Sit-and-Wait Versus Active-Search Hunting: A Behavioral Ecological Model of Optimal Search Mode

Cody T. Ross[a,c], Bruce Winterhalder[a,b]

[a]*Department of Anthropology, University of California, Davis. United States*
[b]*Graduate Group in Ecology, University of California, Davis. United States*
[c]*Email: ctross@ucdavis.edu*

Abstract

Drawing on Skellam's (1958) work on sampling animal populations using transects, we derive a behavioral ecological model of the choice between sit-and-wait and active-search hunting. Using simple, biologically-based assumptions about the characteristics of predator and prey, we show how an empirically definable parameter space favoring active-search hunting expands as: 1) the average rate of movement of prey decreases, or 2) the energetic costs of hunter locomotion decline; the same parameter space narrows as: 3) prey skittishness increases as a function of a hunter's velocity, or 4) prey become less detectable as a function of a hunter's velocity. Under either search tactic, encounter rate increases as a function of increasing prey velocity and increasing detection zone radius. Additionally, we investigate the roles of habitat heterogeneity and spatial auto-correlation or grouping of prey on the optimal search mode of a hunter, finding that habitat heterogeneity has the potential to complicate application of the model to some empirical examples, while the effects of prey grouping lead to relatively similar model outcomes. As predicted by the model, the introduction of the horse to the Great Plains and the introduction of the snowmobile to Arctic foraging communities decreased the metabolic costs of active-search and led to a change in normative hunting strategies that favored active-search in place of sit-and-wait hunting.

Keywords: Foraging Theory, Ambush, Search, Energetics of Hunting, Hunter-Gatherers, Sit-and-Wait

1. Introduction

1.1. Introduction

Evolutionary anthropologists have noted a substantial diversity in hunting strategies across human societies [1, 2, 3, 4, 5, 6, 7, 8, 9], as well as variation in hunting strategies within societies [1, 10] that depend on the behavior of the prey species, individual skills of the hunter, local ecological knowledge, and available technology. Likewise, biologists have noted different normative hunting styles across species [11, 12, 13, 14, 15] and ecologies [16, 17, 18].

Several simple models have been proposed to explain heterogeneity in hunting strategies in 2-dimensional environments [19, 20, 21, 22, 23, 24, 25] in terms of the costs and benefits of active-search versus sit-and-wait, but modeling the linkages between the biological and ecological context of foraging—prey movement velocity, prey skittishness, prey grouping, bioenergetics of predator locomotion, and habitat heterogeneity—and the differential costs and benefits of each strategy to a hunter remains an open problem. In this paper, we attempt to provide a more thorough characterization of the linkages between the biological and ecological characteristics of predator and prey and the costs and benefits of each search mode, by developing a model of foraging behavior that is grounded on the optimization of energetic returns and the dynamics of prey movement through the environment.

Our analysis relies heavily on mathematical tools introduced by Laing [26], Yapp [27], and Skellam [28] to analyze the properties of animal population surveys using transects. These authors rely on a physical analogy (the classical kinetic theory of gases) to make inferences about the population density of a species conditional on the count of individuals observed during a transect walk of specified characteristics. We invert the question and adapt the same tools to investigate encounter rates with prey items observed along a search path conditional on the density and movement of these prey items. We focus on isolating the biological properties of predator and prey that might influence the choice of either an active-search hunting strategy (forager velocity > 0) or a sit-and-wait hunting strategy (forager velocity = 0) by a predator. Similar work on search mode optimization has been conducted in 3-dimensional foraging environments [29], see the *Conclusions* section for a contrast of our findings.

We investigate the role of prey species velocity, prey skittishness, prey detectability, spatial auto-correlation or grouping in prey, habitat heterogeneity, and the energetic costs of active-search on the foraging strategy and optimal velocity of a hunter. We begin by outlining the derivation of our model, and then present the analytical results of our model under simple assumptions concerning the characteristics of prey and hunter. We conclude the analysis by assessing empirical predictions of foraging behavior derived from our model using empirical data on human metabolic expenditure, empirical data on average animal velocities, and ethnographic accounts of human foraging strategies in the Great Plains and Arctic through technological transitions. Finally, we place our analysis and results in the con-

text of related studies concerning the behavioral ecology of the food quest.

Although we describe the predator in question as a human hunter or forager in our prose, our model is general to non-human predators. In the empirical analysis, we focus on the human case studies for two reasons: 1) there is good data on the functions linking energetic expenditure and velocity in humans, and 2) novel technological changes such as domesticated horses, ATVs, snowmobiles, and motorboats have have dramatically changed the energy costs and maximal velocity of active-search in humans; these changes lead to simple, easily tested predictions about hunting strategy change under technological expansion.

1.2. Model Derivation

Closely following the model derived in Skellam [28, passim], we imagine a habitat populated with individuals of a mobile prey species—the gas particles of Skellam's physical analogy—moving in arbitrary paths that are not necessarily independent, with an average velocity u, whose average density over the habitat is $\bar{D}$. Likewise, we imagine a hunter who can chose to remain in a fixed location, or move through the habitat on an arbitrary path at an average velocity, w, Figure 1(a). The hunter carries with him or her a frame of reference, and a convex contour which outlines the area of his or her visual field, as illustrated in Figure 1(b). In contrast to Skellam [28], we do not assume that any prey item that enters the visual contour is necessarily encountered by the hunter, nor do we assume that the density of the prey is the same in neighborhood of the hunter as elsewhere; we do, however, consider these special cases in light of our more general model. For ease of reference, the definitions of these and subsequent parameters and functions are collected in Table 1.

[Table 1 about here.]

[Figure 1 about here.]

We measure the velocity of a prey item relative to the hunter using the hunter's frame of reference. Thus, at any a particular time, t, a given prey item has a relative velocity characterized by a direction, $\theta(t)$, and magnitude, $v(t)$; we allow there to be heterogeneity in these values across prey items. We classify prey items by their directions and magnitudes such that $f(v, \theta, t)\partial v \partial \theta$ represents the proportion of prey items in the neighborhood of the hunter at time t that have velocities in the elementary interval $v \pm \frac{1}{2}\partial v$ and directions in $\theta \pm \frac{1}{2}\partial\theta$.

To calculate the expected encounter rate between the hunter and prey items, we draw the contour of the hunter's convex visual field as illustrated in Figure 1(b). We then draw two parallel tangents to the contour having direction θ; the distance between the tangents is then $H(\theta)$. We mark off a border of width $v(t)\partial t$, and shade the area laying within the tangents, the contour, and the border width. A prey item with velocity $v \pm \frac{1}{2}\partial v$ and direction $\theta \pm \frac{1}{2}\partial\theta$ can cross into the visual field from outside it in the elementary interval of time from t to $t + \partial t$ if and only if it lies within the shaded area at time t.

The area of the shaded region is equal to $H(\theta)v(t)\partial t$, so the expected number of prey items in the stated class lying inside it will be $D(w)f(v, \theta, t)\partial v \partial \theta H(\theta)v(t)\partial t$, where $D(w)$ is the density of prey items in the neighborhood of the hunter, when the hunter is moving at velocity w. For generality, we consider D to be a smooth, strictly decreasing function of the hunter's average velocity, w, which equals $\bar{D}$ when $w = 0$, and has a lower bound at 0. D accounts for prey skittishness, allowing for a local decrease in the density of prey to occur as the hunter moves more rapidly, and is thus more conspicuous in the environment.

The expected total number of prey items, $E(P)$, entering contour from outside in the interval ∂t is given by integrating over all values of v and θ; the expected total number of prey items entering into the contour over the course of the hunt from the start time, T_S, to the end time, T_E, is given by integrating over t. Thus, $E(P)$ over the course of a hunt is:

$$E(P) = D(w) \int_0^{2\pi} \int_0^{\infty} \int_{T_S}^{T_E} v(t)f(v, \theta, t)H(\theta)\partial v \partial \theta \partial t \qquad (1)$$

By definition, $T = T_E - T_S$, and the average velocity of the prey items relative to the hunter, V, is:

$$V = \frac{1}{T} \int_{T_S}^{T_E} \int_0^{2\pi} \int_0^{\infty} v(t)f(v, \theta, t)\partial v \partial \theta \partial t \qquad (2)$$

If, for purposes of analytical tractability, the visual contour is defined to be a circle, then all values of H are equal to 2 times the visual radius, R, and Equation 1, reduces to:

$$E(P) = D(w)2RVT \qquad (3)$$

As shown by Skellam [28] using a 2-dimensional analogue of Maxwell's distribution, V can also be expressed in terms of the average velocity of the prey items, u, and the hunter, w:

$$V = \sqrt{u^2 + w^2} \qquad (4)$$

Finally, we consider the expected number of prey encountered during the hunt, $E(\Phi)$, to be:

$$E(\Phi) = E(P)\xi(w) \qquad (5)$$

where ξ is a smooth, strictly decreasing function of the hunter's average velocity, w, with a value of 1 when $w = 0$ and a lower bound of 0. From Equation 5, we see that ξ modulates the rate of encounters to reflect the fact that a hunter moving at an increased velocity may be more likely to overlook prey items that have crossed into his or her visual contour. While $\xi(w)$ appears to have the same effect on encounters as $D(w)$, they affect the model through different mechanisms, where $D(w)$ reflects changes in the local density of prey as a function of hunter velocity (due to prey skittishness), and $\xi(w)$ further decreases expected encounters (due to the hunter being less able to accurately detect prey items as his or her velocity increases).

