

## Currency of Fitness in Foraging Theories

*Hypothesis* Links Behavior to Fitness

*Deduce* Predictions, *Test* Hypothesis

Diet Choice, MVT:

Expected Long-term Rate of Energy Gain =  $\langle \gamma \rangle$

As Total Foraging Time  $T \rightarrow \infty$

$\langle \gamma \rangle = E [\text{Energy Gain/Cycle}] / E [\text{Cycle Duration}]$

Cycle Duration: Search for Food, Handling, etc.

Reward Renewal Theory

Sometimes Works; Problems with Time Horizon?

Max Expected Long-Term Gain rate  
Does Not Discriminate:

Between  $e$  Energy Units Gained Each Cycle

**and**

99 Cycles with No Food, Followed by Cycle with  $100e$   
Energy Units

Suppose Forager Starves (Fitness Penalty) If Fails to Find  
Sufficient Food over  $T$  ( $T < 100$ ) Consecutive Time  
Units: Natural Selection Discriminates

Energy Constraint on Forager's Fitness;  
 $E$  [Long-Term Energy Gain Rate] Misleading ?

*Physiological Requirements*

Nutritional Balance

Time Constraints

Exposure to Predators While Foraging, *etc.*

**Risk-Sensitivity**

Total Foraging *Time Constrained*, Not Infinite

Daily Energy-Intake *Requirement*

Foraging Stochastic Process (*Random, Uncertain*)

Time to Find Food Item Random

Energy per Food Item Random

***Food Patches of Random Size***

Novel Predictions, Testable

## Solitary Forager

$T$  Time Available for Foraging

$R$  Energetic Requirement

Food Intake  $> R$  for **Surviving** Non-foraging Period

*e.g.*, Foraging During Winter, Daylight Hours

Forager Searches for Food Clumps, Neglect Handling Time

*i.e.*, Handling Times  $\ll$  Search Times

Searching, Forager Finds Clumps at Probabilistic Rate  $\lambda$

$\lambda$ : Food Clumps/Search Time

Clumps Discovered: Random Variable  $N(T)$  (*Poisson*)

Expected Number Clumps Found  $\mathbf{E} [N(T)] = \lambda T$

Variance =  $\mathbf{V} [N(T)] = \lambda T$

Random Variation in Number Clumps Found per day

Given Discovery Clump  $i$ , Clump Size Random Variable  $C_i$

Different Clumps: Different Food Levels

Expected Energy per Clump =  $E [C_i] = m$

Variance Energy per Clump =  $V [C_i] = \sigma^2$

Random Variation in Food/Energy per Clump

End of Foraging Day, Time  $T$

Total Energy Intake  $X(T)$

$$X(T) = \sum_{i=1}^{N(T)} C_i \quad \text{Sum Over Clumps}$$

$$E [X(T)] = E [N(T)] E [C_i] = m\lambda T$$

**Average (Expected) Total Amount of Food at Time T**

**Product: Mean Food/Clump & Mean Clumps/Day**

$$\begin{aligned}V[X(T)] &= E [N(T)] V [C_i] + V [N(T)] (E [C_i])^2 \\ &= \lambda T \sigma^2 + \lambda T m^2 = \lambda T (\sigma^2 + m^2)\end{aligned}$$

**Variance (Randomness) of Total Food Intake/Day**

**Increases with Variance of Clump Size**

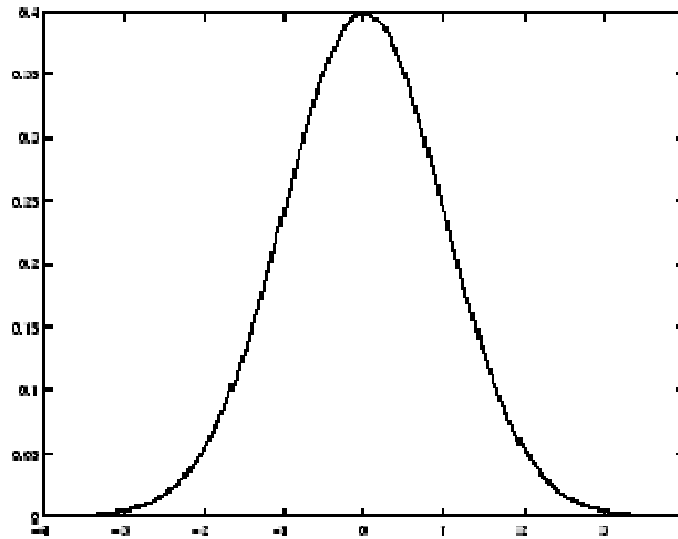
**and Variance in Number of Clumps Found**

