

## Research

### Informational constraints on predator–prey interactions

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The rates of interactions between predators and prey are fundamental to population and food web dynamics. Yet, most ecological theory of predator–prey interaction rates deals exclusively with the first phase of an interaction, an encounter, and not the second phase, a capture or escape. Here, we present a simple dynamical model of prey capture that incorporates empirically observed behavioral strategies of pursuit by predators and evasion by prey. We parameterize the model with data from aquatic systems and analyze its dynamics. Our results show that empirically observed outcomes of predator–prey interactions cannot be predicted solely from biomechanical performance traits of predators and prey. Contrary to previous work, we show that it is only through the inclusion of informational constraints – constraints on the rate at which predator and prey process and respond to incoming sensory information – that the full range of empirically observed prey capture rates are predicted by the model. Our analysis also revealed that the outcome of predator–prey interactions can largely be predicted by the product of two measurable traits: the maximum speed of the prey and the sensory-motor delay that characterizes the time taken for the predator to respond to a change in the relative position of prey. Both of these traits exhibit power-law scaling with body size, suggesting that simple allometric relationships may characterize the outcome of predator–prey interactions across species. More broadly, our results suggest that informational constraints can have a dominant effect on predator–prey interactions, and that these traits should be considered alongside biomechanical performance to capture the fundamental properties of predator–prey interactions in nature.

**Keywords:** capture success, encounter rate, evasion, interaction rate, predator–prey, pursuit

#### Introduction

The rate of trophic interactions between predators and prey is perhaps the most important rate in population and food web ecology. The magnitudes and functional forms that describe predator–prey interaction rates can determine whether ecological communities exhibit stable equilibria, cycles or chaos (Oaten and Murdoch 1975, McCann et al. 1998, Gross et al. 2009, Hein and Martin 2020), how these

communities respond to perturbations and environmental change (Scheffer et al. 2001, Gil et al. 2020), and how energy and materials flow through food webs (de Ruiter et al. 1995, Berlow et al. 2004). Thus, a longstanding goal in ecology is understanding how predator–prey interaction rates vary with the densities and traits of predator and prey species.

To a large extent, the theoretical study of predator–prey interaction rates in ecology has been synonymous with the study of encounter rate: the rate at which predators and prey come into close enough proximity to interact. Ecologists have long modelled the rate of encounters between predators and prey by assuming this rate is given by mass-action (Lotka 1926), and although mass action is still widely used in many areas of ecology, this simplest of encounter rate models has also been substantively extended to account for processes like handling time, central-place foraging, interference, variable speed and directed search (Holling 1959, Skalski and Gilliam 2001, Williams et al. 2007, Gurarie and Ovaskainen 2012, Hein and McKinley 2013, Hein and Martin 2020, Martinez-Garcia et al. 2020). These theoretical extensions toward more biologically-motivated models of encounters are encouraging. However, an encounter between a predator and prey does not guarantee a trophic interaction; the predator must still capture the prey.

Given all the attention paid to the theory of encounter rates, it is somewhat surprising that the second phase of a predator–prey interaction – prey capture – has received comparatively little theoretical attention. Empirically observed capture success rates of predators are often remarkably low (often < 10%), but also quite variable (Vermeij 1982, Stander 1992, Sancho et al. 2000). Moreover, in highly productive ecosystems (e.g. a coral reef), densities of predators and prey can be so high that rates of prey consumption are unlikely to be limited by the frequency of predator–prey encounters (Stewart and Jones 2001), but instead by the fraction of encounters that result in capture. Taken together, these observations suggest that the ability of predators to capture prey after encountering them is likely to be an important constraint on trophic interaction rates, at least under some conditions. Determining the regimes in which capture success is a rate-limiting process, and identifying how predator and prey traits affect capture success are two clear theoretical challenges that deserve more attention than they have received.

The low capture success of predators measured in at least some empirical systems is surprising, given that predators are typically larger, faster and more powerful than their prey. For example, in aquatic systems, predators feed on prey that are on average 1/5th their size in terms of body length (Dunic and Baum 2017). Speed increases roughly in proportion to length in swimming organisms (Hirt et al. 2017), meaning that typical aquatic predators are capable of speeds five times faster than the speeds of their prey. Biologists have primarily tried to resolve the paradox of how capture rates can be low when differences in predator and prey performance are so large by focusing on biomechanical tradeoffs (Domenici 2001, Moore and Biewener 2015, Wilson et al. 2018). This body of theory holds that prey can offset a disadvantage in

speed and power with an advantage in some other performance trait that can aid in escape. For example, while smaller prey are generally slower than their predators (Hirt et al. 2017, 2020), they are also generally more maneuverable (Domenici 2001); thus small prey may be able to escape large predators by outflanking them with a well-timed sharp turn (Howland 1974). Despite the appeal of this idea, mathematical models of this ‘turning gambit’ have been unable to fully explain the high rate of successful escapes by prey (Howland 1974, Corcoran and Conner 2016). For example, applying this theory using empirical estimates of speed (Hirt et al. 2017) and maneuverability (Domenici 2001) for aquatic species, yields the unrealistic prediction that most prey species should be incapable of ever outmaneuvering their predators to avoid capture.

Here, we show that focusing on biomechanics alone misses an essential feature of predator–prey interactions: while biomechanical traits are clearly relevant, their contribution to the outcome of a predator–prey interaction depends entirely on how they are used during the course of an interaction (Hein et al. 2020). For example, a predator’s strike, no matter how swift, will fail to intercept prey if aimed in the wrong direction. We show that the unrealistically high rate of capture success predicted using biomechanical theory of predator–prey interactions (Domenici 2001, Portalier et al. 2019) can be resolved by incorporating the fact that predators and prey are also subject to ‘informational constraints’: that is, constraints on how sensory information is taken in, processed and acted upon during predator–prey interactions. We develop a simple dynamical model of predator–prey pursuit–evasion interactions, in which predators use reactive feedback control to intercept their prey (Brighton et al. 2017), and prey use a collision–detection strategy to time escape maneuvers in response to predators (Peek and Card 2016). To anchor our model to empirical data, we use parameter estimates from predator–prey interactions in aquatic ecosystems.

