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Citation	Moore, Talia Y., and Andrew A. Biewener. 2015. "Outrun or Outmaneuver: Predator–Prey Interactions as a Model System for Integrating Biomechanical Studies in a Broader Ecological and Evolutionary Context." Integr. Comp. Biol. (June 27): icv074. doi:10.1093/icb/icv074.
Published Version	doi:10.1093/icb/icv074
Citable link	http://nrs.harvard.edu/urn-3:HUL.InstRepos:25858000
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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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April 9, 2015

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

30 **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

35 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

40 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

45 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

85   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

90   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

95   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

100   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

125   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

130   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

135   (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

140   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

(Nishiumi 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

340   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

345   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

350   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

355   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

360   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

365   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

370   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

375   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

380   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

385   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

390   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

395   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 variabilitiy 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

440   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

445   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,

450   such as adaptive radiations following invasion of a novel locomotor matrix.

Funding

and a Deakin-Royce Graduate Research Fellowship from Harvard University

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

470   locomotion in horses and spinal circuit function in mice." *Nature* (2012)

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.

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

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

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.

Domenici P, Blagburn JM, Bacon JP. "Animal escapology II: escape trajectory

540   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

Dudley, R. "The Evolutionary Physiology of Animal Flight: Paleobiological and

545   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

Emlen, D J, Corley Lavine, L, Ewen-Campen, B. "On the origin and evolutionary

550   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

Faurie, C, Raymond, M. "Handedness, homicide and negative frequency -

560   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, Triblehorn, 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)

570   212:693-703. doi:10.1242/jeb.019380

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

Hagman, M, Phillips, B L, Shine, R. "Tails of enticement: Caudal luring by an

580   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)

610   88(3):595-605. doi:10.1644/06-MAMM-A-119R1.1

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

615   Affects Locomotion of Four Ecomorphs of *Anolis* Lizards." *Ecology* (2004)

85(4):1111-1124.

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*
650   (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*
655   (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

680   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).

685

Table 1 Studies in various fields, and in various model systems that share a

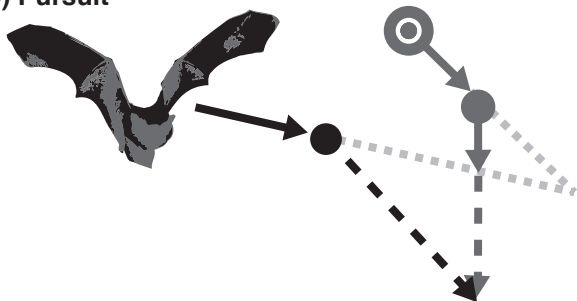common predation strategy. See References for full citations.
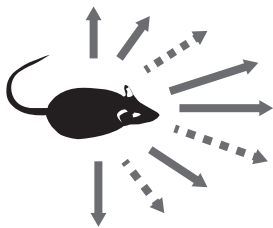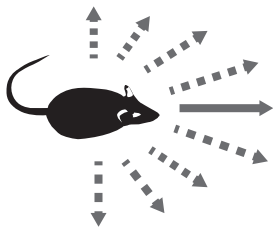
A) Ambush

B) Ballistic Interception

C) Pursuit

High Maneuverability

High Entropy

Low Variance

A) B)

High Variance

C) D)

Low Entropy

Low Maneuverability

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