Thus, the full model we will use to investigate the choice of hunting strategies can be written as:

$$E(\Phi) = 2RTD(w)\xi(w)\sqrt{(w^2 + u^2)} \qquad (6)$$

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Verbally, this model states that the expected number of prey encounters, $E(\Phi)$, is equal to the product of twice the radius of the detection zone, $2R$, the time spent hunting, T, the effective local prey density, $D(w)\xi(w)$, and the square root of the summed squares of hunter and prey average velocities, w and u, respectively. Although different in both scope and derivation, our model shows some similarities with previous work on foraging strategy in zooplankton in 3-dimensional space [29].

2. Results

2.1. Prey Velocity, Energy Expenditure, and Hunting Strategy

If we assume for the time-being that $D(w) = D(0) = \bar{D}$ and $\xi(w) = \xi(0) = 1$, we can model the ecological contexts in which sit-and-wait hunting will be preferred to active-search hunting, when the hunter's velocity has no effect on local prey density or prey detectability. To do so, we investigate the ratio of expected caloric returns from prey encounters to metabolic expenditure across hunting strategies. The expected number of prey encounters is derived from Equation 6, the caloric content of a prey item is defined to be α, and metabolic expenditure is considered to be a smooth strictly increasing function, C, of the hunter's average velocity w, which equals 1 when $w = 0$.

Under these assumptions, sit-and-wait hunting will yield higher returns than active-search hunting when:

$$\frac{2\alpha D(0)\xi(0)RT\sqrt{(0+u^2)}}{C(0)} > \frac{2\alpha D(w)\xi(w)RT\sqrt{(w^2+u^2)}}{C(w)} \quad (7)$$

which is true when:

$$u^2 > \frac{w^2}{\hat{C}^2 - 1} \quad (8)$$

where $\hat{C} = \frac{C(w)}{C(0)}$ is the ratio of energy expenditure rates between active-search at average velocity w, and sitting-and-waiting at average velocity 0.

In our numerical analysis, human energy expenditure per unit time relative to velocity is expressed in terms of METs (Metabolic Equivalents). METs describe the energy required to move at velocity, w, under various kinds of exertion (walking, jogging, running, rowing, horse riding, snowmobiling) in proportion to baseline energy consumption during seated rest [30]. Thus, our parameter $\hat{C} = \frac{C(w)}{C(0)}$ has a direct empirical formulation. As is shown in Figure 2, decreasing the $\hat{C}$ ratio, represented by the shifted indifference curves with identical hunter velocities, but differing MET values, expands the area of the state space favoring active-search hunting.

[Figure 2 about here.]

2.2. Prey Skittishness

If we relax our assumption that $D(w) = D(0) = \bar{D}$ and consider cases where $D(w) \neq D(0)$, while still assuming $\xi(w) = \xi(0) = 1$, we can model the ecological contexts in which sit-and-wait hunting will be preferred to active-search hunting, when the hunter's velocity has an effect on local prey density,

but not prey detectability. We solve Equation 7 under this new assumption, which yields:

$$u^2 > \frac{w^2}{\hat{C}^2\hat{D}^2 - 1} \quad (9)$$

where $\hat{D} = \frac{D(0)}{D(w)}$ is the ratio of local prey densities between sitting-and-waiting and active-search at average velocity w.

If more rapid predator velocity increases the likelihood of alerting prey and thus decreases their local density, and by implication the effective encounter rate, then the area of the state space favoring active-search decreases (Figure 2).

2.3. Prey Detectability

If we relax our assumption that $\xi(w) = \xi(0) = 1$ and consider cases where $\xi(w) \neq \xi(0)$, while assuming $D(w) = D(0) = \bar{D}$, we can model the ecological contexts in which sit-and-wait hunting will be preferred to active-search hunting, when the hunter's velocity has an effect on the detectability of prey that come within its visual range, but not local prey density. We solve Equation 7 under this new assumption, which yields:

$$u^2 > \frac{w^2}{\hat{C}^2\hat{\xi}^2 - 1} \quad (10)$$

where $\hat{\xi} = \frac{\xi(0)}{\xi(w)}$ is the ratio of prey detectability between sitting-and-waiting and active-search at average velocity w.

Similar to the result in Section 2.2, if more rapid predator velocity decreases the likelihood of detecting prey inside the hunters's visual radius, and by implication decreases the effective encounter rate, then the area of the state space favoring active-search decreases (Figure 2).

2.4. Prey Skittishness and Detectability

If we relax both assumptions and consider cases where $\xi(w) \neq \xi(0)$ and $D(w) \neq D(0)$, we can model the ecological contexts in which sit-and-wait hunting will be preferred to active-search hunting, when the hunter's velocity has an effect on prey detection and local prey density. We solve Equation 7 under these new assumptions, which yields:

$$u^2 > \frac{w^2}{\hat{C}^2\hat{D}^2\hat{\xi}^2 - 1} \quad (11)$$

$\hat{D}$ and $\hat{\xi}$ interact multiplicatively, decreasing the scope for active-search hunting as their product increases (Figure 2).

2.5. The Effect of Prey Grouping

The formulas for the mean encounter rates described above do not require that prey items move independently. Thus, the grouping of prey items—for example, whether prey items live and forage in herds, or live and forage solitarily—has no impact on the mean encounter rate under the previous assumptions. The variance of encounters per unit time, however, will be influenced by the grouping of prey items. If the encounter rate is low, and the prey items move in a random walk, then the number of encounters should be distributed approximately as a

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Poisson variate, where the mean and variance are equal [28]. If prey are grouped into clusters composed of G individuals, then the variance of encounters per unit time will be G times the mean number of encounters [28].

The size of the variance in prey encounters may have an impact on the decision of an individual to engage in a hunt, particularly if potential hunters are attempting to mitigate risk [31]. However, as long as the tendency of prey items to form into groups is independent of the search mode used by the hunter, it will have no influence on the preference for one hunting strategy over the other, even when risk-sensitive models are used to analyze the choice of strategies.

To see why, we adopt the Z-score model from Stephens and Charnov [31]. In this model, the strategy that will be preferred by an actor is the strategy which minimizes the probability density lying below the minimum resources needed for survival, R_{min}, which is strictly positive.

Thus, to compare the contexts in which sit-and-wait hunting will be preferred to an active-search strategy using a risk-sensitive model, we write:

$$\frac{\Psi(0) - R_{min}}{\Psi(0)G(0)} > \frac{\Psi(w) - R_{min}}{\Psi(w)G(w)} \qquad (12)$$

where the mean caloric returns per unit time during sit-and-wait hunting, $\Psi(0)$, is given by:

$$\Psi(0) = \frac{\alpha E(\Phi)|_{w=0}}{C(0)} \qquad (13)$$

Here α is the caloric content of prey collected upon encounter, $E(\Phi)|_{w=0}$ indicates the value of $E(\Phi)$ evaluated when $w = 0$, and G is a function which returns prey group size (≥ 1) as a function of the hunter's velocity, w. If the grouping behavior of prey is independent of hunter velocity then $G(0) = G(w)$, and Equation 12 reduces to Equation 7, showing that a hunter's risk-sensitive decision to use sit-and-wait versus active-search is unaffected by degree of prey grouping.

If, on the other hand, prey change their grouping behavior in response to the hunter's velocity, then $G(0) \neq G(w)$, and Equation 12 becomes:

$$\frac{G(w)}{G(0)} > \frac{1 - \frac{R_{min}}{\Psi(w)}}{1 - \frac{R_{min}}{\Psi(0)}} \qquad (14)$$

and as $\Psi(w) \rightarrow \Psi(0)$, and the caloric returns expected from active-search approach those from sit-and-wait, this inequality approaches:

$$G(w) > G(0) \qquad (15)$$

which indicates that sit-and-wait hunting is more likely to be preferred when active-search hunting leads prey items to become more congregated. This effect is driven by the congregation of prey increasing the variance in encounters, leading active-searching hunters to face potentially longer periods with no prey encounters.

2.6. The Effect of Environmental Variability (Patchiness)

If the environment is characterized by heterogeneity (patchiness), then the prey encounter rate for a hunter moving through such an environment (characterized by N distinct patches) is given by:

$$E(\Phi)|_{w>0} = \sum_{i=1}^{N} 2D_i(w_i)\xi_i(w_i)R_iT_i \sqrt{(w_i^2 + u_i^2)} \qquad (16)$$

where T_i is the time spent in patch i, and all other functions or parameters indexed by i are patch specific values.

