FORAGING

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UBCO

Foraging

1. What? Basic OFT
2. When to move on? MVT
3. CPF, a brief mention
4. Constraints I: nutrients
5. Pulling out the goalie: RSB
6. Constraints II: predators (later!)
7. Foraging in groups
8. Constraints III: parasites

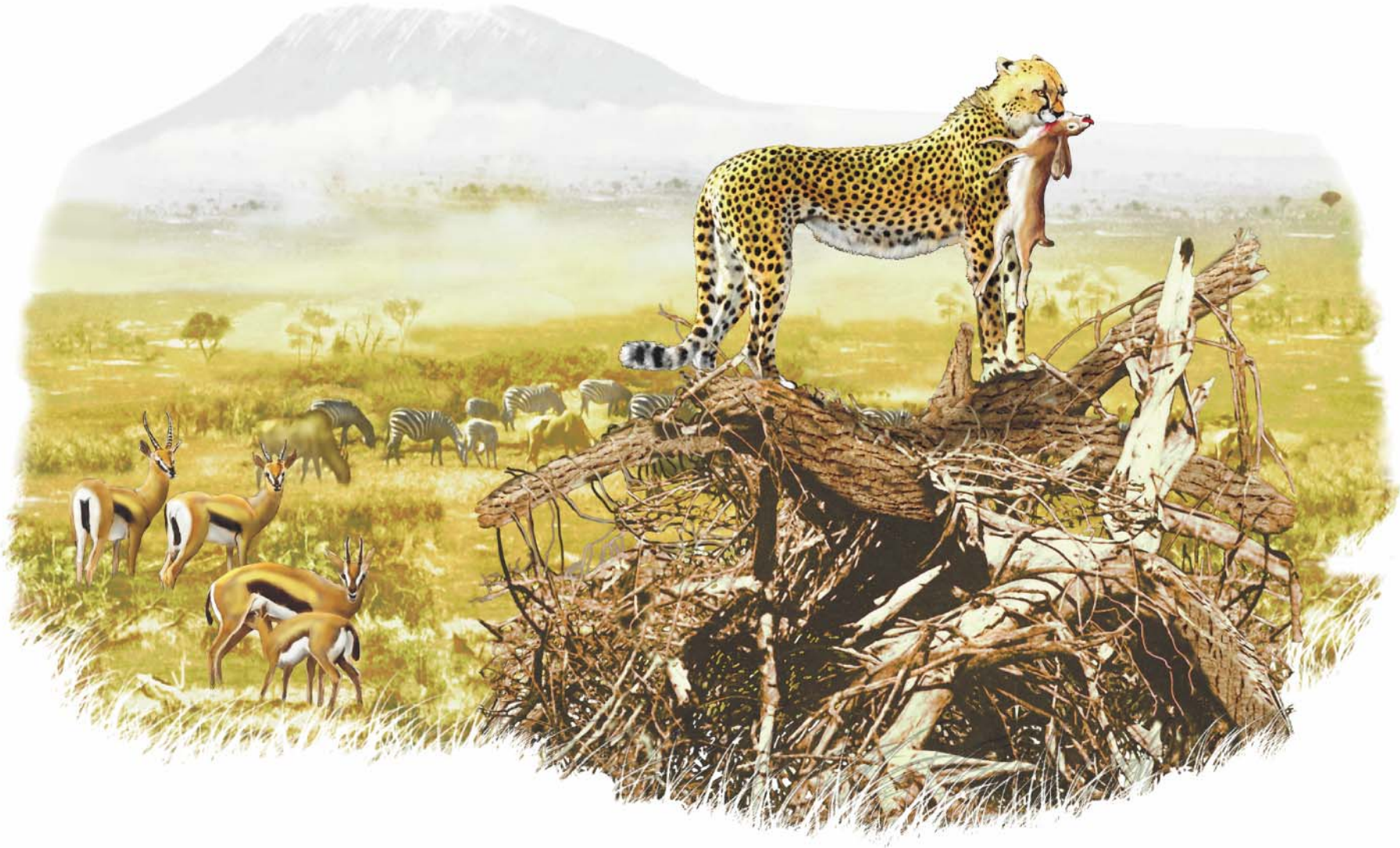


FIGURE 10.5: Foraging decision

Principles of Animal Behavior

1.- What to eat?

- Why not everything?
- Time and effort involved vs. rewards. OFT
- Basic OFT assumptions
  - Measurable prey quality.
  - Non-simultaneous encounter.
  - Instantly recognition.
  - Eating and searching are mutually exclusive
  - There is some currency that animals maximize

The model…verbally

- Imagine 2 prey types, each one with an energy content (e), an encounter rate (λ) and a handling time (h).
- The predator spends time searching for prey (t) and handling prey (t)
- The predator is trying to maximize the rate of energy intake (E/T) CAPS = totals
- When should it take one, not two, and which one?

The model.. algebraically

- Predator maximizes E/T

- $E = t \lambda e$
- $T = t + t \lambda h$

- $E/T = t \lambda e / (t + t \lambda h)$ subscripts for prey 1 or 2
- Simplified to $E/T = \lambda e / (1 + \lambda h)$

- For taking BOTH prey items as they come.

