

The Dickey Dinner Dilemma: Asymmetry in predator-prey risk-taking, a broadly-applicable alternative to the life-dinner principle

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Abstract

40 years ago, the “life-dinner principle” was proposed as an example of an asymmetry that may lead prey species to experience stronger selection than their predators, thus accounting for the high frequency with which prey escape alive from interaction with a predator. This principle remains an influential concept in the scientific literature, despite several works suggesting that the concept relies on many under-appreciated assumptions and does not apply as generally as was initially proposed. Here, we present a novel model describing a very different asymmetry to that proposed in the life-dinner principle, but one that could apply broadly. We argue that asymmetries between the relative costs and benefits to predators and prey of selecting a risky behaviour during an extended predator-prey encounter could lead to an enhanced likelihood of escape for the prey. Any resulting advantage to prey depends upon there being a behaviour or choice that introduces some inherent danger to both predator and prey if they adopt it, but which if the prey adopts the predator must match in order to have a chance of successful predation. We suggest that the circumstances indicated by our model could apply broadly across diverse taxa, including both risky spatial or behavioural choices.

Keywords: Arms-race – Behavioural ecology – Evolution – Life-dinner principle – Predator-prey interaction – Risk-taking

Introduction

Threat of predation is a major aspect to the lives of wild animals, acting as a significant influence on ecology, population dynamics and the evolution of both predator and prey species (Clinchy, Sheriff, & Zanette, 2013; Laundré, Hernández, & Ripple, 2010). Predators are considered to be important selection agents for prey species (Vermeij, 1982), consequently the evolution of antipredator defences in prey has received much attention in the scientific literature (Bateman, Vos, & Anholt, 2014; Caro, 2005, 2014; Edmunds, 1974). However, while predation is undoubtedly a key driver of evolutionary change for many species, a conspicuous but infrequently-discussed point is that predation events do not always (or even usually) conclude with successful capture of prey.

Across a diverse range of taxa, there abound reports of unsuccessful predation (see Vermeij, 1982 for a review). As one extreme example, *Meyenaster gelatinosus* sea stars reportedly catch and consume less than 2% of the moving chiton and gastropod prey that they target (Dayton, Rosenthal, Mahen, & Antezana, 1977). Carnivorous plants are also very inefficient predators, with the pitcher plants *Sarracenia purpurea* (Newell & Nastase, 1998) and *Darlingtonia californica* (Dixon, Ellison, & Gotelli, 2005) capturing only 1-2% of visiting insects (without any evidence of selectivity). Further reports of inefficient predation span such diverse taxa as the crab spider *Misumena calycina* that captures only 1.6% of its preferred bumblebee prey (Morse, 1979), the green tree-frog (*Hyla cinerea*) that successfully captures less than 22% of mosquito prey (Freed, 1980), and Foster's tern (*Sterna forsteri*) that successfully captures fish during only 24% of dives (Salt & Willard, 1971). Even apex predatory mammals, such as lions, usually have predation efficiencies of less than 50% after detecting prey (see Vermeij, 1982 and references therein). Unsuccessful predation can also be indicated by sublethal injuries sustained by prey, for example almost 75% of bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia bore shark-inflicted scars in a 2001 study by Heithaus; and 72% of Australian snubfin (*Orcaella heinsohni*) dolphins bore shark bites in an analysis of photo-identification data by Smith et al. (Smith, Allen, Bejder, & Brown, 2017). Certainly, predation may drive prey to evolve defences in order to reduce their predators' success during attacks; but a fundamental question that has been asked, then, is why does the predator apparently not evolve counter-adaptations at the same rate? That is, why is it that broadly the outcome of

predator-prey co-evolution is that many (if not most) predatory attacks are unsuccessful. The generally well-accepted explanation for this, described in major behavioural ecology textbooks (e.g. Barnard, 2004) and widely taught to students studying predator-prey interactions, concerns asymmetries between predator and prey and, specifically, characteristic differences between them in the relative fitness consequences of different outcomes of a predator-prey interaction.