## Material and methods

### Model setup

Our model of predator–prey interactions describes visually-guided interception and evasion behavior of a predator–prey system in two-dimensional space. We focus on a two-dimensional model because it generalizes well to other ecological systems (e.g. terrestrial interactions), and because predator–prey interactions in many aquatic and aerial systems are at least approximately two-dimensional (e.g. benthic interactions, Hein et al. 2018; aerial predators hunting terrestrial prey, Brighton and Taylor 2019). We focus on the pursuit phase of predator–prey interactions, where the predator has already encountered its prey and initiates pursuit in an attempt to intercept the fleeing prey. The goal of the predator during this phase of the interaction is to adapt its trajectory to intercept the prey. The goal of the prey is to initiate an escape maneuver at the correct time and along the

correct trajectory to avoid capture. While this model does not include all the nuances of predator–prey interactions observed in the field, it contains the essential elements we wish to study: biomechanical and informational constraints on predator and prey maneuvers, and feedbacks between predator and prey behaviors.

## Predator behavior

Many predators, including bats, birds, fish and insects appear to pursue their prey using behaviors that are well-approximated by simple reactive feedback control rules, wherein the predator continually adjusts its attack maneuver in response to incoming sensory information about the prey’s location (Haselsteiner et al. 2014, Bar et al. 2015, Brighton et al. 2017, 2020, Brighton and Taylor 2019, McHenry et al. 2019, Hein et al. 2020). The most widely supported models of such feedback control is known as proportional navigation (PN; Brighton et al. 2017, 2020, Wardill et al. 2017, Fabian et al. 2018, Brighton and Taylor 2019). Predators implementing PN attempt to turn in a way that counteracts perceived changes in the bearing angle to the prey (i.e. the line-of-sight angle to the prey, Fig. 1A), produced by changes in the relative position of predator and prey. This can be achieved using a simple control rule, under which predator turning rate is given by:

$$\frac{dh}{dt} = k \frac{d\theta(t - \delta_A)}{dt} \quad (1)$$

where,  $h$ , is the predator’s heading,  $\theta$  is the bearing angle between predator and prey,  $k$  is a ‘turning gain’ term that determines the sensitivity of turning to perceived change in bearing angle, and  $\delta_A$  is the sensory-motor delay time associated with turning in response to a change in bearing angle (Fig. 1A). Using empirical studies as motivation, we assume that predators attempt to intercept prey using the PN control rule described in Eq. 1. We incorporate biomechanical constraints on turning as a ceiling on the absolute turning rate of the predator, such that the absolute turning rate does not exceed maximum turning rate (Åström and Murray 2010). In this model, the fundamental sensory variable used by the predator is the rate of change in the bearing angle of the prey,  $\frac{d\theta}{dt}$ , which encodes information about the relative motion of predator and prey (Nahin 2012, Brighton et al. 2017). The key informational constraint is the sensory-motor delay,  $\delta_A$ , associated with responding to a perceived change in bearing angle. Sensory-motor delay is a fundamental constraint faced by all organisms: perceiving sensory cues, processing those cues and sending them to the motor system takes time (Borghuis and Leonardo 2015). This means that there is a delay between the time when an event occurs (e.g. a fleeing prey begins a turning maneuver), and the time when the animal is capable of altering its own motion in response to that event. Mathematically, this can be incorporated through delays such as the delay time,  $\delta_A$ , in Eq. 1.

## Initial conditions

Our model focuses on the pursuit phase of the predator–prey interaction, where the predator has encountered and begun pursuit of a fleeing prey, and both predator and prey have accelerated to their maximum speeds. From an ecological perspective, one can think of this as the next step in a predator–prey interaction after an encounter has occurred. In the early stages of this phase, proportional navigation by the predator will quickly guide the predator onto a collision course with the prey by nulling the change in bearing angle (Fig. 1C, Nahin 2012, Brighton et al. 2017). The bearing angle at which predators close in on prey depends primarily on the initial flight direction of the prey. To explore how evasion performance depends on the approach angle of the predator, we simulated scenarios where the predator approaches prey with a constant bearing angle, but bearing angles vary across simulations from 0 (a tail-chase) to  $\pi$  (head-on approach).

## Prey behavior

The use of a timed, high-speed evasion maneuver is a widespread behavioral motif used by prey to evade predators (Domenici et al. 2011). Such maneuvers are often triggered in response to sensory cues produced by an approaching predator (Fotowat and Gabbiani 2011, Peek and Card 2016). We assume prey attempt to evade predators by initiating maneuvers in response to visual sensory cues produced by the predator’s approach. Rather than assuming prey use a distance threshold (Cooper and Blumstein 2015) or some other metric that the prey may not be able to measure directly, we assume prey use visual cues generated by the predator’s approach to determine when to initiate escape maneuvers (Fotowat and Gabbiani 2011, Peek and Card 2016, Hein et al. 2018). Two visual features that are readily accessible to prey are the relative size of the predator in the visual field (i.e. the angle subtended by the predator on the retina of the prey),  $S$ , and the rate of change of this angle,  $S'$ . These variables have been hypothesized to be the raw sensory inputs visual animals use to anticipate a collision, and there is extensive and growing knowledge of how vertebrates and invertebrates measure and encode these variables in the retina and downstream brain regions (e.g. birds: Sun and Frost 1998, locusts: Hatsopoulos et al. 1995, flies: Klapoetke et al. 2017, fish: Dunn et al. 2016, mammals: Zhao et al. 2014; reviewed in Fotowat and Gabbiani 2011, Peek and Card 2016, Branco and Redgrave 2020). Of the range of possible visual cues animals could use to make decisions about when to flee, the perceived angular size and expansion rate of a visual object are particularly valuable because, together, these two visual cues encode an estimate of the time to collision,  $\tau$ , (Lee 1976) between the predator and the prey:

$$\tau \approx \frac{S(t - \delta_E)}{S'(t - \delta_E)} \quad (2)$$

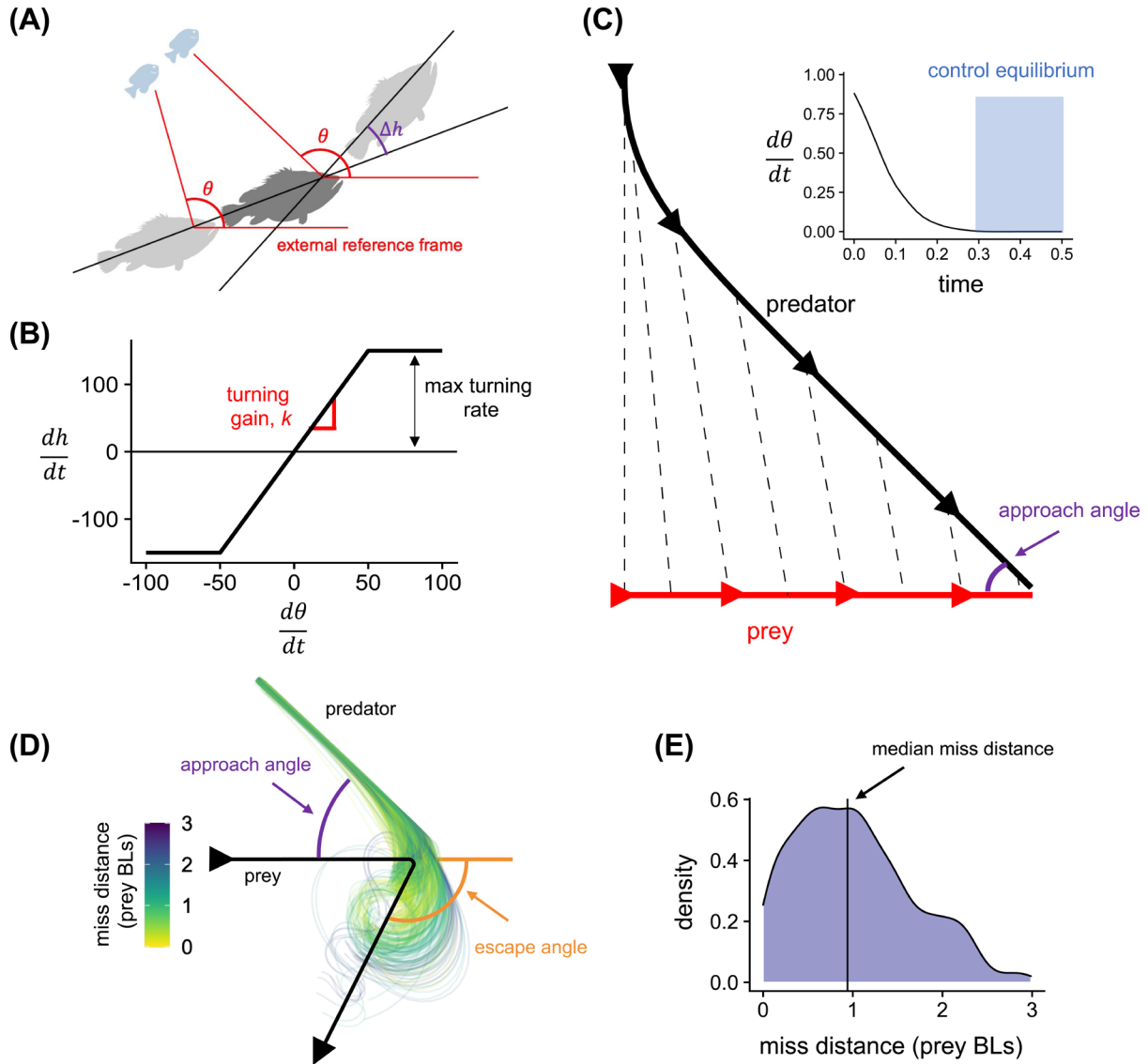


Figure 1. Model setup. (A–B) Schematic of proportional navigation, where predator turning,  $dh/dt$ , depends on the change in bearing angle,  $\theta$ , which is the line of sight to the prey with respect to an arbitrary reference frame, and can be measured from a combination of inertial cues by the vestibular system and the movement of the target’s image along the retina (Brighton and Taylor 2019). In this example,  $\theta$  becomes more negative between consecutive measurements, which in turn triggers a left turn by the predator. The turning rates of predators are capped at the maximum turning capacity of the predator (C). The trajectory of a PN predator as it intercepts a moving prey; dashed lines show the bearing angle to prey at successive times. Early in the interception, the prey’s motion causes a change in bearing angle, which in turn elicits turning by the predator. (Inset) The PN guidance law eventually drives the predator to a control equilibrium where  $\theta$  does not change as the predator closes in on a collision course with the prey. For simplicity, we begin our simulations with predators approaching prey such that  $\frac{d\theta}{dt} = 0$ , and we explore simulations with different approach angles by the predator, ranging from 0 (tail-chase) to  $\pi$  (head on collision). (D–E) For each parameter combination we run 1000 replicate simulations and record the minimum distance (referred to here as ‘miss distance’) of the predator during each attack. Variation among tracks is driven by variability in predator speed and turning gain. We record median miss distance across 1000 simulations as a metric of evasion performance.

We therefore assume that prey initiate an evasive maneuver when  $\tau$  falls below a critical threshold,  $\tau_c$ , where again  $\delta_E$  is a sensory-motor delay of the prey associated with responding to visual input.

We model the prey evasion maneuver by assuming at initiation that the prey begins to turn to a new target heading,

which is shifted from the original heading by an angle,  $\alpha$ . Thus, when an evasion maneuver is triggered, the prey draws a new target heading ( $h + \alpha$ ), turns to this new heading at its maximum turning rate, and then maintains this new heading while fleeing. This sequence approximates the rapid turn-and-accelerate behavior displayed by many species as they flee

(Domenici et al. 2011, Dunn et al. 2016, Hein et al. 2018). To identify optimal evasion strategies against predators implementing proportional navigation, we explore ranges of values for both the threshold critical ratio,  $\tau_c$  (from 0 to 0.5 s), and turn angle,  $\alpha$  (from  $-\pi$  to  $\pi$ ).

### Capture/evasion success

For the purpose of calculating whether a given predator–prey interaction results in a capture or an escape, we assumed that attacks terminate at time  $t$  if the distance between the predator and prey increases above its previous minimum by a factor,  $\epsilon$ . We used a value of 2 for  $\epsilon$ , however our results are qualitatively insensitive to the exact value for reasonable ranges (e.g.  $\epsilon < 4$ ). Our conclusions are robust to this choice of stopping rule as predators rarely came closer to the prey on secondary approaches (Supporting information). We used the minimum distance between the predator and the prey during the entire trajectory as the metric of capture–evasion performance. High values of this distance will correspond to low capture rates (i.e. good for the prey), and low values of this distance will correspond to high capture rates (i.e. good for the predator).

### Reference parameters

The key parameters in our model are the velocities, maneuverability (i.e. minimum turning radius), and the sensory-motor delays of the predator and prey. We compiled data for these traits for aquatic animals to generate an empirically grounded reference set of parameter values, and we explored the sensitivity of evasion performance to the parameters of both the predator and prey within and around this regime.

#### Maximum velocity

For aquatic animals, maximum velocity scales with body mass to the  $1/3$  power over roughly eight orders of magnitude (Hirt et al. 2017). We converted masses (kg) to lengths (m) assuming  $M = 20 L^3$ . For animals larger than approximately

two meters in length, maximum velocity plateaus and then begins to decrease with size (Fig. 2A, Hirt et al. 2017). For simplicity, we restrict our analysis to body sizes below this length. Over the range of interest, maximum velocity is proportional to length:

$$V(L) = bL \quad (3)$$

where for aquatic animals  $b \approx 10$  ( $\text{s}^{-1}$ ; Fig. 2A, Hirt et al. 2017), and thus maximum velocity is approximately ten body lengths per second.

