

Optimizing prey-capture behaviour to maximize expected net benefit

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ABSTRACT

Biologists have long known that predators vary (modulate) their prey-capture behaviour in response to different prey. We propose an optimization model to predict when and why capture behaviour should vary. The predator's attack 'effort' (reflecting any unidimensional kinematic variable such as acceleration) determines both the probability of capturing the prey and the energetic cost of attack. The optimal capture effort then reflects a balance between the marginal benefit of greater success and the marginal cost of added energy outlay. Using this model, we explore how the optimum responds to variation in prey traits (evasiveness and energy value). The model predicts three different types of response to prey variation: (1) no modulation, (2) increased effort for more elusive prey and (3) decreased effort for more elusive or lower energy prey.

Keywords: capture success, foraging costs, modulation, optimal foraging theory, prey-capture.

INTRODUCTION

Many predators vary their prey-capture behaviour in response to the characteristics of the target prey (Liem, 1978; Lauder *et al.*, 1986; Nemeth, 1997a; Ferry-Graham, 1998). For example, large pelagic perch (*Perca fluviatilis*) used significantly different attack initiation distances ('ram distance') when fed *Chaoborus* and mayfly larvae (R. Svanbäck and P. Eklöv, unpublished). This prey-specific capture effort, known as 'modulation', is thought to reflect adaptive behavioural plasticity on the part of the predator. The predator evaluates an individual prey and chooses an appropriate attack tactic. Here, we develop a model of the prey capture costs and benefits that determine the value of a given capture strategy. To do this, we specify three functions: (1) the nature of the reward for an attack, (2) how to model attack behaviours and (3) how prey characteristics and attack behaviours affect the reward for an attack. Applying optimization techniques, we show how such a model could predict the appropriate tactic for a given prey, and use this to hypothesize when a predator will and will not modulate its capture efforts in response to different prey.

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THE REWARD FOR AN ATTEMPTED ATTACK

When a predator attempts to consume a prey, the reward for that action comes in the form of energy income. Empiricists generally measure this value as the number of joules contained in an individual food item, e_{prey} (Sih and Christensen, 2001). However, the value most relevant to the predator, the energy income gained from an attack, is not the same as the energy content in the prey. The net energy income from an attack, e_{net} , is less than e_{prey} because only a fraction (a) of the prey's energy is assimilated during digestion, and because prey capture involves energetic costs (e_{capture}) that must be subtracted from the assimilated income. Consequently,

$$e_{\text{net}} = ae_{\text{prey}} - e_{\text{capture}} \quad (1)$$

assuming that a prey-capture attempt is always successful. In fact, attack success may be quite low in natural settings (Mech, 1966; Nyberg, 1971; McLaughlin *et al.*, 2000) and can significantly alter a predator's diet preferences (Drenner *et al.*, 1978; Vinyard, 1980) and behaviour (Nemeth, 1997a). The predator will only gain a positive e_{net} if capture is successful, otherwise capture energy is expended with no return. If P_{capture} is the probability of a successful capture, then the energetic reward for an attack is a Bernoulli random variable:

$$e_{\text{net}} = \begin{cases} ae_{\text{prey}} - e_{\text{capture}} & \text{if successful} \quad (\text{Pr} = P_{\text{capture}}) \\ -e_{\text{capture}} & \text{if unsuccessful} \quad (\text{Pr} = 1 - P_{\text{capture}}) \end{cases} \quad (2)$$

This formulation assumes that, once an attack is initiated, it is carried out in full, so that the energy expenditure is all or nothing. This may be realistic for some predators, such as fish, which rarely truncate an attack after the strike portion is initiated (the strike is defined here as that portion of the attack beginning with initiation of jaw-opening; L.A. Ferry-Graham and J. New, personal observation). In other settings, prey may escape midway through a capture sequence resulting in an aborted attack. Partial costs can either be modelled explicitly by breaking an attack down into stages, with the possibility of prey escape during each (Appendix 1), or implicitly by weighting the capture costs with a variable representing the fraction of costs expended before prey escape (Sih and Christensen, 2001). These modifications do not change the fundamental results of our model, but do make it harder for empiricists to parameterize the necessary functions.

