

Sih Review

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1. Optimal Foraging

1.1. Optimal Diet

MacArthur & Pianka 1966 essentially introduce the OPTIMALITY approach (see Box 1) to behavior in their model of OPTIMAL DIET, explicitly referencing economics. Insight is to optimize energy per time. Variables are: Energy content E , encounter rate λ , total search time T_s , handling time h , specialize if

$$\frac{E_2}{h_2} < \frac{\lambda_1 T_s E_1}{T_s + h_1 \lambda_1 T_s} \quad (1)$$

Note $\lambda_1 T_s$ is encounter number, T_s drops out. Schoener (1971) notes a different optimal currency is to reach a resource threshold in the minimum amount of time.

Experimental tests Sih & Christensen (2001) review; seems optimal diet theory works best with immobile prey.

1.2. Optimal Patch Use

Charnov (1976) introduces OPTIMAL PATCH USE through its MARGINAL VALUE THEOREM. Individuals should stay in a patch until instantaneous energy gain $E'(t)$ is depressed below the average value of other patches, R , Fig 1.

Experimental tests Stephens & Krebs (1986), qualitative fit to marginal value theorem.

Ideal Free Distribution Should result in a steady-state ESS matching the IDEAL FREE DISTRIBUTION, originally Fretwell & Lucas (1970), many reviews, e.g. Sih (1998). Consumers match resources. Under/overmatching defined by better patches having under/over expected density (note the worse patches experience the opposite effect). Undermatching results when individuals avoid high density, i.e. due to aggression, disease transmission, territoriality, predator avoidance, etc., and seems more common than overmatching, due to herd behavior, facilitation, safety in numbers. MULTIPLE TROPHIC-LEVEL IFD: Predators tend to match resources, prey uniform. Other outcomes also possible, see Sih (1998).

1.3. Uncertainty and risk

Theory Real & Caraco (1986) Risk prone when fitness is accelerating function of risk, risk adverse when decelerating because of JENSEN'S INEQUALITY, $f(E(x)) \neq E(f(x))$, showing the importance of NONLINEARITY in a variable world.

Experimental evidence Typical study offers variable yield and predictable yield with same average. Most studies find risk aversion, but not universal. Animals tend to prefer smaller immediate rewards, showing that they DISCOUNT value over time, qualitatively agrees with economic theory in an unpredictable world.

1.4. Predation Risk

Gilliam & Fraser, (1981) DYNAMIC OPTIMIZATION THEORY, minimize death rate to growth rate ratio: μ/g . Solve backwards by DYNAMIC PROGRAMING, requires a time horizon, terminal fitness function, and is often stochastic and STATE DEPENDENT. Another consequence is the ASSET PROTECTION PRINCIPLE, Clark (1994): Take bigger risks when assets are low, less if high. Effect strongest near a time horizon (about to starve, reproduce, end of life).

2. Social behavior: Altruism, Cooperation & Spite

Classic examples: Food sharing (vampire bats), sentries (prairie dogs), cooperative breeding (eusocial insects). Essential Logic: Altruistic behavior must primarily favor other altruists.

RECIPROCAL ALTRUISM: Trivers (1971). Requires repeated interactions and individual recognition. The PRISONER'S DILEMMA and TIT FOR TAT (TFT) strategy, Axelrod & Hamilton (1981). TFT is stable against invasion from a rare, always-defect strategy. Difficult in large groups to remember all individuals and have ample repeated interactions. POLICING AND PUNISHMENT, Sober and Wilson (1998) can get around this. Policing must be less costly than the altruistic act.

KIN SELECTION: HAMILTON'S RULE: $rB > C$ relatedness r (probability of carrying the altruist gene), recipient benefit B , cost to altruist C . Examples:

- HAPLODIPLOIDY in eusocial insects ensures sisters are more similar ($\frac{3}{4}$) than daughters ($\frac{1}{4}$). Since queens are multiply mated, this cannot work. However, it is still beneficial for workers to police themselves.
- COOPERATIVE BREEDING: benefits of helping (gain parental skills, resources) outweigh benefits of leaving (little territory, mates).