Asymmetries between the fitness consequences for predators and their prey are thought to influence selection depending on their implications for the 'arms-race' between competing sides of ecological interactions (Dawkins & Krebs, 1979). Concerning predator-prey interactions, in 1979 Dawkins and Krebs outlined a particularly salient asymmetry they termed the "life-dinner principle", wherein predators and their prey experience unequal selection pressures. The life-dinner principle proposes that a lineage under strong selection may evolve fitness-enhancing adaptations more rapidly than a weakly selected one where this imbalance in selection concerns significant differences in the penalty of failure for each. For example, if a predator is chasing its prey the prey runs to preserve its life, while the predator runs to secure a meal; the prey experiences a stronger selection pressure to escape as the mortality cost of being caught is greater than the cost to the predator of losing out on a meal. Such an imbalance is suggested to imply that where prey experiences a stronger selection pressure it will have an advantage in that particular arms-race relative to predators (Dawkins & Krebs, 1979).

Dawkins and Krebs' verbal model is widely accepted, with many works continuing to refer to it in much the same words as it was proposed (Barnard, 2004; Colquhoun, 2007; Jacobs & Bastian, 2016). Studies continue to report evidence interpreted with heavy reliance on the life-dinner principle in predator-prey systems, in reference to such diverse traits as activation energies (Dell, Pawar, & Savage, 2011), habitat use (Gvoždík, Černická, & Van Damme, 2013), and chemical recognition abilities (Labra & Hoare, 2015); the prey individuals in all of these examples are considered to be under stronger selection to escape than the predator is to capture. Reactions to simulated predators in primates have also been interpreted to partially support a modification of the life-dinner principle, as cautious reactions to potential threats simply reduce the time available for foraging (i.e. delaying

dinner) rather than risking predation (Barnett et al., 2018). Host-parasite interactions have also been proposed to conform to the life-dinner principle, where asymmetric fitness benefits mean that parasites experience stronger selection to infect hosts successfully than hosts do to resist infection. Cases where parasites experience dramatic fitness reductions in resistant hosts, while not all hosts will be infected and the infection will only cause a small reduction in host fitness, may exemplify this (Wilfert & Jiggins, 2013). The concept has also been extended to plants and insects, where reciprocally specialist species are thought to outpace generalist species due to selection for extreme traits being stronger for specialists than generalists (Anderson, Terblanche, & Ellis, 2010).

However, as an explanation for the frequent escape by prey from predatory attacks, the principle of life-dinner is actually far from as general as Dawkins and Krebs initially proposed. There exists a small literature that demonstrates several ways in which the life-dinner principle specifically rests on under-appreciated assumptions. Firstly, Abrams (1986) argued that the life-dinner principle, as it was originally described (Dawkins & Krebs, 1979), fails in its summary of a predator's situation because predators that catch prey sufficiently rarely would in fact suffer the same cost of failure as prey that get caught (i.e. death). Even though this penalty of failure would occur over a longer timescale its impact on predator success and selection will be significant (Abrams, 1986), and so predators should not be expected to have an inherent disadvantage in coadaptation due to differences in "motivation" to succeed. Further, asymmetries in predator investment in chase adaptations relative to increased prey investment in escape can be explained by reasons beyond the life-dinner principle. For one, improved anti-predator defences in prey may lead to increased prey density and, consequently, increased encounter rate with prey compensating for the reduced per-encounter success for the predator (Abrams, 1986).

Sih (2005) also drew attention to the importance of starvation as a factor for both sides in predator-prey interactions. If a predator is starving, acquiring "dinner" can mean everything while, conversely, for starving prey escaping predation may be futile if they will shortly starve to death. Sih (2005) further made the argument that the spatio-temporal scale of interest is important for predator-prey asymmetries such as the life-dinner principle. While predators can be expected to cope with missing out on a few meals without jeopardising

their fitness, at larger spatial scales predators cannot afford to get caught in large areas with few prey available to them for long periods of time. Keeping track of prey spatial aggregations could be critical for a predator's survival, and so, predators may be selected to overcome prey defences on larger spatio-temporal scales (Sih, 2005).