$$V[X(T)] > E [X(T)]$$

**X(T) Sums Random Variables: Central Limit Theorem**

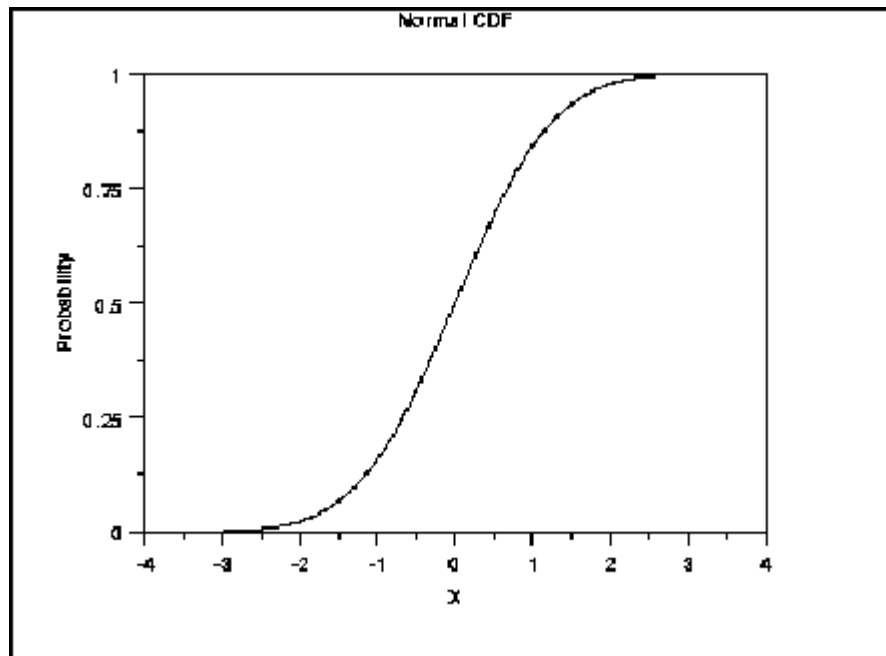
**As Long as Number Clumps Found Sufficiently Large  
X(T) Normally Distributed**

$f[X(T)]$ , Probability Density of Total Food Intake  $X(T)$ :



$m\lambda T$

$\Pr[X(T) \leq x]$ , Use to Infer Starvation Probability



Develop *Currency of Fitness*

$X(T) \leq R$  Fails to Meet Requirement (*Starves*)

$X(T) > R$  No Energetic Failure (*Survives*)

Currency  $\Pr [X(T) \leq R]$

Optimal **Risk-Sensitive** Forager **Minimizes  $\Pr [X(T) \leq R]$**

$$\Pr[X(T) \leq R] = \int_0^R f[X(T)] dX$$

Predictions:

Forager Has 2 Available Habitats

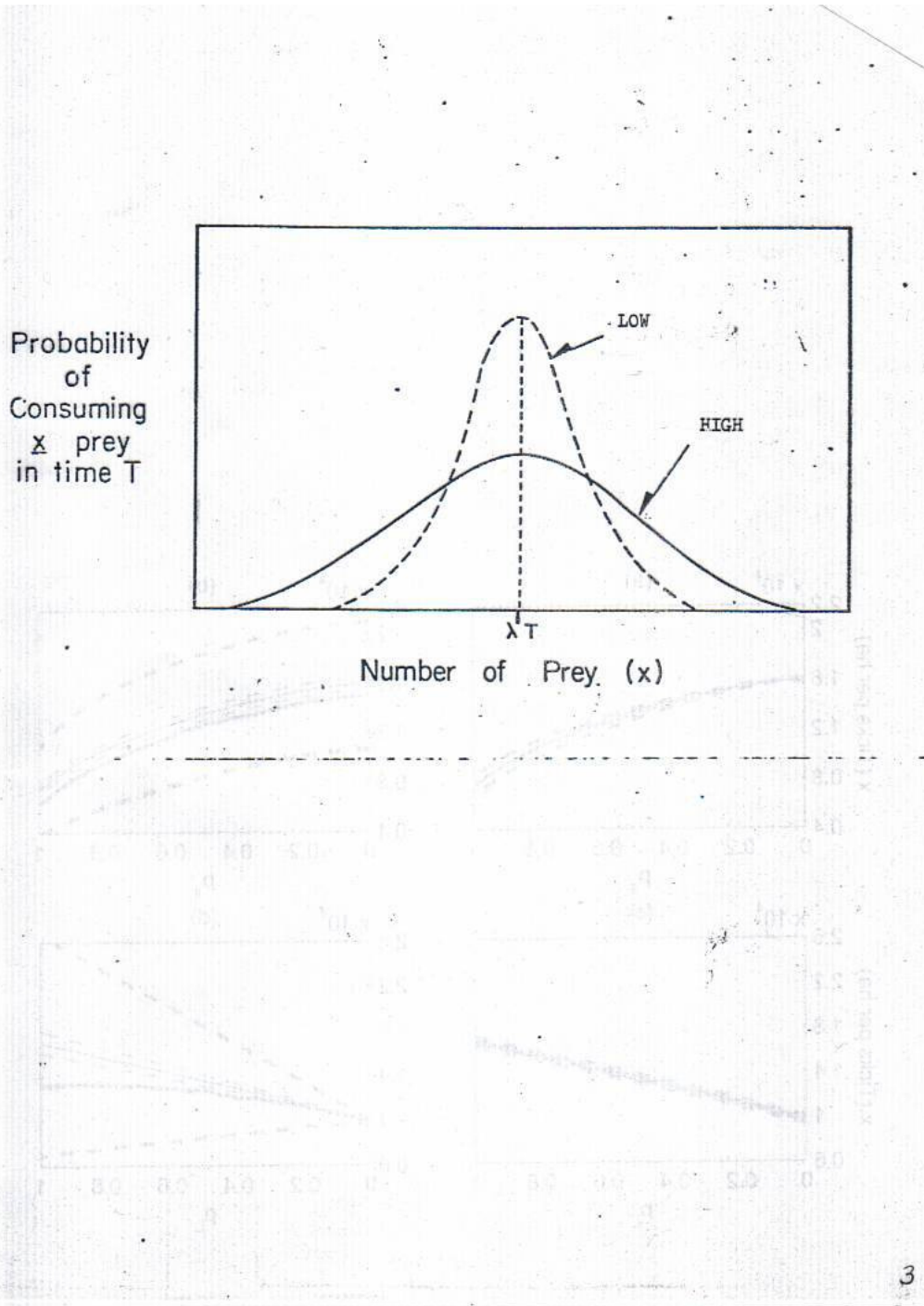
Choose One Habitat, Search for Food Clumps

Assume Same Expected Energy Intake, Both Habitats

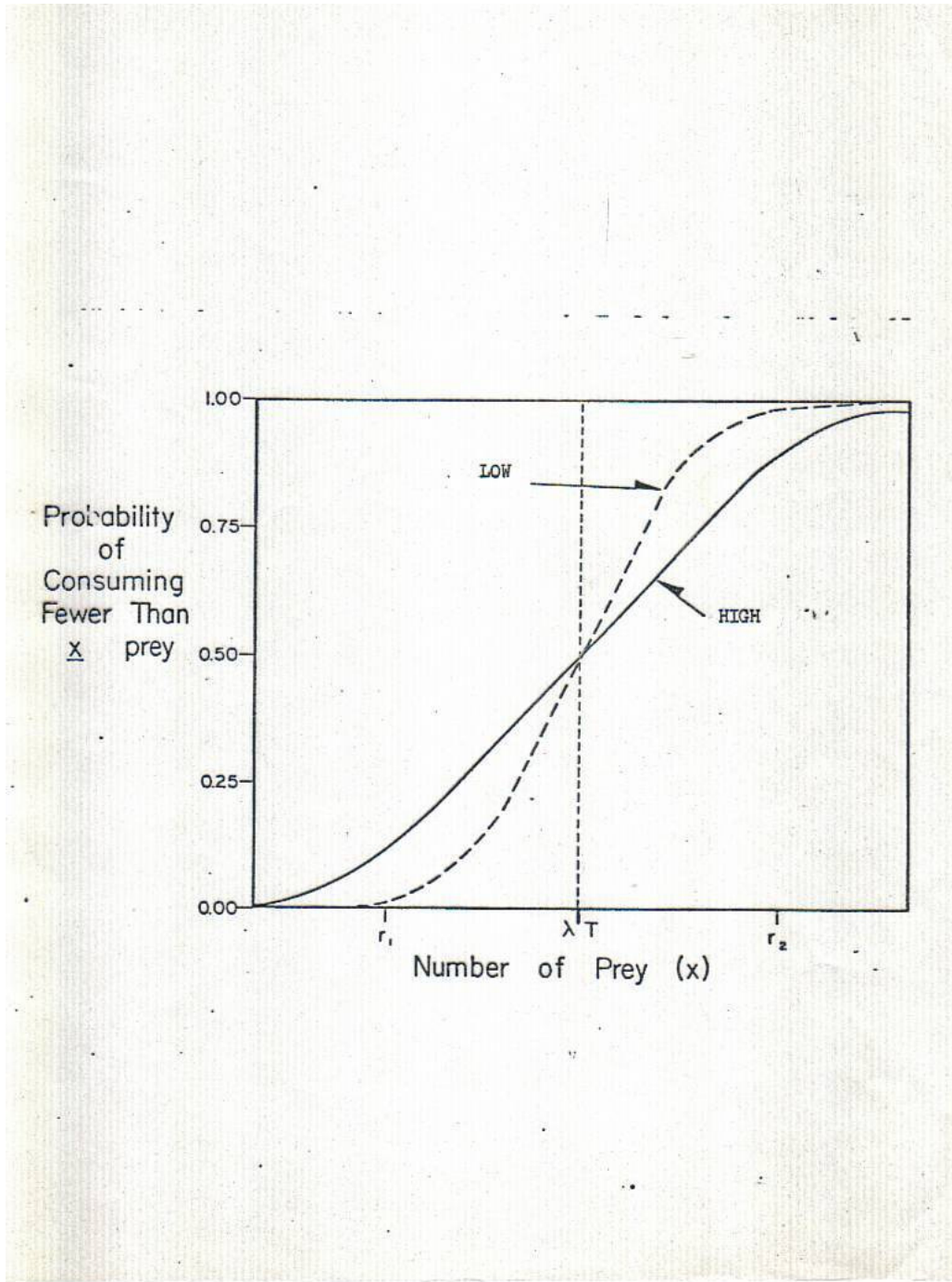
Habitat 1: Low Variance in Energy Intake