#### Maneuverability

We define maneuverability as the minimum turning radius an animal can achieve. For aquatic animals, the maneuverability of an animal is proportional to its length but largely independent of its speed (Fig. 2B, Domenici 2001). Aquatic animals are highly maneuverable, with minimum turning radius typically just a fraction of body length (Domenici 2001). Based on data from Domenici (2001, Fig. 2B) we assumed that minimum turning radii is related to length by:

$$R(L) = cL \quad (4)$$

where  $c$  is 0.15 (dimensionless, Fig. 2B). The maneuverability and maximum velocity, in turn, determine the maximum turning rate of the individual, where  $dh_{\max} (\text{rad s}^{-1}) = V/R$  (Fig. 1B).

#### Prey and predator body size

Because both maximum velocity and maneuverability scale with body size, the relative locomotor performance between prey and their predators is, in large part, determined by the ratio of prey and predator body size. Predator–prey body size ratios tend to be independent of the size of prey, with predators feeding on prey typically five times smaller in length (Dunic and Baum 2017). However, predator–prey body size

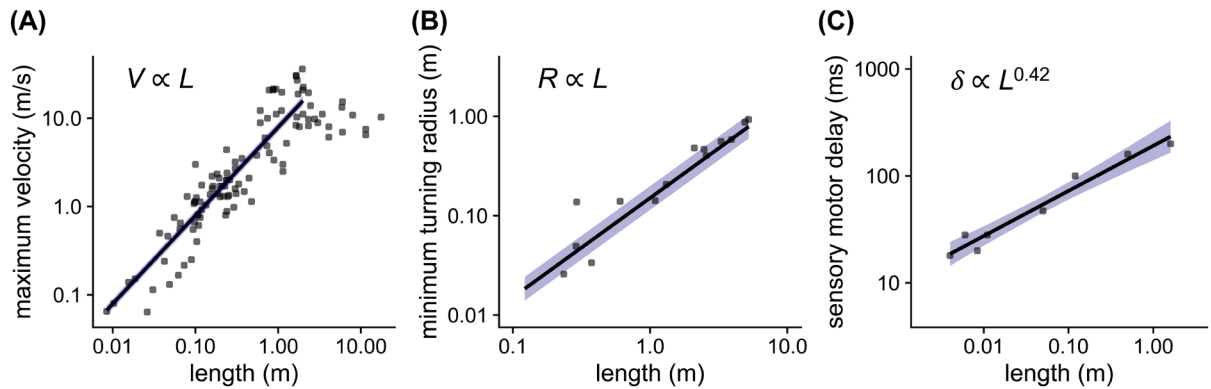


Figure 2. (A) Maximum velocity of aquatic species is proportional length over much of the empirical range of body lengths (data from Hirt et al. 2017). (B) Maneuverability is proportional to length in aquatic animals, and thus minimum turning radius is independent of size. Data from Domenici (2011) for fishes and cetaceans. (C) Visual sensory-motor delay of animals as a function of body size (data compiled in this study).



ratios can also be highly variable (Brose et al. 2006, Dunic and Baum 2017). Therefore, in each simulation, we select a random predator relative size by drawing predator–prey length from an empirically determined log-normal distribution with log-mean 1.6, and log-standard deviation 0.6. Because speed and turning radius are proportional to length, and predator–prey body size ratios are independent of length, the model dynamics are independent of the size of the prey when the spatial dimensions are scaled by the body length of the prey.

### **Sensory-motor delay**

Unlike motor performance variables, there have been few cross-species analyses of the allometry of sensory-motor delays. We therefore searched the literature for estimates of sensory-motor delays for visual tracking tasks, and evaluated whether the duration of the delay scaled with body size (Fig. 2C). Due to the limited data availability for such estimates, we did not restrict our search to aquatic animals, as we do not expect a priori that such delays would differ between aquatic and terrestrial animals.

### **Predator turning gain**

Measured turning gains for predators implementing proportional navigation are variable, but typically range between 1 and 3 (Brighton et al. 2017, Brighton and Taylor 2019). For each simulation, we drew a random value of the predator gain parameter from a uniform distribution between 1 and 3.

### **Simulations**

For each set of parameter values we ran 1000 simulations with independently drawn predator–prey body size ratios and turning gains (Fig. 1D), and recorded the median miss distance of the 1000 simulations (Fig. 1E). Sensory information and control outputs of the prey and predator were updated at 100 Hz. In between updates, the movement of prey and predator were integrated by the ode45 solver in Matlab.

## **Results**

We first present how the ability of prey to evade predators depends on motor and sensory parameters when prey implement maneuvers (maneuver timing and direction) that maximize the miss distance of the predator. We then evaluate which tactics allow for optimal evasion performance. Because the sensitivity of evasion performance to sensory-motor traits was not qualitatively affected by the initial angle of attack of the predator, we first present the results for the tail-chase scenario (initial predator approach is from behind) in detail, before expanding to consider other approach angles.

### **The effects of biomechanical constraints on evasion performance**

For empirically realistic ranges (Fig. 2B), greater maneuverability of the prey did not improve escape performance

in the absence of informational constraints (Fig. 3A). Prey were unable to evade their predators by a significant distance ( $> 5\%$  of prey body length) regardless of the timing or direction of their escape maneuver (Fig. 3A). Although prey are smaller and, thus, generally more maneuverable than their predators, this advantage resulted in negligible miss distances due to the overall high maneuverability of aquatic animals (both predators and prey, Fig. 2B). In general, predators were able to rapidly adapt their interception trajectories to the evasive maneuvers by the prey. Thus, at least in aquatic systems, the greater maneuverability of prey is not sufficient to explain the ability of prey to evade reactive predators.

### **The effects of informational constraints on evasion performance**

While considering biomechanical constraints alone leads to the unrealistic prediction that aquatic prey should be unable to evade an attacking predator, predictions change considerably when informational constraints are included. In the presence of informational constraints (i.e. non-zero sensory-motor delays), median miss distance of the predator increased approximately in proportion to the length of its sensory-motor delay, whereas miss distance was independent of the sensory-motor delay of the prey (Fig. 3B–C). The latter phenomenon is due to the ability of prey to compensate behaviorally for long sensory-motor delay by initiating escape maneuvers earlier (i.e. at a larger value of  $\tau_j$ ).