When a predator initiates a capture attempt, it does not know in advance whether its attack will be successful. Consequently, we assume that the predator evaluates the prey on the basis of the expected, or average, e_{net} rather than the maximum potential e_{net} or e_{prey} that is often used in empirical applications of optimal foraging theory (Sih and Christensen, 2001). Such a predator, when choosing between alternative prey of equal e_{prey} , should prefer the prey with the higher capture probability. The expectation and the variance in energy income are easily calculated:

$$E(e_{\text{net}}) = ae_{\text{prey}}P_{\text{capture}} - e_{\text{capture}} \quad (3)$$

$$V(e_{\text{net}}) = a^2e_{\text{prey}}^2P_{\text{capture}}(1 - P_{\text{capture}}) \quad (4)$$

The 'reward' for an attempted attack on a prey is thus the expected net benefit (ENB = $E(e_{\text{net}})$). This value will vary with the exact nature of the prey, which affects P_{capture} and e_{prey} , and the predator's behaviour, which affects P_{capture} and e_{capture} . We assume in this

model that when a predator is faced with a particular prey, the predator will choose the optimal attack strategy by using the prey-capture behaviour that maximizes the expected net benefit. It is possible that predators do not always perform optimally, or that the predator maximizes some function other than the arithmetic mean benefit, such as some function of expected net benefit weighted by the variance. This latter scenario is likely when the highest expected net benefit is associated with an unacceptably high variance, resulting in the risk of starvation between rare but extremely rewarding successes. Hunger-induced modulation may be one example. It is well known among experimentalists that fish will strike more vigorously at prey after food-deprivation than when nearing satiation (Wainwright and Lauder, 1986). Such modulation does not reflect any change in the parameters affecting expected net benefit (prey value, evasiveness, capture costs), suggesting that hunger ('motivational state') could generate modulation by changing the parameter the predator is trying to optimize. A satiated predator may be more likely to optimize the long-term expected net benefit, whereas a starved one may be better off minimizing the variance in net benefit, even if the total payoff is suboptimal (Kacelnik and Bateson, 1996). Because the variance of e_{net} is easily calculated, it is possible to construct confidence intervals around the expected net benefit. This allows researchers to quantify the extent to which a predator deviates from the theoretically predicted optimum.

OPTIMIZING THE PREY-CAPTURE STRATEGY

Predator attack strategies are complex behavioural repertoires often composed of many steps, such as approach, pursuit, strike, capture and consumption, each subject to prey escape and energy costs. Nevertheless, it is often possible to characterize the 'effort' of an attack as a unidimensional variable, such as acceleration, pursuit time, power output or a biomechanical measure. Examples from fish-feeding mechanics include acceleration rates during fast-starts (Johnston *et al.*, 1995; Wakeling and Johnston, 1998; Hale, 1999), suction pressures (Alexander, 1970; Lauder *et al.*, 1986; Grubich and Wainwright, 1997; Nemeth, 1997b) and the ram-suction index (RSI) in fish (Norton and Brainerd, 1993). In the remainder of this paper, we use the general word 'effort' to mean one of these energetic or biomechanical measures of attack intensity. To model modulation, we assume that a predator has the option to attack a prey with a range of possible levels of effort (x) up to some maximum ($x:[0, x_{\text{max}}]$). The upper limit of capture effort is likely to be determined by physical constraints on the rate of oxygen uptake (Chai and Dudley, 1996), the rate at which chemical energy can be converted to kinetic performance (Wakeling and Johnston, 1998), biomechanical barriers (van Leeuwen and Muller, 1984; Pough and Andrews, 1985; Drucker and Lauder, 2000), or the point where performance generates dangerous levels of strain on tissues (Palmer *et al.*, 1999).