The prey encounter rate for a hunter using the sit-and-wait strategy in a given patch i over the same interval of time, however, is:

$$E(\Phi)|_{w=0} = 2D_i(0)\xi_i(0)R_iu_iT \qquad (17)$$

where the model parameters for a single patch determine the encounter rate.

If the hunter moves across patches, he or she can average over the heterogeneity in patch quality within a hunt, while the sit-and-wait hunter is limited to a single patch of a given quality. If the sit-and-wait hunter has no special knowledge of patch quality, then on average, over many hunts, the comparison of sit-and-wait and active-search under heterogeneity reduces to the model under homogeneity. However, if hunters do have specialized knowledge of patch quality and if any of the model parameters have diverging values across patches, then the effects of patch selection may be significant, and even confound the applicability of this model to empirical data.

Empirically, hunters are likely to have such special knowledge of patch quality. Sit-and-wait hunters often position themselves in optimal patches, for instance, by hiding in watering holes (crocodiles [32]), or waiting near forest trails or passes (puma [23]). Human foragers, especially, use patch constraints to increase the domain of attraction for sit-and-wait hunting, for instance, by creating man-made walls and cairn lines that funnel prey items into a desired location [33]. We leave the specific solution of sit-and-wait versus active-search in a patchy resource environment to another analysis.

2.7. Numerical and Empirical Analyses

To characterize the functions describing when sit-and-wait hunting will be preferred to active-search hunting, we use a combination of numerical and empirical analysis. We focus on illustrating the behavior of the model using numerical analysis and then present a basic empirical test of the model's predictions using examples from the hunter-gatherer literature on the introduction of transportation technology to foraging populations. We leave a more complete comparative analysis of hunter-gather search mode for the future.

2.7.1. Numerical Analysis - Optimal Search Velocity

We assume that the functions $\hat{D}(w)\hat{\xi}(w)$ and $\hat{C}(w)$ take the forms shown in Figure 3(a). We then plot expected return rates as a function of u and w, Figure 3(b). In Figure 3(c), we plot

slices through the contour map presented in Figure 3(b), in order to provide a higher resolution image of the model behavior at small values of u and w.

From Figure 3(b), we note that: 1) above a certain prey velocity (u = 3.3, given our specific numerical assumptions in this example), it always benefits the forager to reduce velocity to zero, 2) below this same threshold, there is an intermediate optimal velocity which declines as prey velocity increases, 3) even if foragers can move faster than their prey, they may benefit by sitting-and-waiting rather than actively-searching if they are hunting fast-moving prey, and 4) even if the foragers are biologically limited to move at slower velocities than their prey, there exist locations in the parameter space where active-search is favored, Figure 3(c). See Supplementary Materials for Simulation Code.

[Figure 3 about here.]

2.7.2. Numerical Analysis - Search Mode Changes

We reproduce a list of METs for various activities published by [30] in Table 2, and use these data to calculate the values of u at which sit-and-wait hunting would be preferred to active-search hunting for various values of $\hat{D}\hat{\xi}$.

[Table 2 about here.]

Figure 4 displays an indifference curve for a hunter selecting between sit-and-wait (at an energy cost of 1 MET) and active-search using various forms of locomotion, as $\hat{D}\hat{\xi}$ changes from $1 \rightarrow 10$.

[Figure 4 about here.]

Figures 4(a) and 4(b) illustrate how the introduction of transportation technology such as all-terrain vehicles, snowmobiles, and motor-boats might alter the behavior of human foragers. Our model would predict foragers to change hunting tactics from sit-and-wait to active-search using vehicles for all combinations of prey rate of movement and $\hat{D}\hat{\xi}$ ratios lying above the indifference curve for the previously optimal hunting strategy and under the indifference curve for vehicle use.

2.7.3. Bison Hunting and the Introduction of Horses to the Great Plains

Until approximately 2000 years ago, the pedestrian Native American hunters of the Great Plains made "exclusive use of natural traps" [34, pg. 32], in their hunts for bison, a major part of their diet. According to Bamforth, around 2000 years ago this tactic intensified, with hunters driving herds which appeared in topographically-suited valleys into cairn-lined lanes leading to visually hidden escarpments, below which the incapacitated or dead animals were butchered and processed. In our terms, these are sit-and-wait tactics, realized through natural and, later, human-modified settings constituting traps.

A dramatic change occurred with the arrival of the horse late in prehistory. The frequency of communal drives, jumps, and pounds diminished, as the increased velocity and mobility of horses allowed mounted hunters, solitary or in small groups, to locate bison over a wide range and quickly overtake and harvest them with the bow or firearms [35]. Among the Hidatsa, a Native American group living along the Missouri River and its tributaries in present-day North Dakota, this shift from sit-and-wait to active-search on horseback is described by Hanson [36, pg. 97-101] in terms we would predict:

> Buffalo hunting on horseback had several advantages over pedestrian methods such as the drive: the mobility and striking speed afforded by mounted hunting allowed groups of hunters to increase their search radius, to report herd locations more quickly to the main camp, and to pursue and surround bison swiftly and efficiently... [Buffalo runners, or horses]... trained for maneuvering in and around buffalo herds, allowing a rider to shoot arrows into an animal at point blank range and yet veer away from the potential danger of a wounded buffalo at precisely the right time... were highly prized and, except in the cases of emergency, were not used for other tasks.

2.7.4. Arctic Big Game Hunting and the Rise of the Snowmobile

Prior to the introduction of the snowmobile and rifle, archaeological data [33, 37, 38] and oral histories [39, 40] indicate that Arctic hunters relied heavily on ambush hunting from blinds to capture large ungulates like caribou, muskoxen, and moose. The introduction of the snowmobile, however, dramatically changed hunting strategies, as long trips to hunting sites were replaced by fast-paced day trips on snowmobiles [41]. Inuit hunters could not usually overtake moving caribou with dog teams, but the introduction of the snowmobile made such active-search possible [42]. The primary hunting strategy of waiting in sheltered blinds, was replaced almost immediately by active-search and chase on snowmobile, followed by firing on the animals after they reached exhaustion [43].

A similar change is noted in the hunting of Tibetan antelope in the western Chang Tang Nature Reserve, where traditional sit-and-wait strategies have been replaced with active-search using motorcycles and guns [44].

It is interesting to note that before the introduction of rapid transportation technology, sit-and-wait hunting (in blinds) was often the preferred hunting strategy for antelope, deer, and other ungulates, even though intuition would suggest that such animals are typically fast-moving prey items. They are fast prey to be sure—even if their average foraging velocity is lower than their sprinting speed [45, 46]—but equally important, they are cursorial ungulates, with highly developed ability to detect moving predators by sound or sight in the open, and typically fairly flat country that they inhabit [47]. As such, the model would suggest that the $\hat{D}\hat{\xi}$ ratio may empirically become unfavorable rapidly if the hunter's velocity is non-zero.

To gain a more rooted understanding of the relationship between our model's implications and empirical data on hunting strategies and prey velocity, we plot published average rate of movement estimates for various prey species on an indifference curve for hiking at 6 Km/hr on a 5 percent slope carrying 20

Kg (Figure 5). The intersection of the indifference curves and the lines describing prey rate of movement are indicative of the $\hat{D}\hat{\xi}$ ratio above which sit-and-wait hunting would be preferred, holding constant prey rate of movement and other model parameters.

[Figure 5 about here.]

Table 3 displays some empirical average rate of movement estimates for various prey items corresponding to Figure 5.

[Table 3 about here.]

3. Conclusions

We provide a behavioral ecological model of the choice between active-search and sit-and-wait hunting strategies that is derived from the biology and ecology of predator and prey; we summarize our findings in Table 4. Under the assumptions of the model, the choice between sit-and-wait and active-search hunting depends on the average rate of movement of the prey and at least three aspects of the hunter's velocity: 1) $\frac{C(w)}{C(0)}$, the ratio of the hunter's energy expenditure moving at velocity w to the energy expenditure at rest, 2) $\frac{D(0)}{D(w)}$, the ratio of local prey density when the hunter is at rest to the local density when the hunter is moving at velocity w, and 3) $\frac{\xi(0)}{\xi(w)}$, the ratio of the ability of the hunter to detect prey when at rest to the ability of the hunter to detect prey when moving at velocity w.

[Table 4 about here.]

Through numerical methods, we show that decreasing the energetic costs associated with elevated velocity should expand the area of the state space favoring active-search hunting. We use case studies of the effect of the introduction of horses into the Great Plains and the introduction the snowmobile into Arctic hunting communities to test if hunting strategies change as the metabolic costs of active-search decrease. In these case studies, we find evidence in support of our model.

However, more wide-ranging empirical work will be needed to evaluate the extent to which this model is predictive of hunting behavior cross-culturally in humans. Such work should investigate the type of search mode used by hunters of a given cultural group as a function of the average velocity and temperament of each of the prey species commonly taken in that cultural group. Additionally, a wider-ranging cross-cultural analysis of the effect of a decrease in the metabolic cost of active-search hunting—due to technological intensification—on hunting style would help to empirically evaluate our model's predictions in human foragers. Further, we envision an assessment of the model through comparative analysis of the use of traps, snares, weirs and similar technologies treated as surrogate sit-and-wait predators by human and some non-human hunters.

