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What determines the attack distance of a stalking predator?

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ABSTRACT

Stalking predation has been identified in many different taxa of animals. Although previous studies have identified environmental conditions that affect hunting success, we still lack a theory that explains diverse stalking patterns on the basis of these conditions. Here, I present an optimization model of a stalking hunt based on a predator's multi-stage decision-making. This incorporates the essential feature of stalking predation: as the predator attacks at a shorter distance and when it attacks before the prey notices it, its hunting success is enhanced. At each step of a hunt, the predator chooses either to shorten the distance by stalking with a risk of being noticed or to attack immediately. Major conclusions are as follows: (1) The predator attains its maximum expected hunting success just by following a simple rule: keep stalking for as long as the merit of proximity exceeds the risk of losing the merit of surprise. (2) The predator attacks at a greater distance as the environmental conditions enhance the risk of losing the merit of surprise compared to the merit of proximity. (3) The optimal attack distance is neither affected by the distance where the predator starts its hunt nor by the previous stalking success as long as the merit of proximity is sufficiently large. This constancy of the optimal attack distance can be used to test if a stalking predator follows the above simple decision-making rule.

Keywords: attack distance, merit of proximity, merit of surprise, stalking predation.

INTRODUCTION

Stalking predation is widespread in many taxa of animals, for example lions and cheetahs in savanna (Eaton, 1970; Elliott *et al.*, 1977; Orsdol, 1984), fish (Hori, 1987) and spiders (Jackson and Pollard, 1996; Bear and Hasson, 1997). Stalking predators show diverse hunting patterns depending on hunting situations (e.g. attack after stalking or attack without stalking) and differences in attack distance. Previous studies have identified environmental conditions that affect the hunting success of a stalking predator, such as kind of prey, size of prey herds, type of vegetation cover, awareness of prey and attack distance (Eaton, 1970; Orsdol, 1984; Bear and Hasson, 1997). For example, Elliott *et al.* (1977) noted how attack distance affects hunting success based on the physiological properties of lions and their prey. However, we still lack a theory that explains diverse stalking patterns on

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the basis of these environmental conditions that affect hunting success. Here, I present an optimization model of a stalking hunt that incorporates essential factors of hunting success. The model provides a unifying framework to understand the essence of stalking predation as a result of a predator's multi-stage decision-making.

THE MODEL

The model consists of the following three elements:

1. *Predator's behavioural options*. A hunt begins when a predator recognizes prey at some distance x_0 (recognition distance) and ends when the predator successfully kills its prey or fails to catch it. In the course of a hunt after recognition of the prey, the predator has two choices at each distance x: stalk or attack (Fig. 1). If it stalks, it aims to shorten the distance at which it does so by a very small length $\mathrm{d}x$. If it attacks, it dashes at the prey immediately. Thus, a predator's hunt is described as a sequence of decisions $\{u(x)\}_x$.

2. *Prey's awareness probability*. In the course of a hunt, the prey is in one of two states: aware or unaware of the predator. The prey is unaware of the predator at the beginning of a hunt. Here, I assume that the probability that the prey becomes aware of the predator while it proceeds from distance x to $x - \mathrm{d}x$ depends on distance x and the predator's decision at x, $u(x)$. That is, if the predator stalks, the prey becomes aware of it with probability $q(x)\mathrm{d}x$, where $q(x)$ is a probability density function. I assume that $q(x)$ is a decreasing function of distance x because the prey detects the predator more easily at a shorter distance. If the predator attacks, the prey notices it immediately. As a constraint, I assume that after the prey becomes aware of the predator, it flees immediately and the predator switches to attack.