Attack effort (x) is likely to have a significant effect on two aspects of the expected net benefit: P_{capture} and e_{capture} . Faster strikes, increased suction, more forceful crushing pressure or other high effort attacks are likely to reduce the chances of prey escape. So why would a predator ever execute an attack below its maximum physiological capacity? Two alternative hypotheses present themselves. First, modulation might reflect the fact that different prey require distinct capture strategies to maximize P_{capture} (Fig. 1). For example, high-velocity attacks may improve capture success for large and elusive prey, but may cause the predator to sacrifice the accuracy needed to capture smaller prey,

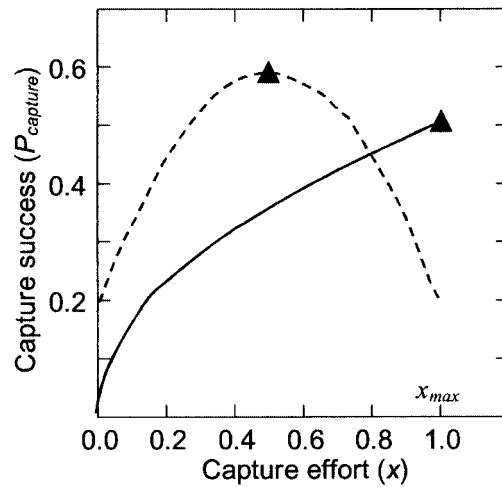


Fig. 1. Capture success (P_{capture}) as a function of both attack effort and prey type. Alternative prey (solid and dotted curves) may have different capture efforts that maximize capture success (optima marked with triangles).

or may be dangerous when approaching prey that are on or near a hard substrate. Alternatively, capture behaviour may represent a balance between two conflicting demands. Higher effort strikes may increase capture success (up to a point) for all prey, but generate higher energetic costs that negate the benefit of additional success rates (Fig. 2). The energetic cost of movement generally increases as a power function of effort, such as acceleration towards a prey (Schmidt-Nielsen, 1972; Evans, 1993; Videler, 1993), crushing bite force (Stein *et al.*, 1984), speed at prey-capture (Beamish, 1970; Glass, 1971; Anderson, 1984), or the costs of subduing the prey (Pough and Andrews, 1985). For elusive prey requiring high effort to achieve maximal success, capture costs may be high enough that lower success strategies yield higher expected net benefit.

Both hypotheses assume that the predator chooses the optimal prey-capture effort $\hat{x}$ that maximizes the expected net benefit for the strike. Taking the derivative of $E(e_{\text{net}})$ with respect to x , and setting it equal to zero, the optimal capture effort $\hat{x}$ will satisfy the equality

$$ae_{\text{prey}} \frac{d(P_{\text{capture}})}{dx} = \frac{d(e_{\text{capture}})}{dx} \quad (5)$$

If capture success and energy costs are both monotonically increasing functions of capture effort, then there will always be a single optimal value. However, the value $\hat{x}$ that satisfies equation (5) may be so large as to exceed the organism's maximum physiological performance (x_{max}). In this case, the organism will choose to operate at its maximum capacity, as close to the optimum as possible.