3.1. The Broader Context

In an early comprehensive review of foraging theory, Schoener [19] distinguished between models developed for sit-and-wait foragers and those developed for foragers incurring the costs of active-search. Although he identified several mathematical representations of active-search, including Skellam's [28], he did not use these to compare the conditions favoring one tactic over the other. Optimal search mode remains to this day insufficiently studied in the behavioral ecology literature [24]. As context for our results, we summarize literature highlights from optimization approaches, and then note the relevance of literature on Lévy walks and game theory models of predator-prey tactics.

In a search mode model similar to ours, but based on search in a 3-dimensional space, Gerritsen and Strickler [29] find that active-searching predators are predicted to prey upon slow-moving animals, and ambush predators are predicted to prey upon fast-moving animals. Our major qualitative findings are, in this way, quite similar. It is informative, however, to contrast our encounter models; in the 2-dimensional foraging environment, we have number of encounters in fixed period of time given by:

$$E(\Phi)_{\text{2-dimensions}} = 2RTD(w)\xi(w)\sqrt{(w^2 + u^2)} \qquad (18)$$

Assuming our functional forms for $D(w)$ and $\xi(w)$ can be directly translated to the 3-dimensional case in which density is prey items per unit volume, in a 3-dimensional foraging environment we have:

$$E(\Phi)_{\text{3-dimensions}} = \frac{\pi R^2 T D(w)\xi(w)}{6} \frac{(w + u)^3 - |u - w|^3}{wu} \qquad (19)$$

which reduces to:

$$E(\Phi)_{\text{3-dimensions}} = \begin{cases} \frac{\pi R^2 T D(w)\xi(w)(3u^2+w^2)}{3u}, & \text{if } u > w, \\ \frac{\pi R^2 T D(w)\xi(w)(u^2+3w^2)}{3w}, & \text{if } u < w. \end{cases} \qquad (20)$$

Although the search mode model is not generally solvable for Equation 19, since we have division by zero if $w = 0$, under the assumption that $u > w$, we can solve the model for the prey velocity u above which the hunter should elect to sit-and-wait:

$$u^2 > \frac{w^2}{3(\hat{C}\hat{D}\hat{\xi} - 1)} \qquad (21)$$

contrasted with the 2-dimensional case:

$$u^2 > \frac{w^2}{\hat{C}^2\hat{D}^2\hat{\xi}^2 - 1} \qquad (22)$$

Now, comparison of the right-hand sides (RHS) of Equations 21 and 22, shows that the RHS of Equation 21 will be bigger than RHS of Equation 22 whenever:

$$\hat{C}^2\hat{D}^2\hat{\xi}^2 > 3\hat{C}\hat{D}\hat{\xi} - 2 \qquad (23)$$

Since $\hat{C}, \hat{D}, \hat{\xi} > 1$, the left-hand side of Equation 23, will grow faster than the right-hand side as a function of increasing inputs, meaning that as locomotion becomes more energetically costly ($\hat{C}$ increases) and depresses the effective local density of prey items ($\hat{D}$ and/or $\hat{\xi}$ increases), the scope for active-search declines for predators in both 2- and 3-dimensional foraging environments, but the effect will be stronger in 2-dimensional

environments. As such, *ceterus paribus*, we might expect to see the sit-and-wait strategy emerge more frequently in land-dwelling animals foraging primarily in two spatial dimensions, than in aquatic, aerial, or other animals foraging in three spatial dimensions.

In an analytical model considering prey density but not movement, Norberg [48] showed that a time-minimizing forager such as an endotherm seeking to meet a set requirement in the least amount of time will optimize by shifting to less costly, perhaps lower velocity methods as prey density decreases, predator size increases, or as prey grow smaller. Field studies have also provided evidence of the importance of prey velocity on search mode. Huey and Pianka [20] hypothesized that sit-and-wait hunting will be favored when high ranked prey choices are mobile, and active-search will be favored when they are not. Empirically, they find that the rate of movement of prey species is the principle driver of search mode between lizard species that specialize in active-search and prey on stationary prey items, like termite mounds, and those that specialize in sit-and-wait hunting. The same pattern was true of the foraging style of snakes, where sit-and-wait snakes specialize in hunting active-searching lizards, and active-searching snakes prey predominately on lizards that rely on sit-and-wait hunting [20].

In a model assessing the success of foragers with access to resource sites classified as either *Good* or *Poor* with switch probabilistically occuring from one state to another, Janetos [21] found that when active foraging, the rule—move if you experience a poor site that day—is favored when relocation is inexpensive, the difference between *Good* and *Poor* sites is elevated, and sites switch between *Good* and *Poor* infrequently. This model provides a useful heuristic for describing how a predator might effectively select between patches in a heterogeneous environment. Our model suggests that the choice between sit-and-wait and active-search itself can be patch-specific. As such, the development of models that integrate patch selection and search mode selection may be of theoretical interest, especially in understanding the behavior of predators whose search mode is variable in space or time.

Models have also shown the importance of directionality in movement. Using simulation, Scharf et al. [25] find that active-search is advantageous when both predator and prey move randomly, but that the relative advantage of active-search diminishes as predator and prey adopt more directional movement. So long as prey movement is random, the predator gains advantage by a modest degree of directional search. If the predator is slower than its prey, active-search has little advantage over ambush; when the predator's velocity can exceed that of the prey, there is a rapidly increasing advantage to active-search. Conversely, ambush becomes more attractive as prey velocity increases. As in our model, these results are largely unaffected by prey density; however, this model did not assign metabolic costs to active-search, so inference about the caloric return rate as a function of search velocity is not possible.

In a broad ranging attempt to determine the relative advantage of the two foraging modes, Higginson and Ruxton [24] model search behavior in a patchy environment as a function of prey abundance, size, and distribution over patches, as well as clumping of patches, for foragers with the goal of maximizing encounters, avoiding predation, and avoiding depletion of food reserves. Their model does not explicitly consider prey mobility, although the effect of mobility is mimicked by a parameter representing patch transience—assuming resource renewal, depletion of a patch requires that prey consumed in one location are offset by prey appearing elsewhere. Patch transience increases the attractiveness of sit-and-wait foraging because prey are more likely to "show up" at the site of a sit-and-wait forager, who thereby avoids the energy costs and potential exposure to predation associated with active-search. Increasing search velocity (without accounting for its metabolic costs) increases the relative advantage of active-search; increasing prey density favors the sit-and-wait mode. Patch "clumpiness" decreases the advantages of active-search in their state-independent scenarios, and increases it in risk-sensitive scenarios when the state of food reserves is taken into account. As in our models, the Higginson and Ruxton [24] model predicts that state-independent choice of foraging mode may change if avoidance of starvation is the immediate goal of the forager.

Our findings generally concur with the hypothesis of Huey and Pianka that increasing prey velocity shifts the advantage toward sit-and-wait foraging [20]. However, some of our specific results differ from those of other studies. For instance, Scharf et al. [25, pp. 355] find that "the optimal strategy for predators that cannot move as fast as their prey is the ambush one." While our results are generally consistent with this pattern, insofar as our model does suggest that predators of high velocity prey can often off-load the energetic cost of movement onto their prey, we note a few nuances. We find that at low prey velocities, predators can increase their payoffs by moving, rather than sitting-and-waiting (Figure 3(c)). We also find that for high prey velocities, predators can often increase their payoffs by sitting-and-waiting, even if they are capable of moving at higher velocities than their prey. And, unlike the results of Higginson and Ruxton [24], who find in their state-independent analyses that increased forager search rate always favors active-search, we show that increasing costs and decreasing search effectiveness at higher velocities will expand the parameter combinations over which the sit-and-wait mode is advantageous. However, when considering risk sensitivity, our model results match those of Higginson and Ruxton [24] in predicting that prey clumping increases the risk of long intervals without encountering prey.

While there is empirical literature suggesting directionality to prey and/or predator movements (summary in Scharf et al. [25]), evidence suggests that a wide range of searching predators adopt Lévy or Lévy-like walks [49, 50], including humans [51], while others conform to Brownian movement (examples in [52]). Lévy walks, are characterized by a distribution of step lengths with randomized turns equally likely in any compass direction. At specific parameter settings, Lévy and Brownian walks appear to differ little in outcome, although Lévy walks can display more heavy-tailed step lengths, and may thus lead to higher efficiency in exploring an environment over a greater range of conditions, especially when prey encounters are rare. This advantage diminishes and may reverse as prey be-

come more common [49]. Lévy walks also produce fewer long "famine" intervals of no encounters [49]. Sorting out the applicability of these various models of movement is difficult because detailed quantitative geographic and behavioral descriptions of search and pursuit for predator-prey systems remain "exceedingly rare" [53, pp. 1].