3. *Predator's hunting success*. Essentially, two variables affect the predator's hunting success: the distance at which it attacks and whether it attacks before the prey notices it. Let

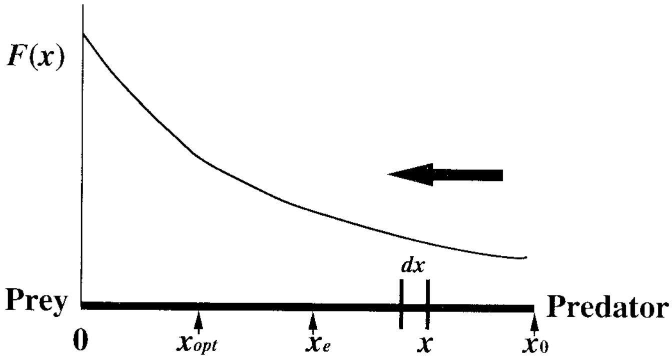

Fig. 1. Schematic representation of the model. The origin of the x-axis is where the prey remains. The predator recognizes its prey at distance x_0 and begins its hunt by approaching the prey. At each distance x, it can either shorten the distance by a very small length $\mathrm{d}x$ (> 0) by stalking or attacking immediately. Let x_{opt} and x_{e} denote the optimal attack distance and the expected attack distance, respectively. The curve represents the maximum expected hunting success, $F(x)$. Note that $F(x)$ increases as the predator succeeds in shortening the distance while x_{opt} is kept constant.

$p(x)$ $(0 \le p(x) \le 1)$ be the attack success probability when the predator attacks at distance x before the prey notices it. I assume that $p(x)$ is a decreasing function of the attack distance x because the predator is more successful as the distance at which it attacks is shortened (Eaton, 1970; Elliott *et al.*, 1977). On the other hand, if the predator attacks its prey after it has been noticed, the hunting success is reduced from $p(x)$ to $\sigma p(x)$ (Eaton, 1970; Elliott *et al.*, 1977), where σ $(0 \le \sigma \le 1)$ is a discounting rate.

At each distance x, a predator chooses the *optimal* decision $u(x)$ that leads to the *maximum* expected hunting success $F(x)$ if it continues to make decisions the same way afterwards. $F(x)$ satisfies the following recursive equation (Mangel and Clark, 1988):

$$F(x) = \max\{p(x), \sigma p(x)q(x)\mathrm{d}x + F(x - \mathrm{d}x)(1 - q(x)\mathrm{d}x)\} \tag{1a}$$

$$F(0) = p(0) \tag{1b}$$

The two terms in brackets in (1a) represent the predator's hunting success when it attacks and stalks respectively. When it stalks, it fails with probability $q(x)\mathrm{d}x$ and succeeds with probability $1 - q(x)\mathrm{d}x$. If it fails, the hunt ends, with an expected hunting success $\sigma p(x)$; if it is successful, the outcome of the hunt is put off until the next stage, and thus the expected hunting success is given by $F(x - \mathrm{d}x)$. As terminal condition (1b), I assume that the predator always chooses attack at $x = 0$. By recursively calculating (1a) from $x = 0$ to x_0 backward with the terminal condition (1b), the optimal decision $u(x)$ and the expected hunting success $F(x)$ are obtained sequentially (Fig. 1).

RESULTS

Optimal attack distance x_{opt}

The predator's optimal sequence of decisions takes the form: $(u(x_0), u(x_0 - \mathrm{d}x), \ldots, u(x_{\mathrm{opt}} + \mathrm{d}x), u(x_{\mathrm{opt}}))$ = (stalk, stalk, . . . , stalk, attack). Thus, the problem is reduced to finding the optimal attack distance, x_{opt}. x_{opt} is determined from the *marginal gain* of stalking at distance x, $\varphi(x)\mathrm{d}x$; that is, an increase in the predator's hunting success when it chooses to stalk instead of immediate attack (see Appendix):

$$\varphi(x) = -p'(x) - (1 - \sigma)p(x)q(x) \tag{2}$$

$\varphi(x)\mathrm{d}x$ consists of two terms: $-p'(x)\mathrm{d}x = p(x - \mathrm{d}x) - p(x)$, the benefit of successful stalking (the *merit of proximity*), and $(1 - \sigma)p(x)q(x)\mathrm{d}x = \{p(x) - \sigma p(x)\}q(x)\mathrm{d}x$, the cost to hunting of unsuccessful stalking (the risk of losing the *merit of surprise*) (Fig. 1). The optimal attack distance x_{opt} is one of the following depending on the sign of $\varphi(x)$:

(A) $x_{\mathrm{opt}} = x_0$ (attack without stalk): $\varphi(x) < 0$ in $[0, x_0]$ – that is, the risk of losing the merit of surprise always exceeds the merit of proximity.