In addition to being sensitive to the sensory-motor delay of the predator (Fig. 3B–C), the evasion performance of prey also depended on prey speed. Faster prey generated larger miss distances, and the median miss distance was approximately proportional to the product of prey speed and the length of the sensory-motor delay of the predator (Fig. 3C inset). Perhaps surprisingly, while the miss distance did depend on the speed of the prey, it was largely independent of the predator's speed (Fig. 3D), provided that the predator's maximum speed was greater than that of the prey. This suggests that it is not the relative speed advantage of predators per se that determine the outcome of an interception attempt. Rather, the outcome is determined by how unpredictable the prey's current location is. The predator is reacting to delayed sensory information, and thus error in the predator's estimate of the prey's location depends on the length of the delay and the rate of change in the prey's position (prey speed). Because maximum velocity of aquatic animals scales in proportion to body length (Fig. 2A), relative body speed (BL/s) and consequently the median miss distance (in units of prey body length) for a given sensory-motor delay is independent of size. However, we found that the length of the sensory-motor delay for visual tracking tasks increased allometrically with body length, with an exponent of 0.42 (95% CI: 0.34–0.50) (Fig. 2C). Thus, our model suggests that on average, due to their longer sensory-motor delays, larger predators will not be able to come as close to their prey (in units of prey body length) as smaller predators.

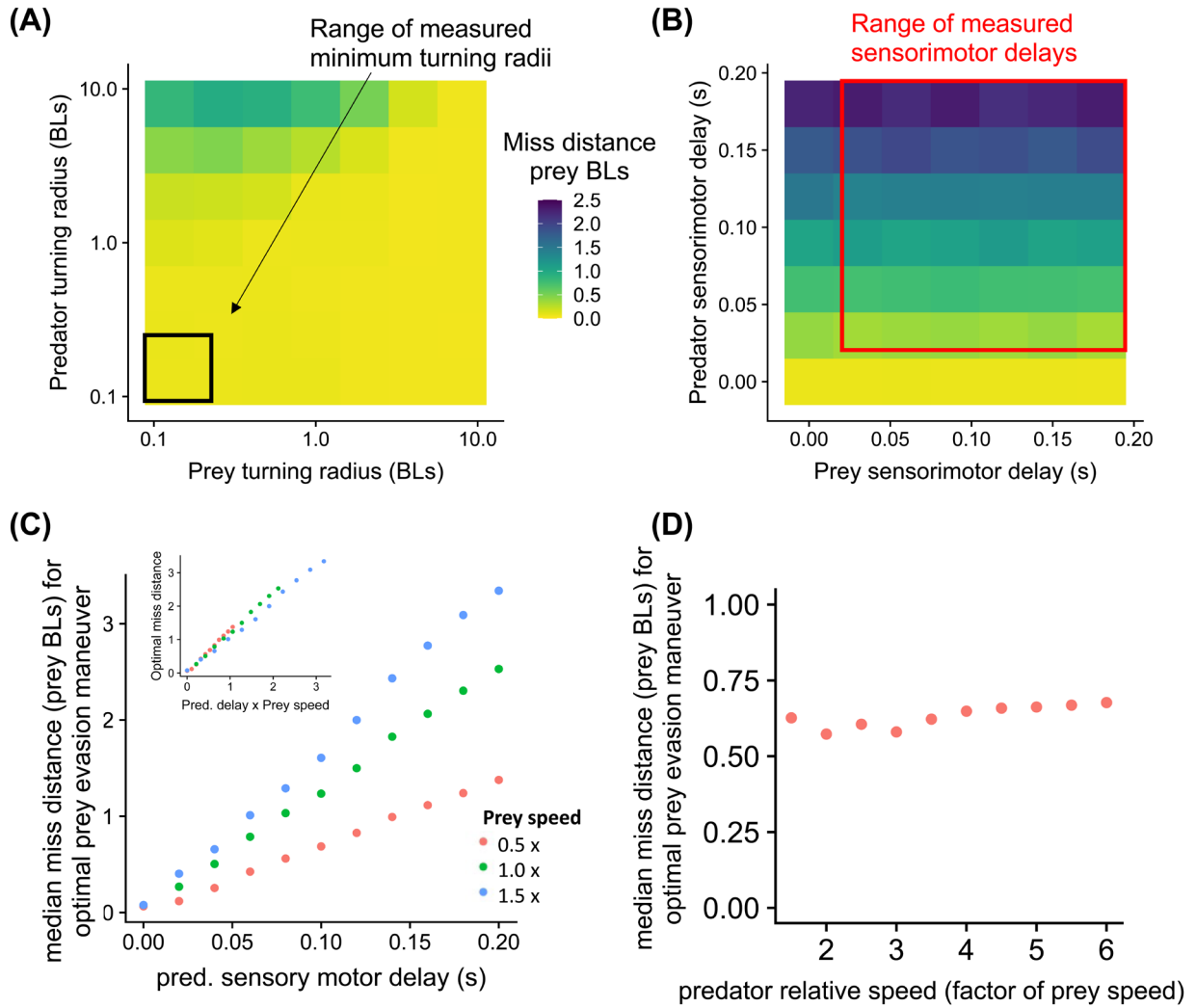


Figure 3. The effect of locomotor and sensory traits on evasion performance. (A) Prey evasion performance as a function of prey and predator minimum turning radii (in body lengths). Color denotes median miss distance in units of prey body length of predators over 1000 simulations, when prey implement optimal evasion behavior (timing and direction). (B) The effect of prey and predator sensory-motor delay on the evasion performance of prey (color denotes same metric as (A)). Red box denotes empirical range of visual sensory-motor delays (Fig. 2C). (C) The effect of prey speed and predator sensory-motor delay on evasion performance. Each point represents the median miss distance over 1000 simulations at a given prey speed and predator sensory-motor delay. Colors indicate simulations in which prey speed was increased (1.5 $\times$ ) or decreased (0.5 $\times$ ) relative to empirical scaling shown in Fig. 2A. (Inset) Miss distance (same data as C) as a function of the product of prey speed and predator sensory-motor delay. (D) Evasion performance is largely independent of predator speed. Data as in (C) (green points) but varying the predator speed between 1.5 and 6 $\times$  the prey speed (sensory-motor delay of predator and prey 0.05 s).