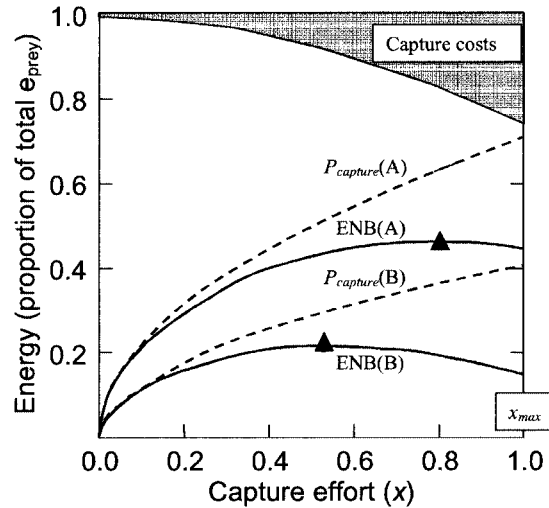


Fig. 2. The optimal capture effort (triangles) for two prey (A and B) of equal energy content (scaled so that $ae_{\text{prey}} = 1.0$). Although capture success (dotted lines) is an increasing function of attack effort for both prey, the expected net benefit (solid lines) for both prey is below the maximum capture effort ($x_{\text{max}} = 1.0$) where success is highest. This submaximal optimum is because the benefits of higher success are balanced by increasing costs (height of the shaded region). The maximum value of the prey is a decreasing function of capture effort (the lower boundary of the shaded region), which, when weighted by the capture success curves, yields the expected net benefit. Note that the more elusive prey (lower P_{capture} curve) justifies lower capture effort. These curves are based on the equations in Appendix 2, with $a = 1$, $s = 2$ (prey A) and 6 (prey B), $d = 0.01$, $b = 2$, $c = 0.25$ and $\hat{x} = 0.79$ (prey A) and 0.55 (prey B). ENB = expected net benefit.

MODULATION: WHY $\hat{x}$ VARIES WITH PREY TYPE

The optimal prey-capture behaviour can be predicted because the expected net benefit depends on capture success and costs, which, in turn, are functions of the attack strategy. However, the expected net benefit also depends on the energetic value of the prey (e_{prey}) and prey elusiveness (which affects P_{capture}). Consequently, different prey will result in different functions describing $\text{ENB} = f(x)$, which may have different optima. Under what conditions do differences in prey result in different optimal strike efforts and hence behavioural modulation?

Above, we outlined two alternative hypotheses for why a predator would attack a prey with anything less than its maximum effort. Hypothesis 1 suggested that P_{capture} is maximized in different ways for different prey (Fig. 1). In contrast, hypothesis 2 assumes that capture success is a non-decreasing function of effort (Fig. 2). The slope of this function can vary with different prey, and can asymptote or reach 100% success, but does not decrease. The first hypothesis explains modulation in a very intuitive way that does not require modelling: predators maximize their capture success and different prey require different strategies. The second hypothesis can produce a more interesting range of results. We used several different models (see Appendix 2 for an

example) describing P_{capture} and e_{capture} as functions of x to examine the types of modulation that result from prey trait variation. We found three distinct forms of modulation in different regions of parameter space (Fig. 3). We will consider each of these three regions in turn.

Region A: no modulation

When prey energy content is high relative to capture costs, the marginal benefit of added capture success may exceed the marginal capture cost throughout the range of physiologically achievable capture efforts. In this case, the theoretical optimum (equation 5) may exceed the highest possible effort that the predator can execute ($\hat{x} > x_{\text{max}}$). Under these conditions, the highest capture effort x_{max} yields the highest possible expected net benefit. Although changes in prey energy content and elusiveness may affect the theoretical $\hat{x}$, the actual capture effort used (x^*) will not change until $\hat{x}$ is reduced to a value below x_{max} . This will be true as long as the cost–benefit ratio is relatively low because capture costs are negligible relative to the potential energy gain ($ae_{\text{prey}}P_{\text{capture}}$). Realistic values of capture effort as a