(B) $x_{\mathrm{opt}} = x^*$ (attack after stalk): $\varphi(x^*) = 0$, $\varphi(x) > 0$ for $x^* < x < x_0$ and $\varphi(x) < 0$ for $0 < x < x^*$ – that is, the merit of proximity exceeds the risk of losing the merit of surprise until x^*.

(C) $x_{\mathrm{opt}} = 0$ (stalk until $x = 0$): $\varphi(x) > 0$ in $[0, x_0]$ – that is, the merit of proximity always exceeds the risk of losing the merit of surprise.

The optimal attack distance x_{opt} is neither affected by the recognition distance x_0 nor by the previous stalking success in cases (B) and (C) because equation (2) does not include x_0 (Fig. 2).

Expected attack distance x_e

The predator should continue stalking as long as the marginal gain of stalking exists. However, it will not always reach the optimal attack distance because the prey may notice it on the way. Thus, the observed attack distance must be compared with the expected attack distance, x_e. This is calculated from the optimal attack distance x_{opt} as follows:

$$x_e = \int_{x_{\text{opt}}}^{x_0} xP(x,x_0)q(x)\mathrm{d}x + x_{\text{opt}}P(x_{\text{opt}},x_0) \tag{3a}$$

$$\geq x_{\text{opt}} \int_{x_{\text{opt}}}^{x_0} P(x,x_0)q(x)\mathrm{d}x + x_{\text{opt}}P(x_{\text{opt}},x_0) = x_{\text{opt}} \tag{3b}$$

$P(x,x_0)$ represents the probability that the predator succeeds to attain x (see Appendix). Inequality (3b) shows that the expected attack distance is usually greater than the optimal attack distance. The two distances coincide *if and only if* x_{opt} coincides with x_0 – that is, when the predator attacks immediately at x_0.

Effects of environmental conditions on x_{opt} and x_e

Environmental conditions, such as kinds of prey and vegetation cover, affect the marginal gain of stalking $\varphi(x)$ through changes in the predator's attack success $p(x)$, the prey's awareness probability $q(x)$ and σ, and thus change the expected attack distance. For example, the prey's poor ability to escape enhances the attack success irrespective of the attack distance x. Short grass and high vigilance increase the prey's awareness probability. Here, I represent the enhancing effect of environmental conditions on attack success and awareness probability by two parameters a and b as $p(x:a)$ and $q(x:b)$, which satisfy $\partial p(x:a)/\partial a > 0$

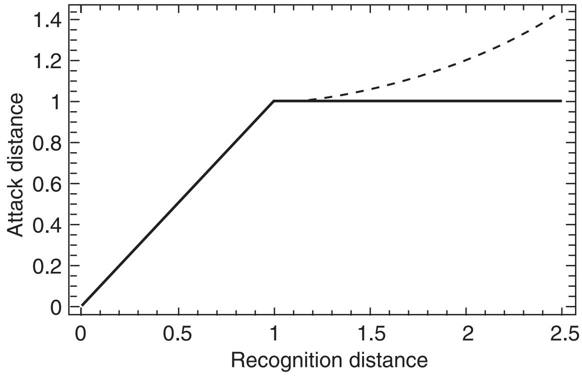

Fig. 2. The optimal attack distance x_{opt} and the mean attack distance x_e as functions of the recognition distance x_0. The solid and dashed curves indicate x_{opt} and x_e, respectively. Here, I assume that $p(x) = 1 - x/a$ and $q(x) = b : a = 5$, $b = 0.5$, $\sigma = 0.5$. $x^* = a - 1/(b(1-\sigma)) = 1$. If $x_0 > x^*$, the marginal gain of stalking is positive until x^*, and thus the predator aims to stalk until x^* and then attack. However, if $x_0 < x^*$, the marginal value of stalking is always negative, and thus the predator attacks immediately at x_0.