Finally, insights about search mode may be gained by considering tactical responses of predator and prey to each other, modeled with a game-theoretic approach [54]. Allowing for strategic interactions can change the manner in which predators seek prey, and how evasive prey inhabit and move among feeding patches [55]. These approaches typically are called search, ambush, or pursuit-evasion games [56]; a variety of them have been proposed and solved [22, 57, 58]. For instance, consider a predator choosing between ambush or active-search that can, when in ambush mode, detect prey only when the prey change location. Prey in turn can elect to hide in one spot or move periodically. Because prey will respond to an ambush predator by remaining stationary, they become more susceptible to active-search, with the result that the equilibrium predator tactic is a mix of ambush and active-searching [56]. Likewise, a predator that begins a foraging bout with active-search may switch to ambush as it narrows the area in which lingering, unexploited prey are isolated. As in our model, Alpern et al. [56] allow for the possibility that prey detection declines with increased predator velocity in their "ambush search" game. In a second model that consists of search or hide-and-seek coupled to pursuit-evasion, Gal and Casas [53] show that prey will respond to a predator that visits each possible hiding location for a probabilistic capture below a threshold number of times by randomizing their positions. However, if the predator revisits particular sites above that threshold, then the prey elect the fixed position with the greatest probability of successfully evading a pursuit once they are spotted.

In the present study, we focus on modeling the choice of optimal search strategy using a model that is grounded on the locomotion dynamics and biological characteristics of predator and prey; this places our model in the realm of optimization rather than game theory, and allows for an analytical approach in place of the simulation models commonly adopted in the analysis of structured environmental settings. Except in the localized and ephemeral effect that predator velocity has on prey skittishness and/or detectability once within observational range, we assume constant prey density based on instantaneous renewal and no effect of hunting on prey distribution [cf. 59]. However, under the assumptions of our model, any change in prey density for densities > 0 will not affect the choice of search mode. We model the metabolic cost of active foraging, but do not assign fitness consequences arising from hazards such as predation or exposure. We also solve the model under the assumption that the forager seeks to optimize return rate, but optimization based on other constraints is possible as well. For example, the forager may only have a fixed number of calories that can be expended before survival is threatened, and optimal search under such a constraint may be different than optimal search under our assumptions. Finally, while we examine prey clumping, we focus on a lone forager or contiguous foraging group, and thus neglect the advantages of information sharing among individuals searching apart from one another [52].

Other literature on foraging strategy has investigated the role of predator hunger or attributes of prey species other than average rate of movement on hunting strategy [60, 61, 62, 63]; our model, reflecting its assumptions, suggests that prey velocity more than any other characteristic has a significant causal role in choice of search strategy by an associated predator. Future empirical research on hunting style across a wider range of animal species that contrasts the effects of average prey rate of movement with other predictors will be of importance in the empirical evaluation of our model and others. Additionally, future theoretical work on optimization of our model under a constrained predator energy budget may help to address how predator hunger might alter search mode.

The modeling and analysis of algorithms that guide optimization of search mode is relevant not only to the food quest of hunter-gatherers or, more generally, predators seeking prey [22], but also to practical matters of attempting to locate criminals [64], capture kidnappers [58], and encountering information in libraries [65] or the internet [66].

References

[1] B. Winterhalder, E. Smith, Hunter-Gatherer Foraging Strategies: Ethnographic and Archaeological Analyses, University of Chicago Press, 1981.

[2] K. Hawkes, J. F. O'connell, N. B. Jones, O. Oftedal, R. Blumenschine, Hunting income patterns among the hadza: big game, common goods, foraging goals and the evolution of the human diet [and discussion], Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 334 (1991) 243–251.

[3] R. Walker, K. Hill, H. Kaplan, G. McMillan, Age-dependency in hunting ability among the ache of eastern paraguay, Journal of Human Evolution 42 (2002) 639–657.

[4] J. M. Koster, Hunting with dogs in nicaragua: an optimal foraging approach, Current Anthropology 49 (2008) 935–944.

[5] B. P. Winterhalder, Canadian fur bearer cycles and cree-ojibwa hunting and trapping practices, American Naturalist (1980) 870–879.

[6] M. S. Alvard, D. A. Nolin, Rousseau's whale hunt? coordination among big-game hunters, Current Anthropology 43 (2002) 533–559.

[7] P. Wiessner, Hunting, healing, and hxaro exchange: A long-term perspective on! kung (ju/'hoansi) large-game hunting, Evolution and Human Behavior 23 (2002) 407–436.

[8] M. Gurven, H. Kaplan, M. Gutierrez, How long does it take to become a proficient hunter? implications for the evolution of extended development and long life span, Journal of human evolution 51 (2006) 454–470.

[9] E. A. Smith, Inujjuamiunt Foraging Strategies: Evolutionary Ecology of an Arctic Hunting Economy, Transaction Publishers, 1991.

[10] R. C. Bailey, R. Aunger Jr, Net hunters vs. archers: variation in women's subsistence strategies in the ituri forest, Human Ecology 17 (1989) 273–297.

[11] T. Bartnick, T. Van Deelen, H. Quigley, D. Craighead, Variation in cougar (puma concolor) predation habits during wolf (canis lupus) recovery in the southern greater yellowstone ecosystem, Canadian Journal of Zoology 91 (2013) 82–93.

[12] M. W. Hayward, G. I. Kerley, Prey preferences of the lion (panthera leo), Journal of Zoology 267 (2005) 309–322.

[13] J. E. Silva-Pereira, R. F. Moro-Rios, D. R. Bilski, F. C. Passos, Diets of three sympatric neotropical small cats: Food niche overlap and inter-species differences in prey consumption, Mammalian Biology-Zeitschrift für Säugetierkunde 76 (2011) 308–312.

[14] B. M. Pierce, V. C. Bleich, R. Terry Bowyer, Selection of mule deer by mountain lions and coyotes: effects of hunting style, body size, and reproductive status, Journal of Mammalogy 81 (2000) 462–472.

[15] M. Ciechanowski, T. Zajac, A. Bilas, R. Dunajski, Spatiotemporal variation in activity of bat species differing in hunting tactics: effects of weather, moonlight, food abundance, and structural clutter, Canadian Journal of Zoology 85 (2007) 1249–1263.

[16] L. M. Hiruki, M. K. Schwartz, P. L. Boveng, Hunting and social behaviour of leopard seals (hydrurga leptonyx) at seal island, south shetland islands, antarctica, Journal of Zoology 249 (1999) 97–109.

[17] M. Nshombo, Foraging behavior of the scale-eater plecodus straeleni (cichlidae, teleostei) in lake tanganyika, africa, Environmental biology of fishes 39 (1994) 59–72.

[18] G. Hohmann, B. Fruth, Culture in bonobos? between-species and within-species variation in behavior, Current Anthropology 44 (2003) 563–571.

[19] T. W. Schoener, Theory of feeding strategies, Annual review of ecology and systematics (1971) 369–404.

[20] R. B. Huey, E. R. Pianka, Ecological consequences of foraging mode, Ecology (1981) 991–999.

[21] A. C. Janetos, Active foragers vs. sit-and-wait predators: a simple model, Journal of Theoretical Biology 95 (1982) 381 – 385.

[22] N. Zoroa, M. Fernández-Sáez, P. Zoroa, A foraging problem: Sit-and-wait versus active predation, European Journal of Operational Research 208 (2011) 131 – 141.

[23] J. W. Laundré, How large predators manage the cost of hunting, Science 103 (2014) 002–004.

[24] A. D. Higginson, G. D. Ruxton, Foraging mode switching: the importance of prey distribution and foraging currency, Animal Behaviour 105 (2015) 121–137.

[25] I. Scharf, E. Nulman, O. Ovadia, A. Bouskila, Efficiency evaluation of two competing foraging modes under different conditions, The American Naturalist 168 (2006) 350–357.

[26] J. Laing, Host-finding by insect parasites ii. the chance of trichogramma evanescens finding its hosts, Journal of Experimental Biology 15 (1938) 281–302.

[27] W. Yapp, The theory of line transects, Bird study 3 (1956) 93–104.

[28] J. Skellam, The mathematical foundations underlying the use of line transects in animal ecology, Biometrics 14 (1958) 385–400.

[29] J. Gerritsen, J. R. Strickler, Encounter probabilities and community structure in zooplankton: a mathematical model, Journal of the Fisheries Board of Canada 34 (1977) 73–82.

[30] M. Jette, K. Sidney, G. Blümchen, Metabolic equivalents (mets) in exercise testing, exercise prescription, and evaluation of functional capacity, Clinical cardiology 13 (1990) 555–565.

[31] D. W. Stephens, E. L. Charnov, Optimal foraging: some simple stochastic models, Behavioral Ecology and Sociobiology 10 (1982) 251–263.

[32] B. M. Galdikas, C. P. Yeager, Brief report: Crocodile predation on a crab-eating macaque in borneo, American Journal of Primatology 6 (1984) 49–51.

[33] J. B. Benedict, Tundra game drives: an arctic-alpine comparison, Arctic, Antarctic, and Alpine Research 37 (2005) 425–434.