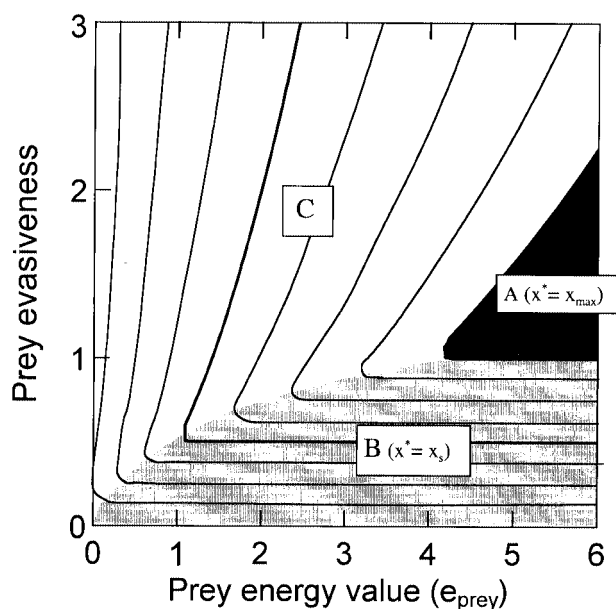


Fig. 3. Contours show how the realized optimal capture effort x^* depends on the interaction between prey evasiveness (higher values indicate more evasive prey) and prey energy value. Three regions with distinct behavioural modulation exist, represented by three levels of shading. If $x_{\text{max}} = 1.0$, variation between prey that remain in the parameter space for region A will not produce any modulation. As long as $\hat{x} > x_{\text{max}}$, the predator will always execute maximum effort attacks ($x^* = x_{\text{max}}$). In region B, the predator executes the minimum necessary effort to ensure that $P_{\text{capture}} = 1.0$ ($\hat{x} = x_s$), so that more elusive prey elicit higher effort attacks. In region C, prey are highly evasive and/or of low value, so that increases in evasiveness justify even less energy outlay, and the optimal effort declines with more evasive prey. Using the functions in Appendix 2, $d = 1$, $b = 2$, $c = 1$. By using $c = 1$, we can interpret e_{prey} in units of capture cost at $x = 1.0$.

percentage of prey value are generally quite low. For instance, the lizard *Chalcides ocellatus* expends about 1% of its assimilated energy in handling its prey (Grimmond *et al.*, 1994). Similar values exist for a range of predators (Anderson, 1984; Pough and Andrews, 1985; Rovero *et al.*, 2000). Such small relative costs imply that, realistically, e_{prey} is approximately 50–200 times the capture cost. In that case, most elusive prey will fall in region A, where maximum strike effort is always optimal.

Region B: maintaining high capture success

Consider a predator whose capture success increases with greater capture effort. For highly elusive prey, P_{capture} could remain low throughout its range of behaviours, while perfect capture success may be possible for less elusive prey ($P_{\text{capture}} = 1$) (Fig. 4). The solution for the optimal capture effort in this context echoes our intuition: the predator should expend only as much effort as is necessary to guarantee successful prey capture. Where $P_{\text{capture}} = 1$, equation (1) describes the net benefit. The derivative of this expected net benefit is uniformly negative with respect to capture effort, because higher effort does not improve success (already 100%) while costs continue to increase. Consequently, predators should execute the minimum effort necessary to ensure capture success. When faced with an easy-