Further arguments against the universality of the life-dinner asymmetry as proposed by Dawkins and Krebs (1979) have also been detailed by Carlsson, Sarnelle, and Strayer (2009). They suggested that the strength and direction of the asymmetry ought to depend on both: (1) the importance of predation from a specific predator as a cause of mortality in the prey species, and (2) the importance of that particular prey item in the predator's diet.

Consequently, the life-dinner principle will apply if a predator is the primary source of mortality for a prey species while the prey is not of great importance to the predator's diet; selection to evolve anti-predator traits will be far stronger for prey than the pressure to evolve means to counter those traits in the predator. Alternatively, though, if the prey is essential to the predator's diet but the predator is not a major risk for the prey the predator will instead be under greater selection to successfully capture the prey than the prey will be under to evolve anti-predator defences (Carlsson et al., 2009). Prey are not usually subject to predation from only one predator species (Sih, Englund, & Wooster, 1998) and so the evolution of predator-specific defence mechanisms is unlikely (Caro, 2005). A few studies have indicated that rather than prey always outpacing predators, as implied by the life-dinner principle, there are in fact cases where predator populations can evolve offensive adaptations as fast or faster than prey defences. The clearest examples of this are predator-prey interactions involving toxic (Brodie III & Brodie Jr., 1999) or in some other way highly dangerous (Robbins, Freidenfelds, & Langkilde, 2013) prey. Where prey are lethal, in particular, the asymmetry between predators and prey is lessened or removed entirely and the fitness consequences of interactions between a predator and its prey can potentially be balanced (Williams, Hanifin, Brodie, & Brodie, 2010).

Therefore, it seems that asymmetry between predator and prey populations in the strength of selection acting, and thus an advantage to members of the prey population in an evolutionary arms race, does not seem a generally applicable explanation for the commonness of unsuccessful predation attempts. However, we believe that there remains a

key and very general asymmetry that has so far received little attention. Beyond evolving more effective anti-predator defences, prey may take greater risks to escape a predator than a predator will to pursue them. Risk-taking by prey would involve the possibility of death by other means than capture by the initial predator and could take the form of: performing more injury-risking activity, increasing speed at the cost of increased risk of slipping and falling (Clemente & Wilson, 2015; Wynn, Clemente, Nasir, & Wilson, 2015), switching to more dangerous terrain during pursuit, or attracting the attention of another predator. Taking a greater risk during the predation sequence could give the prey a genuine advantage over the predator if the predator opts not to match the risky behaviour and thus must give up on the prey individual - but this is not the advantage that was originally proposed by Dawkins and Krebs (1976). Specifically, it has nothing to do with different strengths of selection experienced by predator and prey populations. Rather it relies on asymmetries that exist in the cost-benefit trade-off for the two individuals in an extended predator-prey encounter. The behaviours exhibited by these individuals will of course be evolved (and possibly co-evolved) traits, but our argument involves both individuals expressing optimal behaviours, not one individual behaving sub-optimally because of some “evolutionary lag” in the population of which it is a member.

In situations where prey minimise their risk of mortality by predation through taking a different risk, a predator must weigh up the nutritional benefit of the prey with the newly added element of risk in continuing its pursuit (hence “the dicey dinner dilemma”). Our model in the next section explores the conditions under which this asymmetry could occur and we demonstrate its potential importance as an alternative (or complement) to the life-dinner principle. The situation we model is one where the prey has the option during the process of an encounter with a predator to adopt a behaviour that imposes an additional risk, and the predator has the option to either match the prey’s risky behaviour with risky behaviour of its own, or break off the encounter and lose the prey. We demonstrate theoretically that there are broad ranges of circumstances where the optimal behaviour for the prey will be to accept this risk and the optimal behaviour for the predator will be to decline to match this, thus increasing the overall likelihood of the prey surviving the encounter.