[34] D. B. Bamforth, Origin stories, archaeological evidence, and post-clovis paleoindian bison hunting on the great plains, American Antiquity 76 (2011) 24–40.

[35] G. A. Oetelaar, Better homes and pastures: Human agency and the construction of place in communal bison hunting on the northern plains, Plains Anthropologist 59 (2014) 9–37.

[36] J. R. Hanson, Adjustment and adaptation on the northern plains: the case of equestrianism among the hidatsa, The Plains Anthropologist (1986) 93–107.

[37] B. Grønnow, Recent archaeological investigations of west greenland caribou hunting, Arctic anthropology (1986) 57–80.

[38] T. M. Friesen, The impact of weapon technology on caribou drive system variability in the prehistoric canadian arctic, Quaternary International 297 (2013) 13–23.

[39] A. Stewart, T. M. Friesen, D. Keith, L. Henderson, Archaeology and oral history of inuit land use on the kazan river, nunavut: A feature-based approach, Arctic (2000) 260–278.

[40] A. M. Stewart, D. Keith, J. Scottie, Caribou crossings and cultural meanings: Placing traditional knowledge and archaeology in context in an inuit landscape, Journal of Archaeological Method and Theory 11 (2004) 183–211.

[41] R. G. Condon, P. Collings, G. Wenzel, The best part of life: Subsistence hunting, ethnicity, and economic adaptation among young adult inuit males, Arctic (1995) 31–46.

[42] L. Dick, People and animals in the arctic: Mediating between indigenous and western knowledge, in: A. MacEachern, W. J. Turkel (Eds.), Method and Meaning in Canadian Environmental History, Nelson, 2009.

[43] E. S. Hall Jr, The" iron dog" in northern alaska, Anthropologica (1971) 237–254.

[44] J. L. Fox, T. Dorji, Traditional hunting of tibetan antelope, its relation to antelope migration, and its rapid transformation in the western chang tang nature reserve, Arctic, Antarctic, and Alpine Research 41 (2009) 204–211.

[45] B. K. Johnson, A. A. Ager, J. H. Noyes, N. Cimon, Elk and mule deer responses to variation in hunting pressure, in: Transaction of the 69th North American Wildlife and Natural Resources Conference, The Wildlife Institute, Spokane, WA, USA, pp. 625–640.

[46] A. A. Ager, B. K. Johnson, J. W. Kern, J. G. Kie, Daily and seasonal movements and habitat use by female rocky mountain elk and mule deer, Journal of Mammalogy 84 (2003) 1076–1088.

[47] D. H. Hirth, D. R. McCullough, Evolution of alarm signals in ungulates with special reference to white-tailed deer, American Naturalist (1977) 31–42.

[48] R. A. Norberg, An ecological theory on foraging time and energetics and choice of optimal food-searching method, The Journal of Animal Ecology (1977) 511–529.

[49] N. E. Humphries, D. W. Sims, Optimal foraging strategies: Lévy walks balance searching and patch exploitation under a very broad range of conditions, Journal of theoretical biology 358 (2014) 179–193.

[50] A. Reynolds, Selection pressures give composite correlated random walks lévy walk characteristics, Journal of theoretical biology 332 (2013) 117–122.

[51] D. A. Raichlen, B. M. Wood, A. D. Gordon, A. Z. Mabulla, F. W. Marlowe, H. Pontzer, Evidence of lévy walk foraging patterns in human hunter–gatherers, Proceedings of the National Academy of Sciences 111 (2014) 728–733.

[52] N. P. Tani, A. Blatt, D. A. Quint, A. Gopinathan, Optimal cooperative searching using purely repulsive interactions, Journal of theoretical biology 361 (2014) 159–164.

[53] S. Gal, J. Casas, Succession of hide–seek and pursuit–evasion at heterogeneous locations, Journal of The Royal Society Interface 11 (2014) 20140062.

[54] S. L. Lima, Putting predators back into behavioral predator–prey interactions, Trends in Ecology & Evolution 17 (2002) 70–75.

[55] W. A. Mitchell, S. L. Lima, Predator-prey shell games: large-scale movement and its implications for decision-making by prey, Oikos 99 (2002) 249–259.

[56] S. Alpern, R. Fokkink, M. Timmer, J. Casas, Ambush frequency should increase over time during optimal predator search for prey, Journal of The Royal Society Interface 8 (2011) 1665–1672.

[57] M. Broom, G. D. Ruxton, Perceptual advertisement by the prey of stalking or ambushing predators, Journal of theoretical biology 315 (2012) 9–16.

[58] N. Zoroa, M. Fernández-Sáez, P. Zoroa, Ambush and active search in multistage predator–prey interactions, Journal of Optimization Theory and Applications (2014) 1–18.

[59] D. Fortin, P.-L. Buono, A. Fortin, N. Courbin, C. T. Gingras, P. R. Moorcroft, R. Courtois, C. Dussault, Movement responses of caribou to human-induced habitat edges lead to their aggregation near anthropogenic features, The American Naturalist 181 (2013) 827–836.

[60] T. Inoue, T. Marsura, Foraging strategy of a mantid, paratenodera angustipennis s.: mechanisms of switching tactics between ambush and active search, Oecologia 56 (1983) 264–271.

[61] S. E. Walker, S. D. Marshall, A. L. Rypstra, D. H. Taylor, The effects of hunger on locomotory behaviour in two species of wolf spider (araneae,

lycosidae), Animal Behaviour 58 (1999) 515–520.

[62] D. Ware, Predation by rainbow trout (salmo gairdneri): the influence of hunger, prey density, and prey size, Journal of the Fisheries Board of Canada 29 (1972) 1193–1201.

[63] K. G. ORSDOL, Foraging behaviour and hunting success of lions in queen elizabeth national park, uganda, African Journal of Ecology 22 (1984) 79–99.

[64] P. J. Brantingham, Prey selection among los angeles car thieves, Crime Science 2 (2013) 1–11.

[65] P. E. Sandstrom, An optimal foraging approach to information seeking and use, The library quarterly (1994) 414–449.

[66] P. Pirolli, S. Card, Information foraging, Psychological review 106 (1999) 643.

[67] M. J. Etzenhouser, M. K. Owens, D. E. Spalinger, S. B. Murden, Foraging behavior of browsing ruminants in a heterogeneous landscape, Landscape Ecology 13 (1998) 55–64.

[68] J. R. Potts, S. Harris, L. Giuggioli, Quantifying behavioral changes in territorial animals caused by sudden population declines, The American Naturalist 182 (2013) E73–E82.

[69] G. R. Hepp, Effects of environmental parameters on the foraging behavior of three species of wintering dabbling ducks (anatini), Canadian journal of zoology 63 (1985) 289–294.

List of Figures

(a) Forager and Prey Movement

(b) Prey and the Detection Zone of a Hunter

Figure 1: A Skellam-Inspired Representation of Forager and Prey Movement. Frame (a) Forager and Prey Movement. Arbitrary paths over an interval of time for two prey items (dashed lines) and a forager (solid line). The forager is endowed with a visual detection field demarcated by a contour (lightly shaded circle) and a frame of reference (**F**ront, **B**ack, **R**ight, and **L**eft). Each prey item can be described as having a rate of movement relative to the hunter with magnitude, v, and direction, θ, as indicated at the end of the path for prey 1. Frame (b) Prey and the Detection Zone of a Hunter. The forager's visual detection field is the lightly shaded circle; the dark shaded region represents an area of $H(\theta)v(t)\partial t$. Prey items move from their starting positions, $\Diamond$, to their ending positions, $\blacklozenge$, over the interval of time ∂t. Prey items can cross into the hunter's visual range between time t and $t + \partial t$ if and only if they lie in the dark shaded region at time t. These illustrations are based on sketches in Skellam [28].
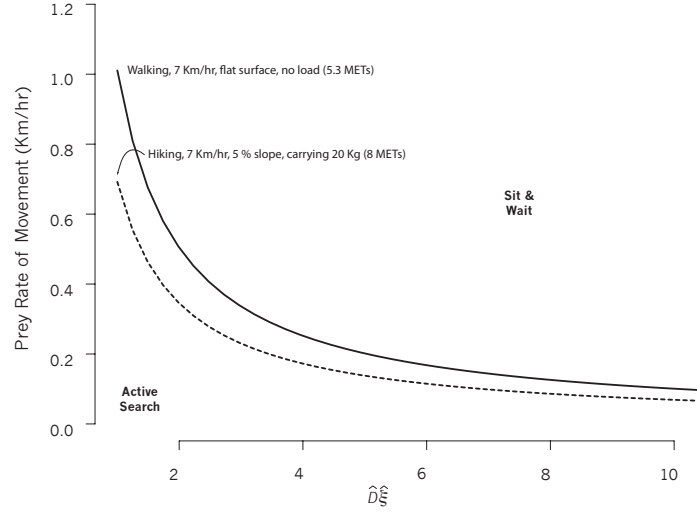
(a) Effect of Caloric Costs of Active-Search on Hunting Tactic