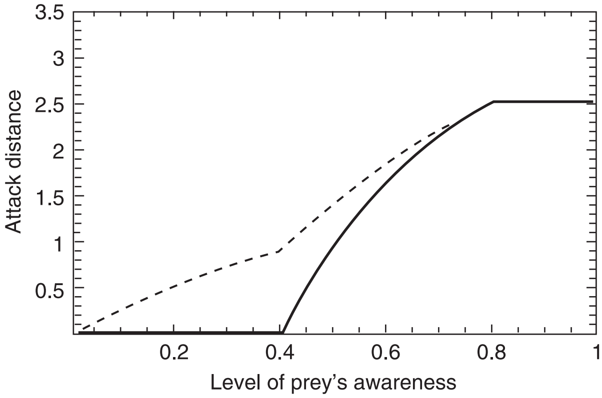

Fig. 3. The optimal attack distance x_{opt} and the mean attack distance x_{e} as functions of the prey's awareness parameter b. The solid and dashed curves indicate x_{opt} and x_{e}, respectively. Here, I assume that $p(x) = 1 - x/a$ and $q(x) = b : x_0 = 2.5$, $a = 5$, $\sigma = 0.5$. $x^* = a - 1/(b(1 - \sigma)) = 1$ at $b = 0.5$. When b is small (here, $b < 0.4$), the marginal gain of stalking is always positive ($x^* < 0$), and thus the predator always stalks. As b becomes large ($0.4 < b < 0.8$), the marginal gain of stalking becomes negative at x^* ($0 < x^* < x_0$), and thus the predator aims to stalk until x^*. When b becomes large enough ($0.8 < b$), the marginal gain of stalking is always negative ($x_0 < x^*$), and thus the predator attacks immediately at x_0.

and $\partial q(x:b)/\partial b > 0$, respectively. Then, the optimal attack distance x_{opt} and the expected attack distance x_{e} are obtained as functions of a, b, σ and x_0.

The sensitivities of x_{e} and x_{opt} to α (α refers to a, b, σ or x_0) are calculated by applying the chain rule of derivatives to (3a) and the implicit theorem to $\varphi(x_{\text{opt}}) = 0$:

$$\partial x_{\text{e}}/\partial \alpha = (\partial x_{\text{e}}/\partial x_{\text{opt}})(\partial x_{\text{opt}}/\partial \alpha) = P(x_{\text{opt}},x_0)\partial x_{\text{opt}}/\partial \alpha \tag{4}$$

$$\partial x_{\text{opt}}/\partial \alpha = -\,(\partial \varphi(x_{\text{opt}})/\partial \alpha)/(\partial \varphi(x_{\text{opt}})/\partial x_{\text{opt}}) \tag{5}$$

From (4), because $P(x_{\text{opt}},x_0) > 0$ holds, the sign of $\partial x_{\text{e}}/\partial \alpha$ coincides with that of $\partial x_{\text{opt}}/\partial \alpha$ – that is, the optimal attack distance and the expected attack distance behave in qualitatively the same way to the changes in environmental conditions.

The predator attacks at a greater distance as either b increases or σ decreases. This is intuitive because both changes increase the risk of losing the merit of surprise $(1 - \sigma)p(x:a)q(x:b)\mathrm{d}x$, while keeping the merit of proximity $-p'(x:a)\mathrm{d}x$ the same (see Appendix). Because parameter a affects both factors through $p(x:a)$ from (2), it depends on the details of the function $p(x:a)$ how a changes the expected attack distance. Figures 2 and 3 provide examples when $p(x:a) = 1 - x/a(x < a)$ and $q(x:b) = b$.