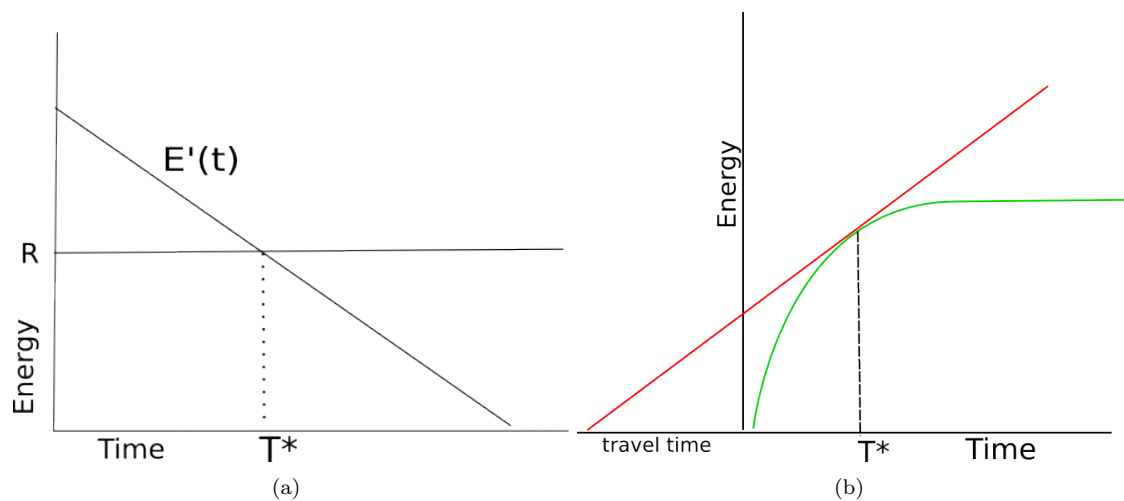


Fig. 1. Charnov's Mean Value Theorem

Box 1: The Optimization Paradigm **Steps:** Specify: (1) Currency, (2) options and constraints, (3) functional relationships, (4) then do the mathematical optimization.

Other considerations: State dependence, depends on choice of other foragers (= GAME), uncertainty in parameters, temporally variable parameters, other currencies to optimize.

Reasons for non-optimality: [Pierce & Ollason \(1987\)](#) 8 reasons why *Optimal Foraging is a complete waste of time*. Natural selection optimizes fitness. Cannot necessarily partition fitness into linear combinations of contributions from different behaviors and optimize each independently, because they are connected – foraging behavior influences predation risk, mate search, etc. Other reasons too – haven't chosen correct variables or constraints, hasn't had time to reach optimum in changing environment/coevolution, etc.

- Modern view is cooperation-conflict mix, [Mock \(1998\)](#), between parent-offspring and also sib-sib.

GROUP SELECTION, [Wilson & Wilson \(2007\)](#): small groups meet in large groups, mate randomly, and randomly re-assort into small groups. Some groups have mostly altruists, some mostly cheaters. Altruist groups do better on average, allowing them to spread. Partitioning group vs individual selection, as vectors, or ANOVA/regressions ([Goodnight, Wolf](#)). Examples: cooperative warfare in chimps, multi-queen eusocial insects, MAJOR TRANSITIONS (eukaryotes, multi-cell, colonial, social groups).

3. Sexual selection

3.1. Behavioral Mechanisms

Bateman principle: differential investment potential implies:

- MALE-MALE COMPETITION
 - Scramble: help find/attract female (search)
 - Interference: help win male competitions
 - Post-mating: displace sperm, mate guarding
- FEMALE CHOICE
 - Direct: treat males differently by phenotype
 - Indirect: treat all phenotypes equally, but induces non-random mating (i.e. attempt to resist all matings).
 - Cryptic: decide on sperm usage post-mating

3.2. Evolution of Female choice

Direct benefits: territory, nuptial gifts, paternal care. Indirect benefits:

- Choose GOOD GENES. Many potential mechanisms: HAMILTON-ZUK HYPOTHESIS: ornaments imply parasite resistance. Genetic complementarity offers more complete set of MHC loci. Moller's Fluctuating asymmetry: symmetry indicates good genes. [ZAHAVI \(1975\)](#) HANDICAP PRINCIPLE: cost makes the signal honest.
- SENSORY EXPLOITATION
- SEXY SONS
- FISHER RUNAWAY PROCESS
- multiple traits

3.3. Sexual conflict

Complicated interactions between who wants and doesn't want who to mate with whom.

Salmon: sneaker Jacks vs large territorial hooknose – Females actually prefer jacks and hooknose are the coercers! Rowe: water striders. PATH ANALYSIS of Sewall Wright, [Sih \(2002\)](#) consider interactions multiple aspects.