Our model

Some predator-prey encounters are extended in the sense that the prey is afforded time to take behavioural countermeasures after it detects that the predator has begun an attack on it. That is, this model rests on the assumption that prey have time to take countermeasures during the predatory encounter they find themselves in, although this possibility can be disregarded in certain cases of predation. During an extended predator-prey interaction between two individuals (predator and prey) there is an important asymmetry between prey and predator that might offer the prey the potential to enhance its probability of escape. This asymmetry relates to the aims of the two interacting individuals. The prey should be selected so as to minimise its risk of mortality during the interaction; the predator should be selected to find the optimal trade-off between the nutritional benefits of catching the prey and any potential costs and risks associated with pursuing the attack. Such costs might be energetic expenditure, risk of injury or heightened predation risk to itself.

It is worth bearing in mind that all our discussion in this model centres on the optimal behaviour for predator and prey after the predator has made an initial decision to attempt to catch the prey. There is a huge body of literature associated with optimal diet choice that relates to whether predators should attempt to capture all prey types that they encounter (Hughes, 2013), that need not concern us here since we are interested only in circumstances where the predator has made that initial decision. There is also a substantial literature on where and when predators should search for prey (Stephens & Krebs, 1986), but again this does not impact on the scenario under study (the optimal behaviour for predator and prey after the predator has encountered the prey and made the decision to attempt to capture it). However, the success of the predator that we model here will influence optimal choices of where and when to look for prey and what discovered prey to attack (see Discussion).

We encapsulate the crux of the behavioural choices open to both parties involved in an extended predator-prey interaction in terms of a simple binary decision. Imagine that the prey is being pursued by the predator and comes to a T-junction: their decision is to choose which fork to take. The key thing from our perspective is that the two paths differ in their inherent riskiness. We will label the two paths – safe and risky (denoted s and r respectively). The risky path might involve less sure footing with heightened risk of injury, or

a stronger water current with risk of being washed away, or exposure to another predator. In principle, some prey may be adapted to withstand falling, dropping, being washed away in a current or blown away by wind, for example, perhaps even using these forces to aid their escape from predators. But in the context of this model we pre-suppose that the risky path is considered to pose a high risk of injury to both prey and predator. We assume that the prey makes a choice (s or r) and then the predator makes the choice whether to pursue or abandon the chase (p or a respectively).

If the prey chooses the safe path, then we assume that the predator will always pursue and the probability of the pursuit leading to prey capture is some fixed value C_s between zero and one.

If the prey chooses the risky option, then its probability of mortality is dependent on whether the predator pursues or not. If the predator does not pursue then we assume that the prey suffers probability of mortality through the inherent riskiness of the environment rather than through predation with some fixed value C_a lying between zero and one. If, however, the predator pursues it then the prey has a probability of being captured given by C_p but also the same independent probability of mortality through other sources C_a . The prey's overall probability of surviving is therefore $(1-C_a)(1-C_p)$ and so its overall probability of mortality is $1-(1-C_a)(1-C_p)$. The prey should be selected to pick the route with the lower risk of mortality, but this may depend on whether or not the predator is willing to pursue the prey if it takes the risky path. Notice that if the predator does pursue the prey then we defined capture by the predator and extrinsic mortality as independent processes. Thus, mathematically both will sometimes be predicted to occur in the same interaction – in such cases, practically, what matters is which event comes first. We do not have to define a rule for this, since both outcomes lead to mortality for the prey and the same nutritional value for the predator (see below).

Turning to the predator, we need to express risk of injury and prey capture in the same currency – which we will call fitness. If we assume that whether the prey dies as a result of the risky path or successful capture by the predator, the predator still gets to consume the prey if it chose to pursue it down the risky path, then the paragraph above defines the

probability of the predator getting a nutritional benefit in all circumstances. If the nutritional value of the prey delivers the same fitness increment B in all circumstances, then we can express the expected fitness benefit to the predator in all circumstances. However, the predator suffers a possible fitness cost Q due to injury if it decides to pursue down the risky path.

So if the prey chooses the safe route then the expected fitness return to the predator is simply $C_s B$.

If the prey chooses the risky route, then the predator gets expected benefit of 0 if it does not pursue and expected benefit of $B(1-(1-C_a)(1-C_p)) - Q$ if it pursues down the risky route.