DISCUSSION

The significant property of the optimal decision is that the predator has only to follow a simple rule: keep staking for as long as the marginal gain of stalking exists. In other words, the predator can obtain the maximum expected hunting success simply by relying on the local information summarized in $\varphi(x)$. This suggests that this decision rule could be realized by a very simple rule, such as 'rule of thumb' (Stephens and Krebs, 1986). The Markovian property that the predator's optimal decision and the prey's state at position x are not affected by the past, and the constraint that a hunt ends once the predator attacks, make the past history of stalking success and the future path of the hunt after the attack superfluous information. This reduces the complexity of multi-stage decision-making to a simple local information-based rule. The locality of this decision rule leads to why the optimal attack distance x_{opt} is constant irrespective of the distance at which the predator begins its hunt (Fig. 2, corresponding to cases B and C in the Results section). On the other hand, the maximum expected hunting success $F(x)$ increases as the predator is able to reduce the distance x (Fig. 1).

When a predator adopts the merit of proximity by stalking, it runs the risk of losing the merit of surprise; conversely, when it adopts the merit of surprise by immediate attack, it must abandon any further merit of proximity. This is the essence of the trade-off in the course of a stalking hunt (Bear and Hasson, 1997). The balance between these two conflicting factors determines the predator's optimal decision and thus its stalking pattern. Environmental conditions change the expected attack distance through change in the balance of these factors. This allows us to test if a stalking predator follows the above decision-making rule.

The predicted changes in the expected attack distance shown in Fig. 3 can explain some jumping spiders' observed attack distance (Bear and Hasson, 1997). Spiders were shown to attack at a greater distance when the prey was an adult house fly than a house fly maggot. With the former prey, the attack distance changed even more when spiders were on a non-camouflaged background than on a camouflaged background. In both cases, the prey's awareness probability $q(x:b)$ appeared to be enhanced. The discounting rate σ of an adult house fly appears smaller than that of a house fly maggot. These changes increase the risk of losing the merit of surprise, which makes spiders attack at a greater distance.

A more clear-cut test is to show the constancy of the optimal attack distance x_{opt}. This test needs to distinguish optimal attack distances from non-optimal attack distances in the observed attack distances; in other words, discrimination between *active* and *passive* attacks that occur once a prey is aware of its predator. A limiting case when the predator is not successful after it has been noticed by its prey ($\sigma = 0$), would provide a good opportunity for this test because the predator may abandon its hunt or even flee if it loses the initiative. For example, scale eaters (predatory fish that feed on the scales of other living fish; Hori, 1987) are smaller than their prey fish and escape when noticed.

The logic and the scope of the model presented here are not restricted to stalking predators. It does not matter whether the predator or the prey moves and shortens the attack distance as long as the predator's merit of proximity is intact. Thus, the model is also applicable to *ambush* predators, which hide themselves by camouflage or attract prey by aggressive mimicry (e.g. Jackson and Wilcox, 1990), and to cases when both the predator and prey move. Stalking behaviour appears to occur when the merit of proximity exceeds the risk of losing the merit of surprise. The prevalence of stalking predation in animal hunts, irrespective of taxa, thus reflects the prevalence of the merit of proximity. This might ultimately be due to a co-evolutionary arms race between predator and prey that is advantageous for the latter because of the 'life-dinner principle' (Dawkins and Krebs, 1979).

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APPENDIX

Derivation of (2)

The predator's optimal sequence of decisions determined by (1) is uniquely represented as follows. Here, '#' represents either stalk or attack:

$$(u(x_0), u(x_0 - \mathrm{d}x), \dots, u(x_{\mathrm{opt}} + \mathrm{d}x), u(x_{\mathrm{opt}}), u(x_{\mathrm{opt}} - \mathrm{d}x), \dots, u(\mathrm{d}x), u(0)) = (\text{stalk, stalk}, \dots, \text{stalk, attack}, \#, \dots, \#, \text{attack}) \quad \text{(A1)}$$