4. Optimal life history

- COLE'S PARADOX [Cole \(1954\)](#): SEMELPAROUS (reproduce once and die) organisms need to produce only one more offspring on average than ITEROPARIOUS (reproduce throughout life). Resolved by [Charnov & Shaffer \(1973\)](#), need to add juvenile mortality.
- OPTIMAL REPRODUCTIVE EFFORT Shaffer graphical models, maximize current potential fitness b plus potential future fitness pV (future reproductive value V times chance of survival p) as a function of reproductive effort R_E . b increases with R_E (probably to saturation) while pV decreases with R_E

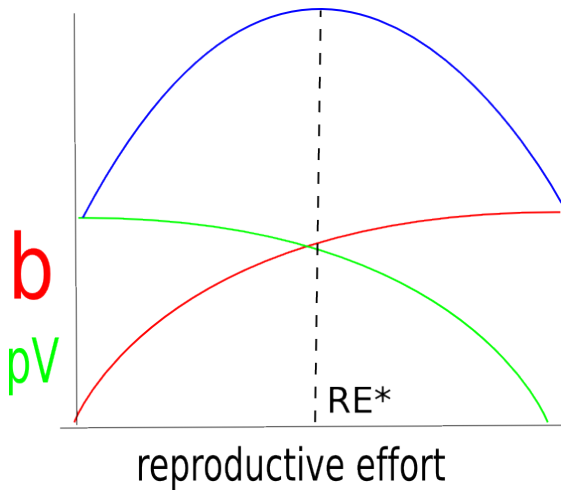


Fig. 2. Optimal reproductive effort.

(less resources available for survival and future reproduction). Graphical argument in Fig 2, maximum at:

$$\frac{d}{dR_E} [b(R_E) + p(R_E)V(R_E)] = 0$$

$$\left[b' = -p'V - pV' \right]_{R_E^*} \quad (2)$$

- Temporal heterogeneity: bet hedging reproductive effort
- Spatial heterogeneity: Adding migration means reproductive effort should be higher in sink than without migration, while effort in source is about the same.

4.1. Timing of reproduction, life stages

- **Model:** AGE OF FIRST REPRODUCTION, α . Without cost, delay α only if pop declining, [Sibly & Calow](#). With cost, switch to reproducing when effect of future increased size w on reproduction f , $\frac{df}{dw}$ less than mortality.
- **Experiments:** Delay if larger offspring preferred, i.e. Predation higher on smaller guppies, favors larger offspring, [Reznick](#). Reverse when predation higher on large guppies.

4.2. Investment in offspring

- **INVESTMENT PER OFFSPRING:** Determining the seed/egg size (possibly quality). Basic model: [Smith & Fretwell \(1974\)](#). Set investment $R = nS$ means trade-off between number n and size S . Notes: Maximize female fitness, $W_F = nW(S) = RW(S)/S$. Assume offspring fitness $W(S)$ increases with size S with diminishing returns and a minimal investment size to get viable offspring. The optimization is seen in Fig 3(a). Further things to consider: simultaneously consider reproductive effort R_E and invest per offspring S , i.e. [Parker & Begon \(1986\)](#), also stochasticity, state dependence.
- **Experimental Tests** [Sinervo](#) remove yolk lizard eggs, get miniature offspring. Ablate some follicles, get giant offspring. Demonstrate good fit to optimized S^* maximizing fitness. Other reasons to favor fewer, larger offspring: (1) *Greater resource limitation*: e.g. shaded plants, [Salisbury \(1942\)](#); (2) *Predation*: [Reznick](#) guppies, others done in salamanders; (3) *Ephemeral habitat*: e.g. need to get out of vernal pool before it dries.

- PARENT-OFFSPRING CONFLICT, i.e. [Trivers \(1974\)](#) offspring want more than parents want to give. Depends on power, uncertainty, etc.
- BI-PARENTAL CARE: [Houston & Davies \(1985\)](#), [Royle et al. \(2002\)](#): Both parents should under-compensate, Fig 3(b).

5. Adaptive plasticity

Graded vs discrete, irreversible (developmental) vs reversible.