Figure 2: Effect of Caloric Costs of Active-Search on Hunting Tactic. The area to the lower-left of an indifference curve (with its value of $\hat{C}$ given in METs) represents values of prey rate of movement, u, and local effective density ($\hat{D}\hat{\xi}$; see definitions in text), where active-search is favored. The area to the upper-right of a curve for a given form of locomotion indicates parameter states at which the sitting-and-waiting tactic (at an energy cost of 1 MET) is favored. As slope and load of the forager moving at a constant velocity increase, his or her metabolic costs (METs) grow, and the parameter space favoring a sit-and-wait tactic expands. Conversely, the lowering of metabolic costs favors active-search. As $\hat{D}\hat{\xi}$ increases, the effective local density of prey items for an active-searching hunter is $\frac{1}{\hat{D}\hat{\xi}}$ times the effective local density for a hunter searching at velocity 0.
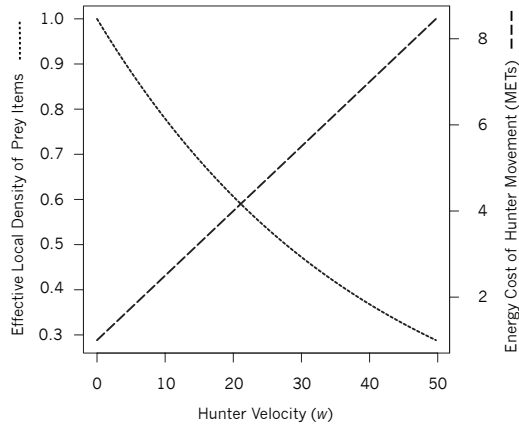
(a) Energetic Costs of Movement and Local Prey Density as Functions of Predator Velocity
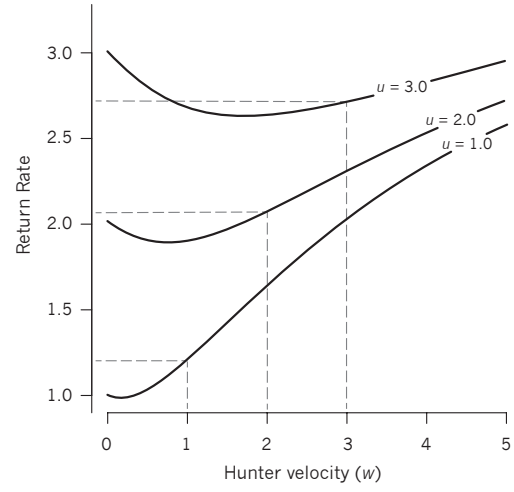

(c) Optimal Search Velocity at Small Values of w and u
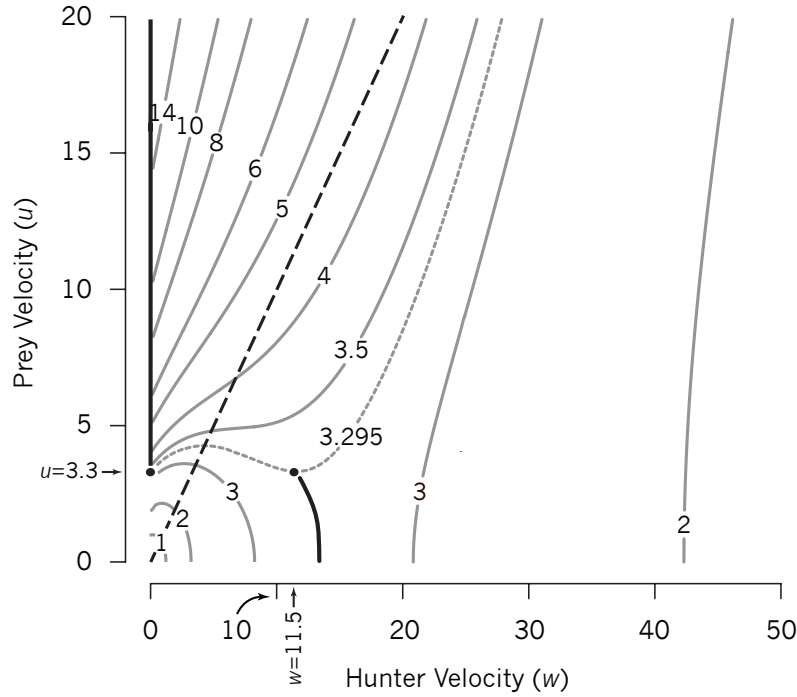
(b) Optimal Search Velocity

Figure 3: Effect of Relative Predator-Prey Velocity on Search Mode and Optimal Velocity of Active-Search. Frame (a) Energetic Costs of Movement and Local Prey Density as Functions of Predator Velocity. We make simple assumptions concerning the functions $\hat{D}\hat{\xi}$ (scaled exponential decline) and $\hat{C}$ (linear growth). Frame (b) Optimal Search Velocity. The gray contours plot the encounter rate experienced by a forager as a function of forager and prey velocities under the functional forms assumed in Frame (a). The solid black lines represent the optimal search velocity; there is a discontinuity at $u = 3.3$, where the hunter is indifferent to active-search at the optimal velocity of $w = 11.5$ and sitting-and-waiting at $w = 0$. The diagonal dashed line represents equal predator and prey velocities; to the upper-left of this line are values of prey velocity greater than forager velocity, and *vice versa* for the lower-right. Frame (c) Optimal Search Velocity at Small Values of w and u. We plot three slices from the contour plot in Frame(b) for small values of u. The black curves are the return rate contours for $u = 1$, $u = 2$, and $u = 3$, as a function of w. The dashed vertical lines at $w = 1$, $w = 2$, and $w = 3$ intersect their respective u contours, such that all value of u to the left of the vertical lines have $u > w$. The dashed horizontal lines show the return rate for $u = w$. For $u = 3$ we see that the return rate for sitting-and-waiting exceeds the return rate for active-search, under the constraint that $u > w$. However, for slower prey, we see that return rate can frequently be maximized by increasing foraging velocity under the constraint $u > w$.

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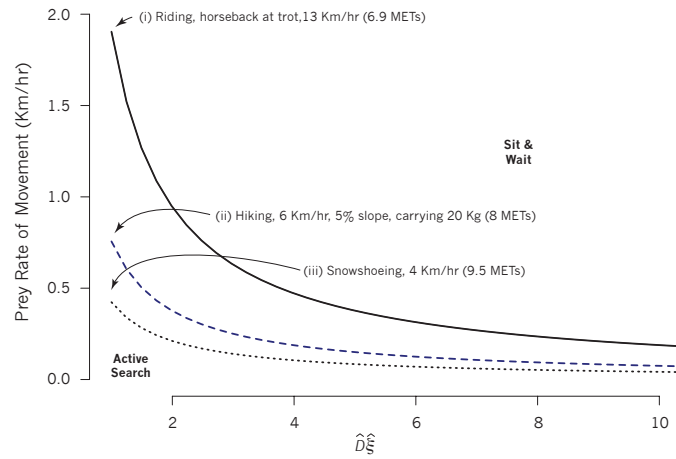
(a) Effect of Search Velocity and Caloric Costs on Hunting Tactic
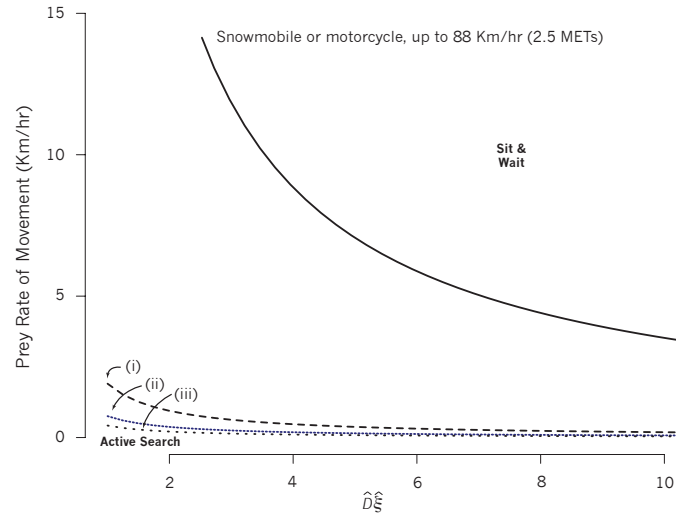
(b) Impact of Mechanical Transportation Technology

Figure 4: Energetic Costs and Transportation Technology. Frame (a) Effect of Search Velocity and Caloric Costs on Hunting Tactic. Increased velocity and lessened metabolic cost to the hunter expand the parameter space favoring active-search. Frame (b) Impact of Mechanical Transportation Technology. Curves (i), (ii) and (iii) are repeated from (a) with the parameter space now showing the consequence of using a snowmobile or motorcycle at search velocities of up to 88 Km/hr (2.5 METs). The introduction of high velocity search at low caloric cost greatly expands the conditions under which active-search is favored, even after accounting for significant decreases in effective local prey density, $\hat{D}\hat{\xi}$, arising from factors such as increased prey avoidance due to noise or failure of the forager to detect some prey items due to rapid search velocity. The state space represented here is meant to depict model outcomes over a wide range of theoretically possible parameter conditions, without implying that all locations in the state space are attainable (e.g., prey rate of movement) or desirable (forager velocity).