### Effective maneuvers for prey evading reactive predators

The optimal timing of evasive maneuvers by prey depended on the sensory-motor delay of the predator. In general, prey could initiate earlier evasive maneuvers that generated larger miss distances against predators with longer sensory-motor delays. For a given sensory-motor delay of the predator, the value of  $\tau_c$  that optimized prey escape performance was intermediate (Fig. 4A), suggesting a balance between two opposing mechanisms. If prey initiated responses too early (large  $\tau_c$ ) the predator adapted its trajectory to the new course of the prey. However, if the prey initiated a maneuver too late

(small  $\tau_c$ ) it was unable to move far enough from its original trajectory to create a significant miss distance. With longer sensory-motor delays, it became increasingly difficult for predators to adapt to earlier maneuvers by the prey, thus prey could initiate evasive maneuvers earlier (larger  $\tau_c$ ; Fig. 4A longer delays), move further out of the original path of the predator, and consequently generate larger miss distances.

In addition to the timing of an evasive maneuver, the direction of the evasive maneuver also had a large effect on the miss distance of the predator. Counterintuitively, optimal evasion maneuvers tended to be directed toward the approaching predator, but offset by approximately 45–60° (Fig. 5A). For example, in the case of a tail-chase, evasive

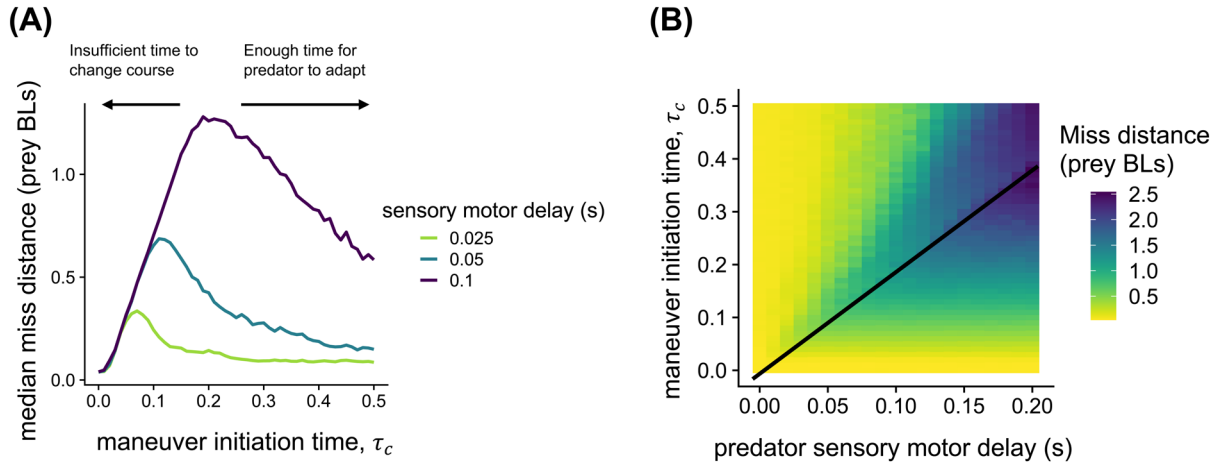


Figure 4. (A) The effect of evasion maneuver initiation time,  $\tau_c$ , on prey evasion performance for different predator sensory-motor delays,  $\delta_A$ . Prey implement an evasion maneuver when the estimated time to collision falls below a threshold value. The optimal value of this threshold increases with the length of predator sensory-motor delay. (B) Evasion performance as a function of  $\delta_A$  and  $\tau_c$  (The value of  $\delta_E$  did not affect evasion performance (Fig. 3B) and was set to zero). Color of tiles denote the median miss distance. Black line shows the best fit regression for the optimal  $\tau_c$  as a function of the sensory-motor delay of the predator.

turns of  $\sim 120^\circ$  (back towards the direction of the oncoming predator) tended to maximize evasion performance, while for head-on encounters, small turns of  $50^\circ$  maximized performance (Fig. 5A–B). By moving in the direction of the oncoming predator, prey allow a predator less time to adjust its course in response to the prey's maneuver. Additionally,

such turns tend to maximize the change in bearing angle perceived by the predator during an evasive maneuver, pushing the predators further from a control equilibrium.

Prey achieved comparable evasion performance for both tail-chase and head-on interception trajectories (Fig. 5A). However, optimal evasion maneuvers against predators

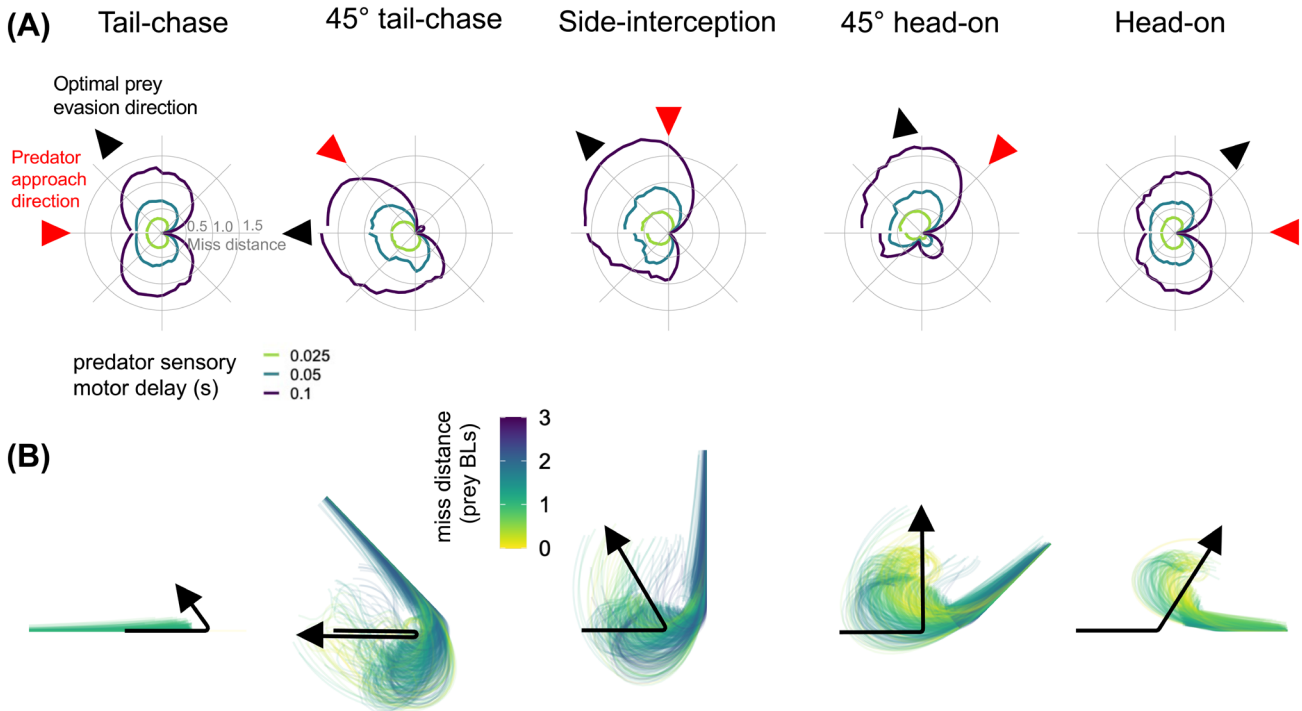


Figure 5. (A) Optimal evasion directions as a function of the approach angle of the predator. Lines denote the median miss distance from 1000 simulations for prey implementing an evasive turn to that direction for various sensory-motor delays of the predator. Red triangle indicates the approach direction of the predator, and the black triangle denotes the optimal escape angle. (B) Replicate predator interception trajectories (different lines) against prey implementing an optimal turn direction. The color of each predator trajectory is scaled by its miss distance. Shown are results for a predator sensory-motor delay of 0.1 s and  $\tau_c = 0.2$  s.