6. Behavioral syndromes

Examples

- Fishing spider female voracity, [Johnson & Sih \(2006\)](#) See Fig 4(a).
- Great tits *Parus major* Exploratory behavior also more aggressive
- Sticklebacks activity-boldness-aggression: high predation \implies positive correlation (can't hide when predators too common), low predation \implies decoupled, e.g. [Bell \(2005\)](#). May decouple at adulthood too.
- **Stability of syndrome?** Carries over in spiders and salamanders, adults decouple in sticklebacks and water-striders.
- **Impact on invasibility?** Only the invasive *Gambusia* exhibits Boldness-Aggressiveness syndrome, see Fig 4(b).

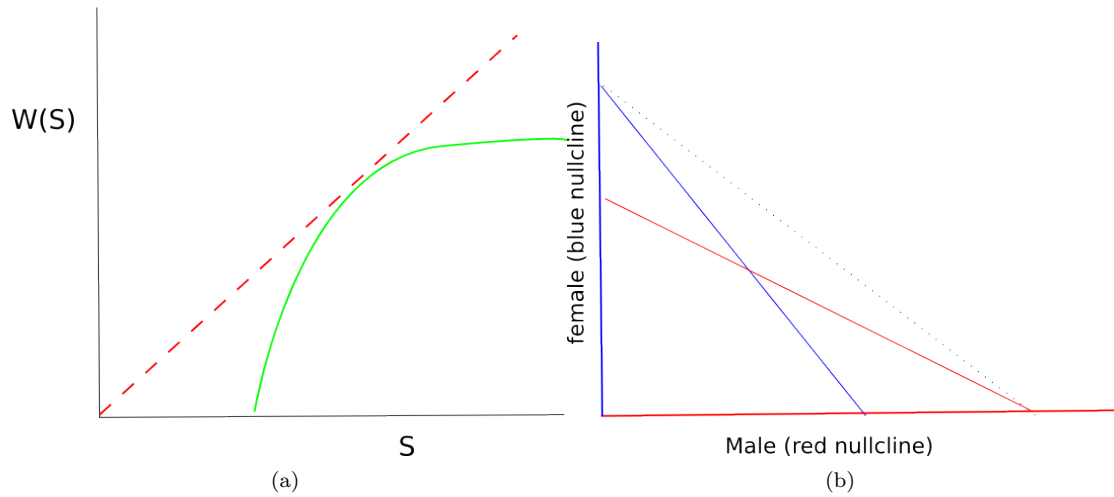


Fig. 3. (a) Optimal investment per offspring where line hits curve. (b) Under-compensation in levels of parental care is stable (intersection).

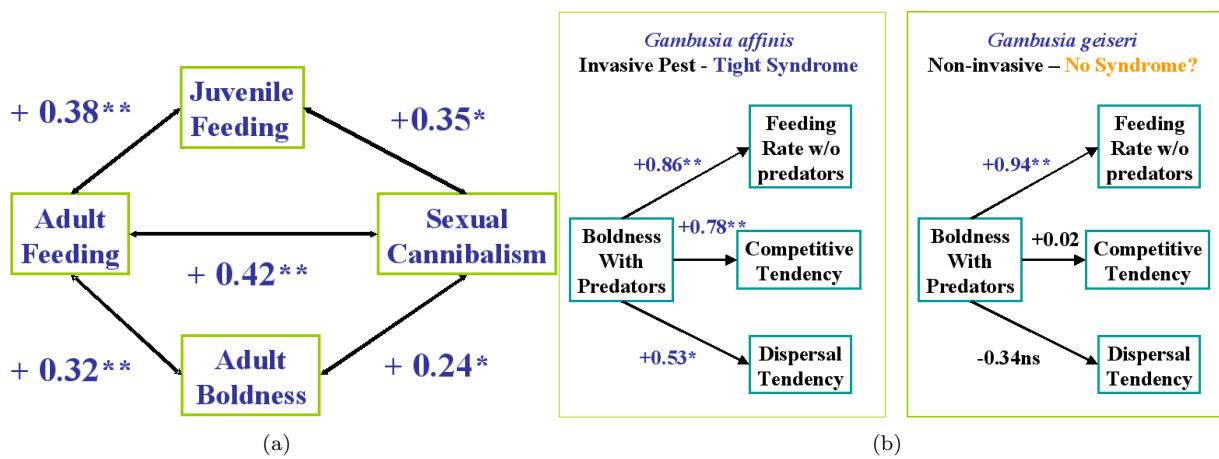


Fig. 4. Behavioral Syndromes