t_1 = handling time for 1

1 **Foraging Decisions: Context**

- 1.1 Importance: consequences for survival, reproduction
- 1.2 Foraging decisions: abundance vs. quality pursue vs. ignore exposure to predation risk
- 1.3 Economic reasoning: maximize gain or minimize cost of some currency
- 1.4 Simple rules: simple organisms need not make complex decisions
- 1.5 3 kinds of foraging behavior:
- (i) active search (ii) sit and wait (iii) mixed strategies

2 **Example 1: Maximizing Energy Gained**

- 2.1 Simple case: 2 prey types, $1 \& 2$ *E* = total energy gained
- 2.2 3 possible strategies $T =$ total foraging time

2.3 Equations for
$$
E_1 \& E_{12}
$$
 a_1 = energy from 1

$$
E_1 = \frac{T a_1}{t_1} \qquad \qquad E_{12} = \frac{T (a_1 + a_2)}{t_1 + t_2}
$$

2.4 Apply to demonstration:

T = 5 sec
$$
a_1 = 10
$$
 $a_2 = 1$ suppose $t_1 = 3$ $t_2 = 1$
\n $E_1 = \frac{5 * 10}{3} = 16.67$ $E_{12} = \frac{5(10 + 1)}{3 + 1} = 55/4 = 13.75$ $(E_2 = 5)$

Conc: eat type 1 only; ignore 2

2.5 Best strategy: ignore 2 if $a_1/a_2 > t_1/t_2$

3 **Example 2: Minimizing Foraging Time (what to eat when in a hurry)**

- 3.1 Intuition: when prey rare, eat all prey types when prey abundant, selective
- 3.2 Simple case: 2 prey types
- 3.3 3 possible strategies
- 3.4 Compare strategies: Equations for T_1 vs. $T_1 \& 2$:

$$
T_1 = \frac{1}{a_1} + t_1 \qquad T_{1\&2} = \frac{1}{a_1 + a_2} + \frac{a_1 t_1}{a_1 + a_2} + \frac{a_2 t_2}{a_1 + a_2}
$$

 $T =$ mean search & handling time =handling time *t* = abundance *a*

 3.5 Best strategy: ignore prey type 2 if 2 ι_1 1 1 $t_2 - t$ $a_1 > \frac{1}{t_2 - 1}$ >

 3.6 Conclusion: foragers should be more selective when overall prey abundance high foragers should be less selective when overall prey abundance low

4 **Diet Breadth**

- 4.1 If increase variety in diet: a) decrease search time (T_s) (more prey available) b) increase handling time (T_h) (include difficult prey)
- 4.2 Optimal diet breadth = $min(T_s + T_h)$
- 4.3 Increase environmental productivity \rightarrow decrease $T_s \rightarrow$ increase specialization

5 **Optimal Foraging Theory**

- 5.1 Theory to predict behavior of efficient forager
- 5.2 Basic argument: optimality results from natural selection for efficient organisms 5.2.1 survival & reproduction require energy (food)
	-
	- 5.2.2 food resources are limited
	- 5.2.3 efficient foragers have more energy for survival & reproduction \Rightarrow have more offspring \Rightarrow higher fitness
	- 5.2.4 optimal forging evolves because natural selection favors efficient foragers
- 5.3 Approach
	- 5.3.1 Identify currency that forager should optimize.
		- 2 primary currencies: time (minimize foraging time)
			- energy (maximize energy gained)
	- 5.3.2 Develop models of foraging strategies in terms of currency
	- 5.3.3 Determine strategy that optimizes currency; predict animals will use it
- 5.4 Other Currencies
	- 5.4.1 Maximize rate of energy gain
	- 5.4.2 Maximize efficiency (max gain / min time)
	- 5.4.3 Minimize starvation risk
	- 5.4.4 Maximize survival
- 5.5 Critique of Optimal Foraging Theory
	- 5.5.1 Assumptions often violated in the field
	- 5.5.2 Often contradicted by observations & difficult to test
	- 5.5.3 "Adaptationist Programme" (cf, S.J. Gould)

6 **Limitations of Optimal Foraging Theory**

- 6.1 Nutritional considerations ignored
- 6.2 Predation risk may affect foraging
- 6.3 Ignores learning
- 6.4 Ignores efficiency of experience (search images)

7 **Marginal Value Theorem**

- 7.1 Decision: when to change foraging area
- 7.2 Assumptions: knowledge of environment
	- 7.2.1 know rate of food capture in current patch
	- 7.2.2 know projected rate of food capture in other patches
	- 7.2.3 know travel time to other patches

7.3 Marginal Value Theorem:

 Leave current patch when food capture rate = average yield of entire habitat. Equivalently, "leave when can do better elsewhere."

Derivation:

 $F(t)$ = amount food obtained in a patch during time *t*; assume $F(0) = 0$. $R(t)$ = rate of food gathering, including travel time between patches, τ . $+ \tau$ $=\frac{1000}{1000}$ = *t* $R(t) = \frac{\text{food/visit}}{\text{if } t} = \frac{F(t)}{t}$ time/visit $f(t) = \frac{\text{food/visit}}{\text{if } t \text{if } t} = \frac{F(t)}{t}$ Determine *t**, time to leave patch that maximizes *R*. $R'(t^*) = 0$ and $R''(t^*) < 0$, for some time $t^* > 0$ \Rightarrow *F*'(*t*^{*}) = *R*(*t*^{*}) Example: $F(t) = bt - at^2$; $F'(t) = b - 2at$ $+\tau$ $-2at^* = \frac{bt^* - b}{t^*}$ * $2at^* = \frac{bt^* - at^*}{t}$ 2 *t* $b - 2at^* = \frac{bt^* - at^*}{t}$ $at^{*2} + 2a\pi * -b\tau = 0$ Apply quadratic formula: $t^* = -\tau \pm \sqrt{\tau(\tau + b/a)}$

- 7.4 Prediction: optimal Giving Up Time (GUT) decreases as travel time betw/ patches decreases
- 7.5 Implications for various taxa
- 7.6 Few tests of Marginal Value Theorem

8 **Learning and Foraging Behavior**

9 **Foraging Theory: different philosophical approach to science** − primacy of individual agenda vs. primacy of mechanism

10 **Behavior in Groups**

Complex group behavior emerges from simple individual rules.

References:

Adam JA. 2009. *A Mathematical Nature Walk*. Princeton Univ. Press, Princeton, NJ, pp.25-27.

Couzin I. 2007. Collective minds. *Nature* 445:715.

Feder T. 2007. Statistical physics is for the birds. *Physics Today* (Oct. 2007, pp. 28-30)

- Zimmer C. 2007. From ants to people, an instinct to swarm. *New York Times*, Tue. 13 Nov. 2007, pp. D1,D4
- National Geographic Magazine. Swarm behavior, photo gallery. July 2007. http://ngm.nationalgeographic.com/ngm/0707/feature5/gallery1.html