The predator should decide to pursue if:

$$B(1-(1-C_a)(1-C_p)) - Q > 0$$

That is if $B(1-(1-C_a)(1-C_p)) > Q$

Tidying this up, we get:

$$B(C_a + C_p - C_a C_p) > Q \tag{1}$$

The question now is what is the optimal behaviour for the prey?

If condition (1) is met then the predator will always pursue and so the prey should take the risky path if:

$$1-(1-C_a)(1-C_p) < C_s \tag{2}$$

If condition (1) is not met then the predator will never pursue and then then the prey should take the risky route if:

$$C_a < C_s. \tag{3}$$

So there exists a set of circumstances (a combination of parameter values) where condition (3) is met but (1) is not, where the prey will adopt a riskier behaviour and so enhance its probability of surviving the attack (because the predator declines to also adopt the risky behaviour).

Turning to the specific parameters, it is easy to understand condition (3). The prey will only select to take the riskier route if the potential mortality risk of this in the absence of the predator pursuing it is lower than the mortality of allowing the predator to continue pursuing it down the safer path. We are interested in situations where the prey opts for the riskier route. This will more readily occur when the risk of successful capture by the predator if the prey opts for the safer route is high and if the inherent mortality risk from factors unrelated to successful capture by the predator (should it opt to pursue) down the risky route is relatively lower.

We now turn to the condition (conditional on the prey having chosen the riskier route) that the predator opts not to pursue it, from above this can be expressed as:

$$C_a + C_p - C_a C_p < (Q/B) \quad (4)$$

The higher the fitness cost of the riskier environment (Q) relative to the reward from prey capture (B) the less willing the predator will be to pursue the prey down the riskier path and the easier this condition is to satisfy. It is also easier to satisfy this condition the smaller the values of C_a and C_p , these are the independent probabilities of the two types of events occurring that would lead to the pursuing predator getting reward B from consuming the prey. Thus, it makes sense that the lower these are the less willing the predator would be to continue pursuit when the prey heads down the riskier path. The probability (conditional on the prey having gone down the risky path) that the predator will break off pursuit is shown graphically in Fig 1, the region that satisfies equation (4) lies above the relevant line.

The key set of circumstances needed to trigger this advantage to the prey is the availability of a behaviour that introduces some inherent danger to both predator and prey if they adopt it, but which if the prey adopts the predator must match in order to have a chance of

catching the prey. This will occur very generally whenever the predator-prey encounter is extended such that the prey can influence its outcome through its behavioural choices. We have encapsulated this choice as a spatial route choice, but it need not be. The risky behaviour could simply be, for example, running faster or turning more tightly, each invoking a greater chance of slipping and falling (potentially incurring an injury).

Discussion

While unsuccessful predation can indeed be a selective force for the evolution of adaptations in prey (Vermeij, 1982) it is certainly not proof of predators failing to adapt in response to improvements in prey antipredator defences (Abrams, 1986, 1989). The life-dinner principle (Dawkins & Krebs, 1979) is insufficient as an explanation of why diverse predators may miss out on prey. Further, its foundation in assuming that the predator side of predator-prey interactions experiences weaker selection pressure is not secure in general (Abrams, 1986; Carlsson et al., 2009; Sih, 2005). However, we here present a (potentially broadly applicable) case where asymmetries between the relative costs and benefits to predators and prey of selecting a risky behaviour could lead to an enhanced likelihood of escape for the prey. The advantage to prey here requires only that (i) the prey can respond behaviourally to predatory attack, (ii) the behaviour introduces a potential cost to both the predator and their prey, and (iii) that the predator must also adopt an analogous behaviour if it is to have any chance of capturing a prey that has chosen to adopt the risky behaviour.

