Aggregation Economy

Replace general fitness function w_i(*Group size*)

Probability of energetic failure

Risk-sensitivity affects solitary vs group foraging?

Affects equilibrium group size?

Recall **risk-sensitivity** as hypothesized currency of fitness,

then

Apply to social economy, foraging for clumps of food

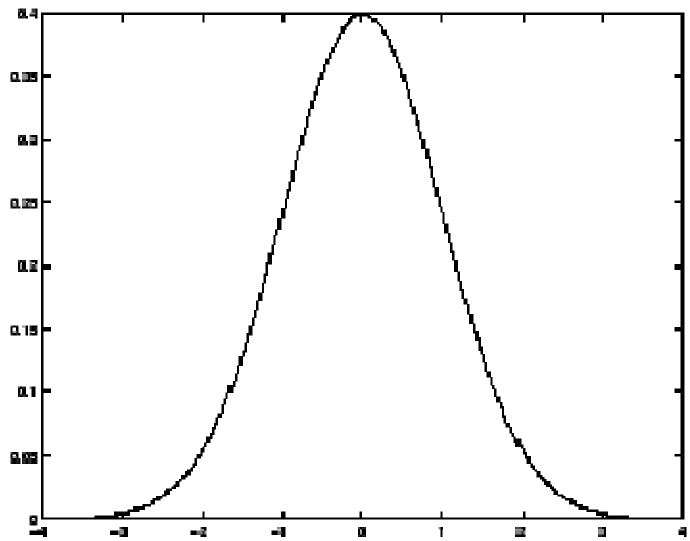
Theory, elements

Test, Ekman & Hake (1988, *Behav Ecol Sociobiol* 22:91)

Forager's total food/energy intake varies **randomly**

Sum of gains & losses over time T

(Approximately) normal density



Abscissa: Food/energy intake (X, RV)
Ordinate: Pr density of intake [X(T)]

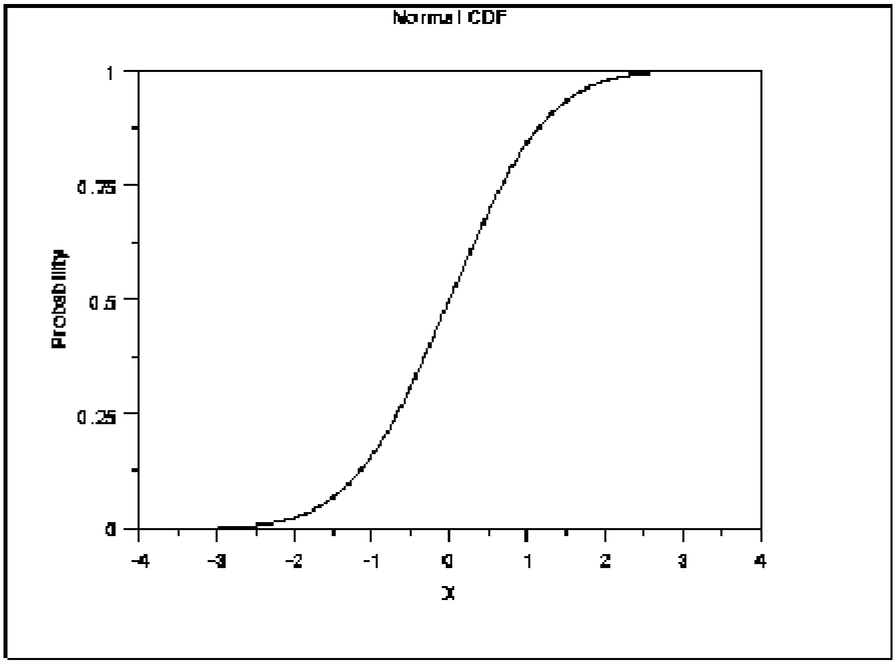
Intake exceeds physiological requirement, forager survives

Intake fails to exceed requirement, forager starves

Requirement = R

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

Minimize Pr[X(T) ≤ R]



Different behavioral strategies

Different mean intake, intake variance

Different Pr[X(T) ≤ R]

Apply to solitary/group foraging

Group has G members; $G = 1, 2$; all search for food

Encounter divisible food clumps rate λG^{α} (λ, $\alpha > 0$)

Solitary's ($G = 1$) encounter rate λ

$\alpha < 1$, the average rate at which food is discovered *per group member* decreases with group size

$\alpha < 1$ either inefficiency (*e.g.*, groups alert their prey) or competitive interference among foragers

If $\alpha > 1$, the average rate at which food is discovered *per group member* increases with group size

$\alpha > 1$ mutualism: enhanced searching efficiency or group members forage cooperatively

$\alpha = 1$, independence during search

Clumps divided equally; handling time negligible

Number clumps discovered: random variable

mean = variance = $\lambda T G^{\alpha}$ (Poisson)

Food per clump: random variable

Individual's energy intake X(T): random variable

Expected intake (mean, average):

(Expected no. clumps) (Expected clump size)/G

= $\lambda T G^{\alpha - 1}$ (Expected clump size)

Intake variance:

(Expected no. clumps) (Clump size variance)/G^2

\+ (Variance no. clumps) (Expected clump size)/G^2

= $\lambda T G^{\alpha - 2}$ [Clump size variance + Expected clump size]