approaching from the side resulted in larger median miss distances (Fig. 5A). During side-interceptions, the predator's trajectory leads the prey's position, in order to null the change in bearing angle. Thus, as soon as the prey initiates a turn, it is already well out of the interception path of the predator (Fig. 5B). Prey evading predators in either a head-on or tail-chase engagement do not have this advantage, and their evasion performance is limited by the distance they can travel away from the original interception path of the predator.

## Discussion

Questions of how predators should behave to best capture their prey, and how prey should behave to best evade their predators have long fascinated biologists. Moreover, because capture rates vary considerably (Vermeij 1982, Stander 1992, Sancho et al. 2000), processes that influence capture rate have the potential to impact rates of trophic interactions. Classical biomechanical theory of prey capture and predator evasion posits that the motor performance capabilities of predator and prey determine the outcome of predator-prey encounters (Howland 1974, Domenici 2001). By extending this body of theory to allow for sensory-driven feedbacks between predator and prey movements, we show that, in empirically-grounded parameter regimes, the outcomes of such interactions are unlikely to be determined by biomechanics alone. Information acquisition and processing are essential. Ignoring informational constraints can lead to conclusions that are at odds with data from real ecological systems: for example, the prediction that aquatic prey cannot evade their predators (Fig. 3A–B, predator and prey sensory-motor delay = 0).

Our analysis reveals that the effectiveness of evasive maneuvers by prey can be predicted from two variables: the speed of the prey, and the sensory-motor delay of the predator. The product of these two variables is a measure of the distance between the true location of the prey at any time, and perceived prey location to which the predator is currently reacting. When prey implement an evasive maneuver, the distance they travel before the predator begins to perceive the turn is proportional to the product of the prey's speed and the predator's sensory-motor delay. It is this sensory constraint that appears to determine the outcome of predator-prey interactions when predators use an interception strategy consistent with proportional navigation. This conclusion differs from those drawn from existing theory of attack and evasion behaviors, where, typically, the outcome of predator-prey interactions is hypothesized to depend on differences in predator and prey motor performance (e.g. speed, maneuverability; Howland 1974, Domenici 2001). In our analysis, so long as predators are faster than prey, predator speed has little effect on capture success (Fig. 3D). This unexpected result occurs because, for a given distance from the prey, faster moving predators with sensory-motor delays have less time to adjust their headings to the new trajectory of the prey. This disadvantage of moving quickly toward a target negates any advantage the predator gains by prey having less

time to alter their course as the predator closes distance. As a result, the evasion performance of the prey is largely independent of predator speed. Thus, in the presence of perceptually delayed (via sensory-motor delays) feedbacks between predator and prey behaviors, it is not a biomechanical arms race (Wilson et al. 2018) between predator and prey per se, but an information race that determines the outcome of the interaction.

Our analysis revealed an asymmetry in the effect of sensory-motor delays on performance for predators and prey. The outcome of predator-prey encounters depended on the sensory-motor delay of the predator but not on that of the prey. This surprising result is caused by an information asymmetry inherent to attack and evasion behaviors. Information encoded in the apparent size and expansion rate of oncoming predators provides predictive information about the future trajectory of the predator. If the predator is to remain on a collision course with the prey, it must maintain its trajectory, and thus the behavior of the predator now must contain information about its behavior in the near future. On the other hand, the prey's trajectory is only predictable to a predator that is implementing proportional navigation if the prey does not change course. Because the objective of the prey is to avoid being captured, prey have an incentive to initiate an evasive maneuver, to which predators can only react with delay. This difference in objectives and the predictive information available to predator and prey helps to explain the advantage of 'brinkmanship' – waiting until the last moment to respond to an adversary – in predator-prey interactions. A prey's evasion performance is maximized when it responds not as early as possible, but at intermediate times before collision with the predator (Fig. 4A). Timing an escape maneuver such that it is close to the time of collision ensures that the predator does not have time to correct course. As the predator's delay gets shorter, the optimal response time draws closer to the time of collision (compare curves in Fig. 4A). One strategy that we have not studied here by which predators could potentially improve performance is to accelerate or decelerate during the terminal stages of attacks. This would introduce error in the prey's estimate of time to collision (assuming the prey uses a constant-speed approximator like the one assumed in Eq. 2), potentially causing prey to initiate an evasive maneuver earlier or later than the optimal time. However, because prey could generally achieve large miss distances over a range of evasion times, we expect that this strategy would only lead to modest reductions in the evasion performance of prey.

Our analysis suggests that differences in maneuverability between predators and prey cannot fully explain the outcomes of predator-prey interactions in aquatic systems. Although we used a different modelling framework, our results agree qualitatively with predictions from the turning gambit theory of Howland (1974) within the range of measured speeds and maneuverabilities for aquatic animals. The key result from the turning gambit is that slower, more maneuverable prey can escape their predators with a sharp turn when their relative velocity,  $v$  ( $V_{\text{prey}}/V_{\text{predator}}$ ), is greater than the square root of their relative turning radius,  $r$ :  $v > r^{0.5}$ .

Because both velocity and minimum turning radius are proportional to body length for aquatic species, this condition will not be met, except in cases where predators are substantially slower or less maneuverable than expected for their sizes, or in cases where the ratio of predator to prey body size is extremely large (Cade et al. 2020). Moreover, even in such cases, the small turning radii of aquatic species only allow for small miss distances, which would likely be within the capture radius of a predator; typical turn radii are less than 0.2 body lengths, and aquatic predators are on average five times longer than their prey; thus, the best case scenario for a turning gambit would result in a miss of only  $\sim 4\%$  of the body length of the predator. Incorporating realistic sensory-motor delays completely changes this prediction, suggesting that prey can generate miss distances an order of magnitude larger than those predicted under turning gambit theory. While our model idealizes predator and prey strategies, we based the model on the finding that many predators use interception strategies well-approximated by proportional navigation (Haselsteriner et al. 2014, Brighton et al. 2017, 2020, Wardill et al. 2017, Fabian et al. 2018, Brighton and Taylor 2019), and that many prey species use visual cues related to the apparent size and expansion rate of an approaching object to trigger escape maneuvers (Fotowat and Gabbiani 2011, Peek and Card 2016, Hein et al. 2018).