Our model presents a situation where pursued prey encounter a turning point at which they have to choose between a safe route or a risky route. A risky route could entail terrain that increased the risk of injury, a stronger flowing current that may result in them being swept away, or exposure to some additional predator that poses a risk to both the prey and other predatory animals, such as the prey's initial predator. The model is not restricted to choices in fleeing route, though, as it could just as readily apply to prey opting to perform more injury-risking activity which the predator would have to emulate in order to continue its pursuit. Some forms of aggressive defence by the prey may also be adopted as a risk-taking strategy by prey that incurs extra risk to them, but which the predator must also counter with a behaviour that incurs some risk to themselves if they are to maintain the potential for prey capture. Alternatively, risky behavioural change in the prey could also include

conspicuous movements or noise production, for example, to attract the attention of a predator to both species involved in the pursuit, whereby the predator would then have to decide whether to remain in close association with the prey whose actions may endanger them both. Such choices between relative safety and risk-taking will be very general in prey and could explain a great number of purportedly “unsuccessful” predation events, wherein the predator may instead be weighing up the relative nutritional benefits of capturing the prey with the risk of injury to itself in adopting a risky behavioural choice.

Of course, what we present here is not a complete predictor of predator behavioural decisions. In some ways modelling will always fall short as a predictor of behaviour for any specific situation, in large part because of the assumption of every individual of a given species hunting in the same way with the same prey preferences (Caro, 2005). Marked individual differences in hunting behaviour are in fact evident in many studies (Caro, 2005), and so while the model we present here suggests what might be the most optimal decision-making for predators and the prey they pursue we acknowledge that such choices are unlikely to play out completely consistently across predation events in any taxa. Nonetheless, we suspect that will be many cases where our model could explain observations of predators breaking off pursuit of prey. A wider ecological understanding would certainly be necessary to fully understand the various risks that a particular route choice or other behaviour might pose for both parties, but a very real advantage may exist for prey where they are willing to adopt a tactic where the predator must then accept some additional risk itself in order to continue the attack.

We would strongly encourage researchers to further explore the application of our principle of asymmetry in risk-taking to real-world situations, both through laboratory studies and fieldwork where possible. The first stage of such further study would be to explore the fundamental assumptions of our model. Unresolved questions include whether responses of prey to detection of impending predatory attack can be linked to both raised risk to themselves (even in the absence of successful predation) and a raised risk of the predator if it is to pursue its attack. Following explorations of this, it may be predicted that predators should break off attacks in response to the risky prey behaviour in situations (either naturally occurring or experimentally manipulated) where their risk is higher (e.g. when the

terrain features less sure footing). We also agree with Caro (2005) that further exploration of the impact of an unsuccessful or a successful attack on the subsequent behaviour of any given predator could bring a very insightful further dimension to modelling of predator-prey interactions, building up a bigger picture of how individual predation events influence long-term behaviour changes, fitness consequences and fit into the wider ecology of a system.

In the interests of simplicity, our model assumed that the added external risk (encapsulated in C_a) was the same for predator and prey. The qualitative predictions of our theory would be unchanged if this symmetry were broken, with predators being more willing to pursue prey if the incremental increase to their external risk was lower (providing the additional risk to the predator is non-negligible – it does not have to be equal or even similar to that of the prey for our general concept to apply). However, the quantitative impacts of such asymmetries would be a valuable extension of the analysis presented here. Another potential extension to our model would be to explore situations where prey that suffer a source of extrinsic mortality are lost to the predators and yield no nutritional reward for the predator. As we discussed earlier, this would require modelling of the timing of the two possible sources of mortality for prey (should they occur), so that the relative timing of them in one particular outcome can be modelled. The mathematics of the situation would thus be complicated, but will not affect the fundamental asymmetry on which our model relies and thus the major qualitative predictions made here. Another useful extension of the work presented here is to explore how optimal-decision making by the predator in terms of declining to pursue attacks that have been launched on some prey affect decisions about which types of prey to attack in the first place, and about when and where to actively search for prey to attack.

As we emphasized earlier, our proposed mechanism does not hinge on arguments about the rates of co-evolution of traits of predators and prey (unlike the life-dinner principle). However, of course we could expect that the traits that we model will have been subject to evolution. A more complex but interesting extension to the work introduced here would be to explore the extent to which predators might invest in adaptations that reduce the inherent risk to them of the riskier path versus, for example, investment in traits that allow them to capture the prey before it has had opportunity to select the riskier path itself, or

investment in traits that allow increased discovery rates of prey. Such exploration would be very much in spirit to the work of Abrams (1986 & 1989) in other predator-prey contexts.