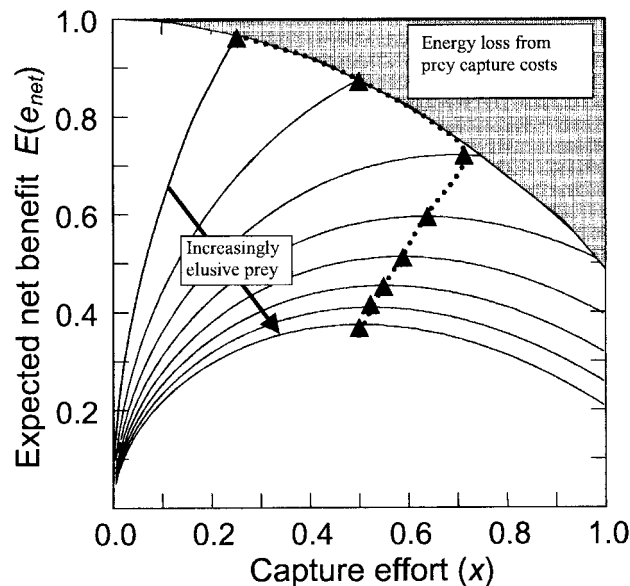


Fig. 4. The shape and optimum (triangle) of the expected net benefit (ENB) curve depends on prey elusiveness. The prey value is scaled to 1.0 and the potential energy income (e_{net} given $P_{\text{capture}} = 1.0$) is the lower boundary of the shaded region representing capture costs. Less evasive prey have an optimum $\hat{x}$ such that $P_{\text{capture}} = 1.0$. As prey become more evasive, capture effort must increase to maintain high success rates up to the point where capture costs are too high. As capture costs become higher, more evasive prey justify less capture energy expenditure, and more evasive prey inspire lower capture effort. This progression is tracked by the thick dotted line. Using the functions in Appendix 2, $d = 0$, $b = 2$, $c = 0.5$, s ranges from 0.25 to 2.0.

to-catch prey, a predator will therefore expend little effort, while a more elusive prey will inspire a higher effort strike. In these conditions, modulation simply allows a predator to maintain maximal capture success for a range of different prey, while prey value (e_{prey}) has little or no influence on the capture effort. Although this result is intuitive, it has a profound implication: e_{capture} is sufficiently large to affect the expected net benefit of a prey-capture event and hence the predator's behaviour.

Region C: the apathetic predator

The third type of modulatory behaviour predicted by our model is somewhat counter-intuitive. To understand this result, first consider why the effective net benefit function has a maximum. This function is the difference between the gains made by increasing the value of the prey ($ae_{\text{prey}}P_{\text{capture}}$) and the costs of extra effort (e_{capture}). Extremely elusive prey and prey with relatively little energy content reduce the first term and hence do not justify high-cost capture behaviours (second term). Although such a prey item could simply be ignored, the predator could also execute a lower effort capture attempt, the costs of which are reduced so that the expected net benefit remains positive. As a result, highly evasive and low-energy prey can result in optimal prey-capture efforts that are below x_{max} even for monotonically increasing P_{capture} functions (Fig. 4). In these circumstances, an even more elusive prey (or one with less energy content) would justify even lower outlays of capture energy, and so result in lower capture effort. The result is an apparently apathetic predator that reduces its capture effort when faced with a harder-to-catch prey, so as to ensure that the expected net benefit remains positive. This effect may be quite rare. Numerical simulations suggest that capture costs must exceed 20% of the prey's expected gross value ($ae_{\text{prey}}P_{\text{capture}}$) to see the 'apathetic predator' form of modulation.

Although capture costs may frequently be small, there are instances where predators have exceptionally high foraging costs. Wild dogs (*Lycaon pictus*) average 25 times their basal metabolic rate while hunting (Gorman *et al.*, 1998). Although that measure is an average that reflects foraging as well as prey-capture, wild dogs have their highest energy use when actively running down prey. These capture costs are large enough to severely limit the geographic distribution of wild dogs (Gorman *et al.*, 1998). Within fish, some recent bioenergetic models suggest that capture costs may be higher than traditional methods have indicated (Hughes and Kelly, 1996). A study of optimal diet in the redear sunfish (*Lepomis microlophus*) found that different prey types required significantly different handling energy expenditure, and that energy-based cost-benefit optimization performed better than energy-time measures (Stein *et al.*, 1984). Other studies have shown that it is possible to accurately predict optimal swimming speed in non-foraging contexts, suggesting that locomotion costs are significant enough that fish will optimize their swimming speeds (Weihs *et al.*, 1981; Parsons and Sylvester, 1992).

DISCUSSION

Different species of predators modulate their prey-capture behaviour to different degrees. For example, the temperate marine fish (*Hexagrammos decagrammus*) uses significantly different attack speeds, initiation distances and premaxillary protrusion when feeding on different species of shrimp, crabs and shrimp fragments, using higher attack effort on more elusive prey (Nemeth, 1997a). In contrast, Reilly and Lauder (1989) found that

aquatic salamanders (*Ambystoma mexicanum*) did not modulate when fed a wide range of prey (see also Ferry-Graham, 1997). As far as we are aware, no general theory has been proposed to explain when and why a predator will modulate its prey-capture behaviour. Yachi (2000) used an optimization model to describe when a stalking predator should abandon stealth and begin a charge. In contrast to our model, Yachi (2000) assumed that predators act to maximize their capture probability. We have shown that this is true for a subset of parameter space, but predators' behaviours are simultaneously constrained by capture costs and prey value, which may favour behaviours with submaximal capture success.