Our model is only slightly more complex than the open-loop models commonly used in biomechanics to study prey capture and predator evasion (Howland 1974, Kawabata et al. 2020). However, it is significantly more detailed than common approaches taken in ecology to model capture success. Indeed, one of the most widespread assumptions in ecological models is that capture success per predator-prey encounter is simply a constant. A critique one could levy against the added complexity of our model is that a model with this level of detail is unlikely to lead to any generalities that would prove useful in ecological studies that do not explicitly model or measure pursuit and evasion behavior. On the contrary, a central conclusion of our analysis is that, at least in aquatic ecosystems, a key quantity that determines capture success – the minimum distance between predators and prey during an interaction – is a function of two simple, measurable traits: the sensory-motor delay associated with the predator’s steering, and the speed of the prey during rapid evasion maneuvers (Fig. 3C). Maximum speed is proportional to body length across a wide range of body sizes ( $V \propto L_{\text{prey}}$ ; Fig. 2A, Hirt et al. 2017), and while more comprehensive measurements of sensory-motor delay are needed, this quantity also appears to scale predictably with body size (delay  $\propto L_{\text{pred}}^{0.42}$ ; Fig. 2C). Thus, the outcome of dynamical interactions between predators and prey can be understood, at least to a first approximation, in terms of an informational constraint (predator sensory-motor delay) and a biomechanical constraint (prey escape speed), both of which scale with the body sizes of predator and prey in predictable ways. These findings point toward the possibility of a general scaling theory of capture rate that would express capture probability during a predator-prey interaction as a function of predator and prey

traits. While our results rely on numerical solutions to control equations across a range of initial conditions and parameters values (Fig. 3–5), it is worth noting that one could also pose the problem of predator-prey pursuit-evasion interactions as a differential game. Indeed, there is a significant literature on such pursuit-evasion games, and much of this literature is applicable to predator-prey interactions (Ho 1965, Nahin 2012). Casting the model developed here as a differential game could provide insights about what behaviors predators and prey should use during encounters, however the main challenge will be retaining sufficient biological realism (e.g. movement constraints, sensory-motor delays) while maintaining analytical tractability.

We modelled relatively simple predator-prey interactions between a single predator and prey in two-dimensional space, however this framework can be extended to consider more complex interactions. For predator-prey interactions that occur in three-dimensions, proportional navigation guides predator turning along both a horizontal and vertical axis (Fabian et al. 2018, Brighton et al. 2019). We expect that the qualitative conclusions from our analysis, that delays in the time it takes predators to act on sensory information allow prey to evade biomechanically superior predators, will hold in three dimensions. However, we hypothesize that sensory motor delays benefit prey even more in three-dimensions as predators must respond to prey maneuvers by turning appropriately along two axes rather than one. Extensions of this model could also be applied to consider predator-prey interactions between multiple predators or prey. For example, some predators hunt in groups (Handegard et al. 2012), which may improve their capture success because a well-timed evasive maneuver against one predator may be poorly timed with respect to other approaching predators. Conversely, the interception abilities of predators that hunt groups of prey may be diminished by disruptions to proportional navigation when the focal prey becomes temporarily occluded by other prey, providing a mechanistic basis for the so-called ‘confusion effect’ (Landeau and Terborgh 1986). We expect that extensions of the simple dynamical model developed here will shed light on the behavioral and biomechanical determinates of predator-prey interactions across a diverse range of systems.

The result that informational constraints can dictate the outcome of predator-prey interactions has implications for human impacts on predator-prey interaction rates in the Anthropocene. In particular, sensory pollution – the addition of novel chemical and physical stimuli to the environment by humans (Dominoni et al. 2020) – has the potential to disrupt interactions by changing key parameters of the behavioral algorithms predators and prey use to interact with one another. For example, noise pollution can disrupt perception of predator acoustic cues, and chemical pollution can disrupt or mask perception of prey scent cues (Dominoni et al. 2020). Because both predators and prey rely on sensory cues to detect and interact with one another, how sensory pollution will ultimately impact predator and prey performance is not totally straightforward to discern. In this respect, the type

of algorithmic models we present here are particularly useful because they provide a quantitative framework with which to evaluate outcomes. As an example of this, anthropogenic eutrophication of freshwater as well as runoff can increase turbidity. High turbidity decreases visual ranges but it also interferes with perception of contrast (Cronin et al. 2014). From the perspective of prey, contrast is an important driver of escape responses: animals exhibit higher probability and more rapid escape responses to high contrast objects than to low contrast objects (Evans et al. 2018, Fernandes et al. 2021). This effect could be manifested in prey behavior, for example, by shorter detection ranges, noise in loom rate and size perception and increased sensory-motor delays in Eq. 2 above, and in predator behavior by changes in visual range and error in bearing angle estimates due to reduced visual perception of the prey's body. Importantly, the algorithmic models developed here provide a way of connecting measurable changes in the sensory abilities of predators and prey with their consequences for predator-prey interactions.

In contrast with the predictions of classical models of the outcome of predator-prey interactions, our analysis reveals that, at least in aquatic systems, it is informational constraints, not motor constraints, that grant smaller, slower prey the ability to evade their predators. The modeling framework introduced here to study predator-prey interactions represents a first step toward explicitly considering feedbacks between predator and prey behavior and the informational constraints involved in such feedbacks. Although our model includes only a small set of sensory variables – measurements of relative angles and sizes of visual objects and the sensory-motor delays associated with responding to such measurements – explicitly including these variables makes it possible to link these models with lower-level, mechanistic models of neural implementation (Hein et al. 2020). We view this as an essential step in the future development of models of predator-prey interactions in ecology. As new discoveries are made in the neuroscience and ethology of natural behaviors, these findings can be used to inform our understanding of the ecology and evolution of predator-prey interactions.

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## Data availability statement

Code and data are available from the GitHub repository: [https://github.com/btmarti25/Informational\\_constraints\\_on\\_predator-prey\\_interactions](https://github.com/btmarti25/Informational_constraints_on_predator-prey_interactions).

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