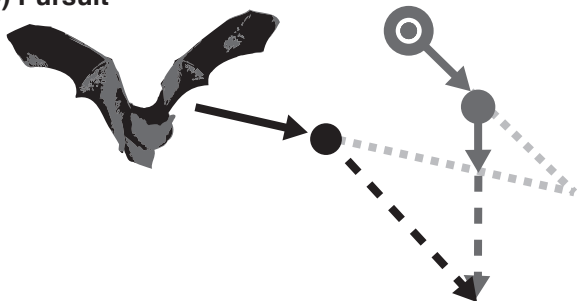
A) Ambush



B) Ballistic Interception

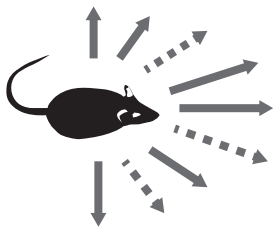
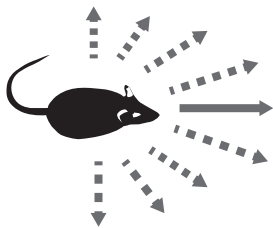


C) Pursuit



High Maneuverability

High Entropy



Low Variance

A) B)
C) D)

High Variance



Low Entropy

Low Maneuverability

	Ambush	Ballistic-Interception	Pursuit
Theory	Caraco 1986 <i>Spider</i>	Rossell 2002 <i>Archer fish</i>	Howland 1974 <i>Falcon</i> Broom 2005 <i>Theoretical</i>
Biomechanics	deVries 2012 <i>Stomatopod</i>	Peters 1996 <i>Leopard Frog</i> Anderson 2012 <i>Chameleon</i> Mischianti 2014 <i>Dragonfly</i>	Ghose 2009 <i>Brown bat</i> Kane 2015 <i>Goshawk</i>
Behavioral Ecology	Fouts 1999 <i>Angel shark</i> Bradley 1996 <i>Trapdoor spider</i>	Combes 2010, 2012, 2013 <i>Dragonfly</i> Nishiumi 2014 <i>Snake</i>	Wilson 2013 <i>Cheetah</i>
Application	Ewert 2001 <i>Frog</i>	Scott-Samuel 2011 <i>Torpedo</i>	Yuan 1948 <i>Target-seeking devices</i>