Predators that act to maximize the expected energetic benefit from a prey-capture event must balance the benefits of increased capture success against capture costs. Variation in the specific parameters and shape of these cost and benefit functions will alter the location of the optimal capture behaviour. When faced with several different food items, the predator will have a different optimal capture behaviour for each, depending on the prey-specific balance of costs, evasiveness and energy value. When these optima all exceed the maximum capacity of the predator, the predator should theoretically perform at that maximum and show no modulation. In contrast, predators with high capture efficiency should modulate to use the minimum capture effort necessary to ensure success, thus expending more effort on more elusive prey. Many studies of fish feeding have found that predators increase their capture effort on more elusive prey (Liem, 1978, 1979; Norton, 1991; Nemeth, 1997a). Although these results are consistent with the modulation observed in our model, most studies confound the effects of prey evasiveness and prey value. An exception is the study by Nemeth (1997a), which showed that *Hexagrammos decagrammus* uses higher velocity strikes at evasive shrimp than shrimp carcasses. Finally, modulation can occur in exactly the opposite direction: less effort for more elusive prey. This only occurs for relatively inefficient predators whose capture success is low, or whose costs are a significant portion of the potential income.

As with previous optimization models of foraging behaviour, the utility of the model presented here depends on how effectively it can be applied to predict prey-capture behaviour in empirical systems. Using this model to generate quantitative predictions about prey-capture effort, and to test whether a predator behaves as predicted, will not be a trivial undertaking. A researcher must identify a continuous variable describing capture effort and then determine empirically the functions relating capture success and energy costs to effort. Parameterizing these functions will require high replication across a wide range of behaviours, using laboratory techniques sensitive enough to measure the energy expenditure from single attacks. The shape of these functions may be sensitive to ambient environmental conditions (Macy *et al.*, 1999). In our review of the literature, we found no systems with sufficient data on attack costs and success rates to apply our model. Nor do many of the current studies of modulation separate the effects of prey elusiveness and prey value. However, we are optimistic that a few technical advances will make it possible to parameterize the appropriate prey capture and energy cost equations to develop a quantitative tool for testing the causes of modulation in prey-capture behaviour.

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APPENDIX 1

Most prey-capture sequences involve multiple variables that must be optimized simultaneously or sequentially. For example, fish attempting to capture prey can vary the distance at which they initiate their strike, strike acceleration and the amount of suction they generate through head expansion. To model this multi-step process, we assume that each variable x_k represents modulation of part of a sequence of n strike components ($\mathbf{x}$ is a vector of n components x_k : $1 \leq k \leq n$) and then determine $E(e_{\text{net}} | \mathbf{x})$. Let p_k and $e_{\text{capture},k}$ be the success probability and energy cost of a given strike component k . A failure at any stage of capture would result in an aborted capture attempt and less than total energy expenditure. Hence, $e_{\text{capture},k}$ is zero if the previous strike component ($k - 1$) failed.

Net energy income after stage k	Probability of stopping at stage k
e_{net} (failure at step 1) $= -e_{\text{capture},1}$	$\Pr(f_1) = (1 - p_1)$
e_{net} (failure at step 2) $= -(e_{\text{capture},1} + e_{\text{capture},2})$	$\Pr(f_2) = p_1(1 - p_2)$
e_{net} (failure at step 3) $= -(e_{\text{capture},1} + e_{\text{capture},2} + e_{\text{capture},3})$	$\Pr(f_3) = p_1p_2(1 - p_3)$
$\vdots$	$\vdots$
e_{net} (success) $= ae_{\text{prey}} - \sum_1^n (e_{\text{capture},k})$	$\Pr(s) = \prod_1^n p_k$