Because $F(x_{\mathrm{opt}}) = p(x_{\mathrm{opt}})$ holds, the next equation follows by sequentially calculating (1a) backward from x_{opt} to x_0:

$$F(x_0) = \sum_{k=1}^{(x_0-x_{\mathrm{opt}})/\mathrm{d}x} \sigma p(x_{\mathrm{opt}} + k\mathrm{d}x) q(x_{\mathrm{opt}} + k\mathrm{d}x) \prod_{j=k+1}^{(x_0-x_{\mathrm{opt}})/\mathrm{d}x} (1 - q(x_{\mathrm{opt}} + j\mathrm{d}x)\mathrm{d}x) + p(x_{\mathrm{opt}}) \prod_{j=0}^{(x_0-x_{\mathrm{opt}})/\mathrm{d}x} (1 - q(x_{\mathrm{opt}} + j\mathrm{d}x)\mathrm{d}x) \quad \text{(A2)}$$

Because $\mathrm{d}x$ is very small, $F(x_0)$ coincides with $W(x_{\mathrm{opt}}, x_0)$, where $W(x, x_0)$ is the predator's expected hunting success when it begins its hunt from x_0 and continues stalking until distance x and attacks from there:

$$W(x,x_0) = \int_x^{x_0} \sigma p(y)P(y,x_0)q(y)\mathrm{d}y + p(x)P(x,x_0) \tag{A3a}$$

where

$$P(x,x_0) = \exp(-\int_x^{x_0} q(y)\mathrm{d}y) \tag{A3b}$$

$P(x, x_0)$ and $P(y, x_0)q(y)\mathrm{d}y$ represent the probabilities that the predator succeeds to attain distance x and that the prey becomes aware of the predator at distance y, respectively. Thus, the first and second terms of (A3a) represent the predator's expected hunting success when it fails to attain the distance x and when it succeeds, respectively. Because $F(x_0)$ is the predator's maximum expected hunting success when it begins its hunt at distance x_0, $W(x_{\text{opt}}, x_0)$ coincides with the maximum value of $W(x, x_0)$. Thus, the optimal attack distance obtained from the dynamic optimization (1), x_{opt}, is equivalent to the attack distance that makes $W(x, x_0)$ maximum.

By differentiating (A3a) with x, we obtain the following equation:

$$\partial W(x, x_0)/\partial x = -\varphi(x)P(x, x_0) \tag{A4}$$

Because $P(x, x_0) \geq 0$, $\varphi(x)$ determines the sign of $\partial W(x, x_0)/\partial x$.

Parameter dependence

In the following, I assume that $x_{\text{opt}} = x^*$ (i.e. $0 < x^* < x_0$). The local maximum condition of $W(x_{\text{opt}}, x_0)$ requires the following inequality:

$$\partial^2 W(x_{\text{opt}}, x_0)/\partial x^2 = -\partial\varphi(x_{\text{opt}})/\partial x P(x_{\text{opt}}, x_0) < 0 \tag{A5}$$

Because $P(x_{\text{opt}}, x_0) \geq 0$, $\partial\varphi(x_{\text{opt}})/\partial x$ must be positive at x_{opt}, and thus the sign of $\partial x_{\text{opt}}/\partial a$ coincides with that of $-\partial\varphi(x_{\text{opt}})/\partial a$ from (5).

The sensitivity of x_{opt} to σ is always negative as follows:

$$\partial\varphi(x_{\text{opt}})/\partial\sigma = p(x_{\text{opt}})q(x_{\text{opt}}) > 0 \tag{A6}$$

The sensitivity of x_{opt} to b is always positive as follows:

$$\partial\varphi(x_{\text{opt}})/\partial b = -(1-\sigma)p(x_{\text{opt}})\partial q(x_{\text{opt}})\partial b < 0 \tag{A7}$$

Finally, the sensitivity of x_{e} to x_0 is positive as follows:

$$\partial x_{\text{e}}/\partial x_0 = q(x_0)\int_{x_{\text{opt}}}^{x_0} P(x, x_0)\mathrm{d}x > 0 \tag{A8}$$