Habitat 2: High Variance

Pr Density of Energy Intake  $X(T) = f[X(T)]$



# Pr $[X(T) \leq R]$ by Integration



*Energy Budget Rule*

2 Habitats, Same Mean, Pr Density

Plot  $\Pr [X(T) \leq R]$  for Each Habitat/Patch Type

$E [X(T)] > R$  Positive Energy Budget

Choose Low Variance, *Risk-Averse*

$E [X(T)] < R$  Negative Energy Budget

Choose High Variance, *Risk-Prone*

M. Bateson

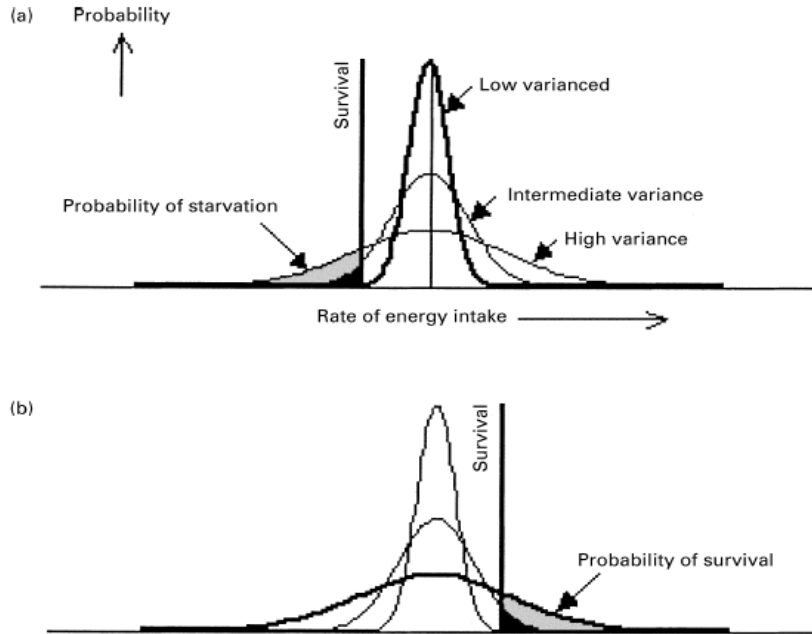


Fig. 1. The energy-budget rule demonstrated graphically with three alternative foraging options differing in the extent of variance in rate of energy intake (low, intermediate or high). Note that all three options have the same mean rate of energy intake associated with them. (A), The starvation threshold is below the mean rate of intake provided by the three options (i.e. a positive energy-budget situation), and it is thus optimal to be risk-averse, preferring the low-variance option, because this option minimises the probability of starvation. (B), Conversely, the starvation threshold (I) is above the mean rate of intake provided by the three options (i.e. a negative energy-budget situation), and it is thus optimal to be risk-prone, preferring the high-variance option, because this option maximises the probability of survival. (—), The optimal option to choose in both A and B.

Test

Know Mean & Variance “Clump Type”

Body Mass, Energy Requirement