where $\Pr(f_k)$ is the probability of failure at step k , $e_{\text{net}}(f_k)$ is the net energy from failure at step k and $\Pr(s)$ is the probability of success. This is essentially a geometric probability function, the expected net energy income of which can be expressed as:

$$E(e_{\text{net}} | \mathbf{x}) = \sum_1^n e_{\text{net}}(f_k) * \Pr(f_k) + \left(\prod_1^n p_k \right) \left(ae_{\text{prey}} - \sum_1^n (e_{\text{capture},k}) \right) \quad (\text{A1})$$

APPENDIX 2

Here, we provide one of the models used for numerical simulations, which was also used to generate Figs 2–4. Both capture costs and capture success must be described in terms of capture effort (x). We chose

$$e_{\text{capture}} = d + cx^b \quad \text{for } x: [0, x_{\text{max}}] \quad (\text{A2})$$

$$P_{\text{capture}} = \begin{cases} \sqrt{\frac{x}{s}} & \text{for } x \leq s \\ 1 & \text{for } x > s \end{cases} \quad (\text{A3})$$

to reflect that e_{capture} is likely to be an exponential function of effort (Schmidt-Nielsen, 1972; Evans, 1993; Videler, 1993), and P_{capture} is an increasing function of x up to the point ($x_s = s$) where $P_{\text{capture}} = 1$. The parameter s can be thought of as indicative of prey elusiveness. If $x_{\text{max}} < s$, then the predator cannot achieve 100% capture success. We denote the effort necessary for 100% success as x_s . Given these functions,

$$E(e_{\text{net}} | i) = \begin{cases} e_{\text{prey}} \left(\sqrt{\frac{x}{s}} \right) - (d + cx^b) & \text{for } x \leq s \text{ and } x: [0, x_{\text{max}}] \\ e_{\text{prey}} - (d + cx^b) & \text{for } x > s \text{ and } x: [0, x_{\text{max}}] \end{cases} \quad (\text{A4})$$

Taking the derivative of equation (6a) and (6b), we find that the optimal capture effort $\hat{x}$ occurs when:

$$\hat{x} = \begin{cases} \left(\frac{e_{\text{prey}}}{2bc\sqrt{s}} \right)^{\frac{2}{2b-1}} & \text{for } x \leq s \text{ and } x: [0, x_{\text{max}}] \\ \min(x) & \text{for } x \geq s \text{ and } x: [0, x_{\text{max}}] \end{cases} \quad (\text{A5})$$

When $\hat{x} > x_{\text{max}}$, the actual behaviour used (x^*) will be the supremum of the expected net benefit function rather than the maximum, in this case $x^* = x_{\text{max}}$. This results in three possible achieved optimal behaviours:

$$x^* = \min \left\{ x_{\max}, x_s, \left(\frac{e_{\text{prey}}}{2bc\sqrt{s}} \right)^{\frac{2}{2b-1}} \right\} \quad (\text{A6})$$

which correspond to the three regions of modulation behaviour. As long as the variation among prey maintains the condition $\hat{x} \geq x_{\max}$, there will be no modulation ($x^* = x_{\max}$). If variation among prey meets the condition

$$x_{\max}, \left(\frac{e_{\text{prey}}}{2bc\sqrt{s}} \right)^{\frac{2}{2b-1}} \geq x_s \quad (\text{A7})$$

the predator will always strike with the minimum effort necessary to maintain $P_{\text{capture}} = 1$, and so more elusive prey (larger x_s) will require more effort. Finally, when the third condition is fulfilled,

$$\left(\frac{e_{\text{prey}}}{2bc\sqrt{s}} \right)^{\frac{2}{2b-1}} \leq x_s, x_{\max} \quad (\text{A8})$$

more elusive prey (or lower energy prey) will reduce the optimal prey capture effort.