Finally, more system-specific elaborations of the simple model presented here would attach numerical values to parameters and explore quantitative predictions. Although we model only a single predator-prey encounter, we might expect that for a single predator or prey these parameters vary between encounters – through changes in their internal state and/or changes in the external environment – most obviously the local densities of predators and prey. Clearly, if prey density is higher then the predator's willingness to take risks to pursue one prey item might be expected to decline, whereas conversely if predator density is high then evasion of one predator by means that are likely to attract the attention of others should be less attractive. Since the success of individual predator-prey outcomes will affect predator-prey dynamics (as well as being affected by them), the interplay of the mechanism introduced here with population dynamics has considerable scope for generating quite different predictions in different ecological scenarios.

In summary, we argue that the widespread observation of unsuccessful predation events is unlikely to often be explained in terms of the predator-population lagging behind the prey population in terms of adaptation and co-adaptation – but rather will often find explanation in terms of the predator judiciously balancing risk and reward and sometimes pulling out of attacks that it has launched. Escape by prey should not then be seen as indicating some error by the predator, and similarly a fleeing prey individual that slips, falls and is thus captured should not also be interpreted as having made a mistake. The interesting empirical challenge that this theory throws up is differentiating between times when prey escapes because predators decline to continue pursuit, and cases where the predator was not unwilling but unable.

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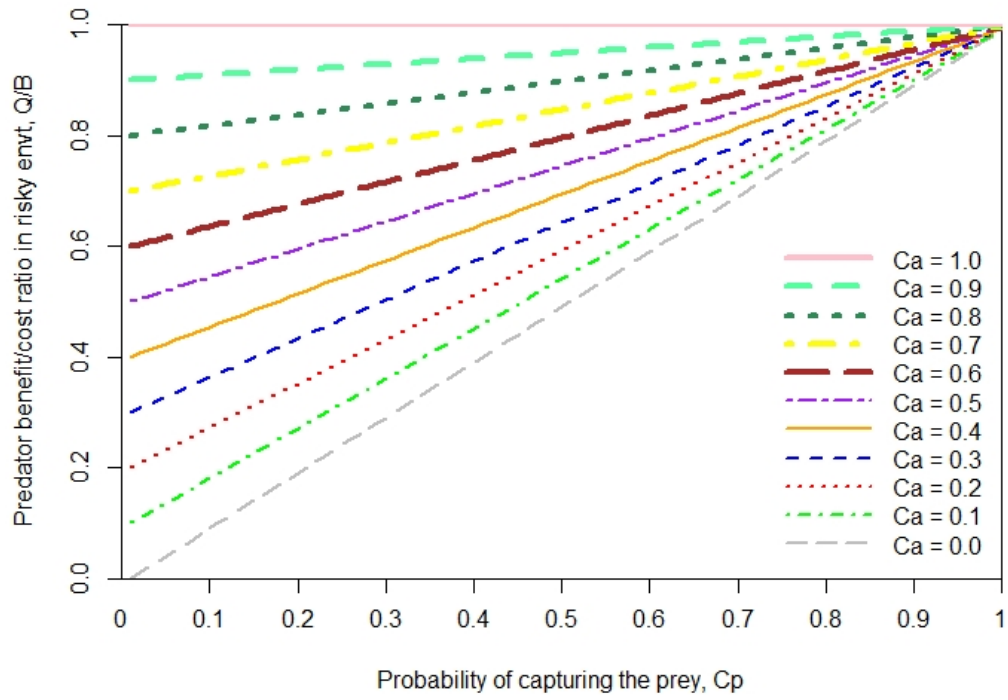
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Fig 1: The parameter ranges in which a predator will break off pursuit of a prey that has chosen a risky route. The region of the plot above each line satisfies equation (4) for the given C_a , that is the inherent risk of mortality associated with the risky path. The higher the probability of the predator capturing the prey (C_p) the less willing it is to give up the chase. However, as C_a increases, the predator becomes more likely to break off pursuit until the risk of mortality down the risky route (C_a) is equal to 1.0, in which case the predator should break off pursuit 100% of the time.



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