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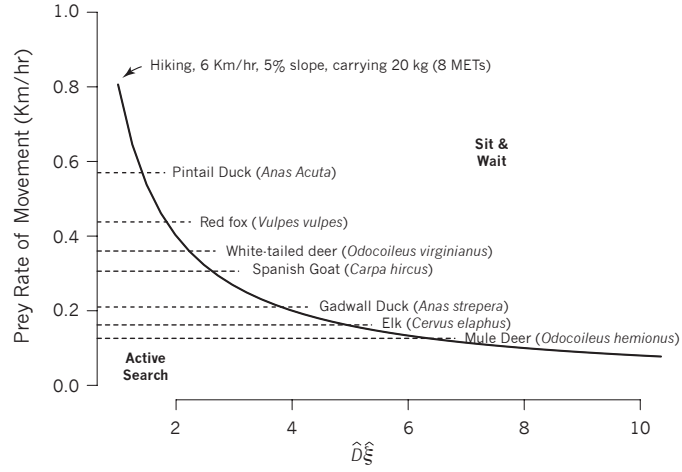
(a) Effect of Prey Rate of Movement on Hunting Tactic

Figure 5: Effect of Prey Rate of Movement on Hunting Tactic. Diminishing rate of movement of prey, shown here via empirically-measured average foraging velocity (see examples in Table 3), favors a shift to active-search on the part of a predator. Conversely, an increase in the average rate of movement of a prey species would favor a shift to the sit-and-wait tactic. The intersection of the indifference curves and the lines describing prey rate of movement are indicative of the $\hat{D}\hat{\xi}$ ratio above which sit-and-wait hunting would be preferred, conditional on the indicated locomotion method of the hunter.

List of Tables

Table 1: Definitions and Limits of Parameters and Functions.

Symbol	Type	Lower Limit	Upper Limit	Definition
w	Parameter	0	·	Hunter's average velocity.
u	Parameter	0	·	Prey's average velocity.
t	·	·	·	Time.
$v(t)$	Function	0	·	Relative velocity of prey item to hunter at time t.
$\theta(t)$	Function	·	·	Relative direction of prey item to hunter at time t.
$H(\theta)$	Function	0	·	Distance between tangents in Figure 1(a).
$\bar{D}$	Parameter	0	·	Average density of prey items in the wider environment.
$D(w)$	Function	0	$\bar{D}$	Local density of prey items when hunter is moving at velocity w.
T_s	·	·	·	Start time of hunt.
T_e	·	·	·	End time of hunt.
T	Parameter	0	·	Duration of hunt.
R	Parameter	0	·	Visual radius of hunter.
V	Parameter	0	·	Average relative velocity of hunter and prey items.
$\xi(w)$	Function	0	1	A function, decreasing with increasing w, that translates between prey crossing into the detection zone and prey items that are actually detected.
$E(P)$	·	0	·	Expected number of prey items crossing into the detection zone during a hunt.
$E(\Phi)$	·	0	·	Expected number of prey items encountered during a hunt.
α	Parameter	0	·	Caloric value of a prey item.
$C(w)$	Function	1	·	Hunter's energy expenditure as a function of w.
$G(w)$	Function	1	·	Group size of prey items as a function of w.
$\Psi(w)$	Function	0	·	Expected caloric returns from hunting as a function of w.
R_{min}	Parameter	0	·	Minimum caloric input per unit time needed to survive.

Table 2: Velocity and Energetic Costs. The velocity (in Km/hr) and energy costs (in METs) of various activities, as well as the prey velocities (u) above which sit-and wait hunting would be favored to active-search for each indicated activity, under $\hat{D}\hat{\xi}$ ratios of 1, 1.25, 1.5, 2, and 5. Backpacking is walking up a 5 percent slope with 20Kg of supplies.

Activity	Km/hr	METs	$u_{\hat{D}=1}$	$u_{\hat{D}=1.25}$	$u_{\hat{D}=1.5}$	$u_{\hat{D}=2}$	$u_{\hat{D}=5}$
Resting	0	1	-	-	-	-	-
Walking	3	1.8	2	1.5	1.2	0.9	0.3
Walking	5	3.2	1.6	1.3	1.1	0.8	0.3
Walking	7	5.3	1.3	1.1	0.9	0.7	0.3
Jogging	9	8.8	1	0.8	0.7	0.5	0.2
Jogging	11	11.2	1	0.8	0.7	0.5	0.2
Running	13	12.9	1	0.8	0.7	0.5	0.2
Running	15	14.6	1	0.8	0.7	0.5	0.2
Backpacking	6	8	0.8	0.6	0.5	0.4	0.2
Backpacking	7	9.6	0.8	0.6	0.5	0.4	0.2
Backpacking	8	11.6	0.7	0.6	0.5	0.3	0.1
Backpacking	10	13.1	0.7	0.6	0.5	0.4	0.1
Backpacking	11	15.5	0.7	0.6	0.5	0.4	0.1
Rowing	4	5.5	0.7	0.6	0.5	0.4	0.1
Rowing	8	10.3	0.8	0.6	0.5	0.4	0.2
Rowing	12	13.5	0.9	0.7	0.6	0.4	0.2
Rowing	16	16.4	1	0.8	0.7	0.5	0.2
Rowing	20	19.1	1	0.8	0.7	0.5	0.2
Snowshoeing	4	9.5	0.4	0.3	0.3	0.2	0.1
Horsebacking-Walk	6	3.2	2.1	1.7	1.4	1	0.4
Horsebacking-Trot	13	6.9	1.9	1.5	1.3	0.9	0.4
Horsebacking-Gallop	44	8.6	5.2	4.1	3.4	2.6	1
Snowmobile/Cart	88	2.5	38.4	29.7	24.3	18	7.1

Table 3: Average Rate of Movement (in Km/hr) of Several Animal Species in Natural Environments.

Species	Name	Location	Average Velocity (Km/hr)	Source
Cervus elaphus	Elk	Oregon, USA	0.162	[45]
Odocoileus hemionus	Mule Deer	Oregon, USA	0.126	[45]
Odocoileus virginianus	White-tailed Deer	Texas, US	0.36	[67]
Carpa hircus	Spanish Goats (Domestic)	Texas, US	0.306	[67]
Vulpes vulpes	Red Fox	Bristol, UK	0.438	[68]
Anas strepera	Gadwall Duck	North Carolina, US	0.21	[69]
Anas acuta	Pintail Duck	North Carolina, US	0.57	[69]

Table 4: Summary of Model Results.

Variable	Direction of Change	Has this Consequence	Notes
Prey's Average Velocity, u	$\downarrow$	+ Active-Search	As average prey velocity declines, the parameter space favoring active-search expands.
Prey Skittishness as a Function of w, $\hat{D} = \frac{D(0)}{D(w)}$	$\uparrow$	− Active-Search	As the hunter moves more rapidly and is thus easier for prey to detect, local density of prey in the neighborhood of the hunter declines, decreasing the parameter space in which active-search is favored.
Prey Detectability as a Function of w, $\hat{\xi} = \frac{\xi(0)}{\xi(w)}$	$\downarrow$	− Active-Search	As the hunter moves more rapidly and is thus more likely to overlook prey items, the effective local density of prey in the neighborhood of the hunter is diminished, again decreasing the parameter space in which active-search is favored.
Hunter's Energy Expenditure as a Function of w, $\hat{C} = \frac{C(w)}{C(0)}$	$\uparrow$	− Active-Search	As hunter locomotion becomes exceedingly costly in terms of energy expenditure as a function of w, the parameter space favoring active-search shrinks.
Group Size of Prey Items as a Function of w, $G(w)$	$\uparrow$	+ Risk of longer periods of no encounters with active-search	This result only occurs if clumping is a consequences of searching actively; otherwise, clumping does not affect choice of hunting strategy.
Caloric Value of a Prey Item, α			The caloric value of prey items is unrelated to the optimal foraging strategy under the assumptions of this model. An increase in α increases caloric return rate under both search modes.
Hunter's Visual Radius, R			The visual radius of the hunter is unrelated to the optimal foraging strategy under the assumptions of this model. An increase in R increases the encounter rate under both search modes.
Hunt Duration, T			The duration of the hunt is unrelated to the optimal foraging strategy under the assumptions of this model. An increase in T increases total encounters under both search modes.
Prey Density, $\bar{D}$			The overall density of prey is unrelated to the optimal foraging strategy under the assumptions of this model. An increase in $\bar{D}$ increases the encounter rate under both search modes.

+ Active-Search := expands parameter space in which forager will elect active-search;
− Active-Search := expands parameter space in which forager will elect sit-and-wait.