Mean intake declines with G when $\alpha < 1$

Interference during search

Variance declines with G when $\alpha < 2$

Special case, independence: $\boldsymbol{\alpha}$ **= 1**

Expected intake = $\lambda T G^{\alpha - 1}$ (Expected clump size)

= λT (Expected clump size)

Same mean for all group sizes

Intake variance =

($\lambda T/G$) [Clump size variance + Expected clump size]

Variance declines as G increases

$\alpha = 1$, individual's clump-discovery rate independent of G

Pr[starvation]

increases with group size if $R >$ *Expected intake*

requirement exceeds expected intake

Forage as solitary to **Minimize Pr[X(T) ≤ R]**

Risk-prone, since highest intake variance

Pr[starvation]

declines with group size if *Expected intake* $> R$

expected intake exceeds requirement

Forage as group member to **Minimize Pr[X(T) ≤ R]**

Risk-averse, since lower intake variance

Demonstrate

Ekman & Hake (1988):

Greenfinches (*Carduelis chloris*)

Aviary, choose to feed alone or in pairs

Expected intake

Solitary: Mean seeds/day = 79.5

Group: Mean seeds/day = 77.8

No significant difference

Pairs found food twice as often as solitaries

Pairs 83% trials, food divided equally

Solitaries 41% trials

Close to $\alpha = 1$

Intake variance

Significantly greater for solitaries

Requirement: 80 seeds/day (10 seeds/hour)

Fed 20 seeds/hour

Expected intake exceeds requirement

80 % choice trials - group

20% choice trials - solitary

Significantly risk-averse

Fed 5 seeds/hour

Requirement exceeds expected intake

35 % choice trials - group

65% choice trials - solitary

Significantly risk-prone

Above: fixed time T available; Energy intake random

Dual: Fix number of food clumps; Time random

Suppose each individual:

Must consume energy = 1 clump by time τ (tau)

Otherwise, individual starves

Solitary, encounters food at rate λ;

Must find 1 clump by time τ

Group of G, encounters food at rate $G\lambda$;

Must find G clumps by time τ

Food clumps divided equally

Waiting time problem

Individual **Min Pr[time to find G clumps $\leq \tau$]**

Solitary ($G = 1$)

Waiting time t exponential

Probability density $f_1(t) = \lambda e^{-\lambda t}$

$$\Pr[t \le \tau] = 1 - e^{-\lambda \tau}$$

Mean time = $1/\lambda$ Variance = $1/\lambda^2$

Group ($G > 1$)

Waiting time t gamma (sum G exponentials)

Probability density $f_G(t) = \dfrac{(\lambda G)^G t^{G-1} e^{-\lambda G t}}{(G-1)!}$

(G - 1)! = (G - 1) (G - 2) … (2) (1)

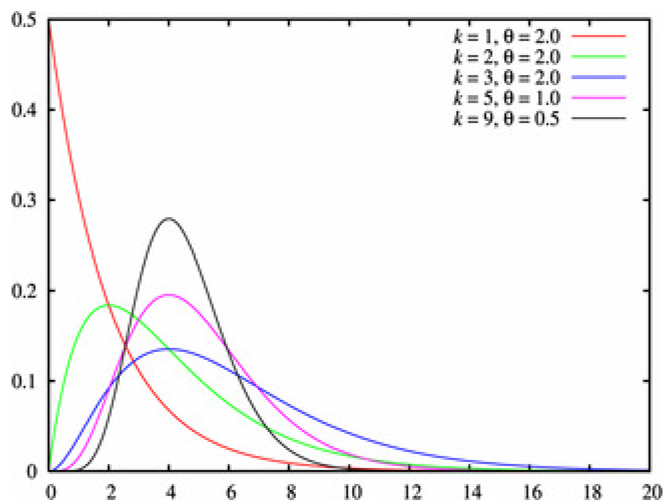
Mean time = $G/G\lambda = 1/\lambda$

Variance = $1/G\lambda^2$

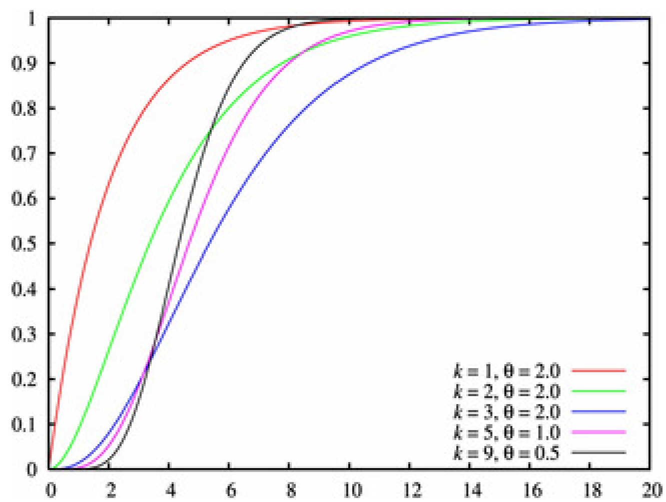
Same mean time to find required food

Variance in search-time declines as group size increases

en.wikipedia.org/wiki/Gamma_distribution



Abscissa: Time t
Ordinate: density f(t)



Abscissa: Time t
Ordinate: $Pr[t \leq \tau]$