- $E = t \lambda e \quad \rightarrow \quad E = t (\lambda_1 e_1 + \lambda_2 e_2)$
- $T = t + t \lambda h \quad \rightarrow \quad T = t + t \lambda_1 h_1 + t \lambda_2 h_2$

- $E/T = t (\lambda_1 e_1 + \lambda_2 e_2) / (t + t \lambda_1 h_1 + t \lambda_2 h_2)$

- Simplified to $E/T = \lambda_1 e_1 + \lambda_2 e_2 / 1 + \lambda_1 h_1 + \lambda_2 h_2)$

- When to take just prey type one?
- When E/T for one > E/T for both

- $\lambda_1 e_1 / (1 + \lambda_1 h_1) > \lambda_1 e_1 + \lambda_2 e_2 / 1 + \lambda_1 h_1 + \lambda_2 h_2)$

- Which can be rearranged to:

$$\lambda_1 > e_2 / (e_1 h_2 - e_2 h_1)$$

$$\lambda_1 > e_2 / (e_1 h_2 - e_2 h_1)$$

- Whether prey 1 is taken depends solely on its encounter rate.
- This does not depend on the encounter rate with prey 2
- Just on their handling costs and energy provided.
- Inclusion of an item depends on the frequency of better items; no matter how common it is.

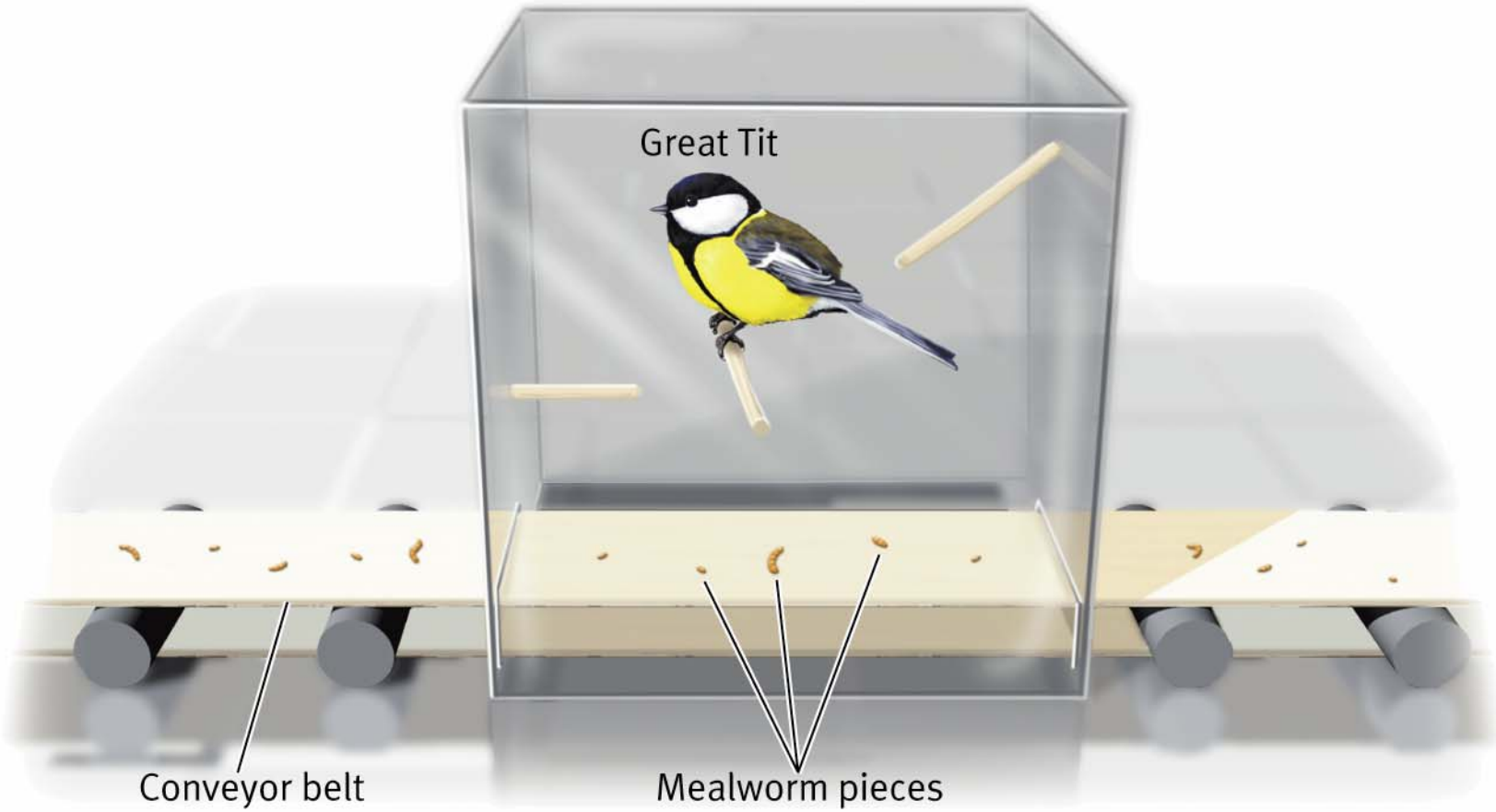
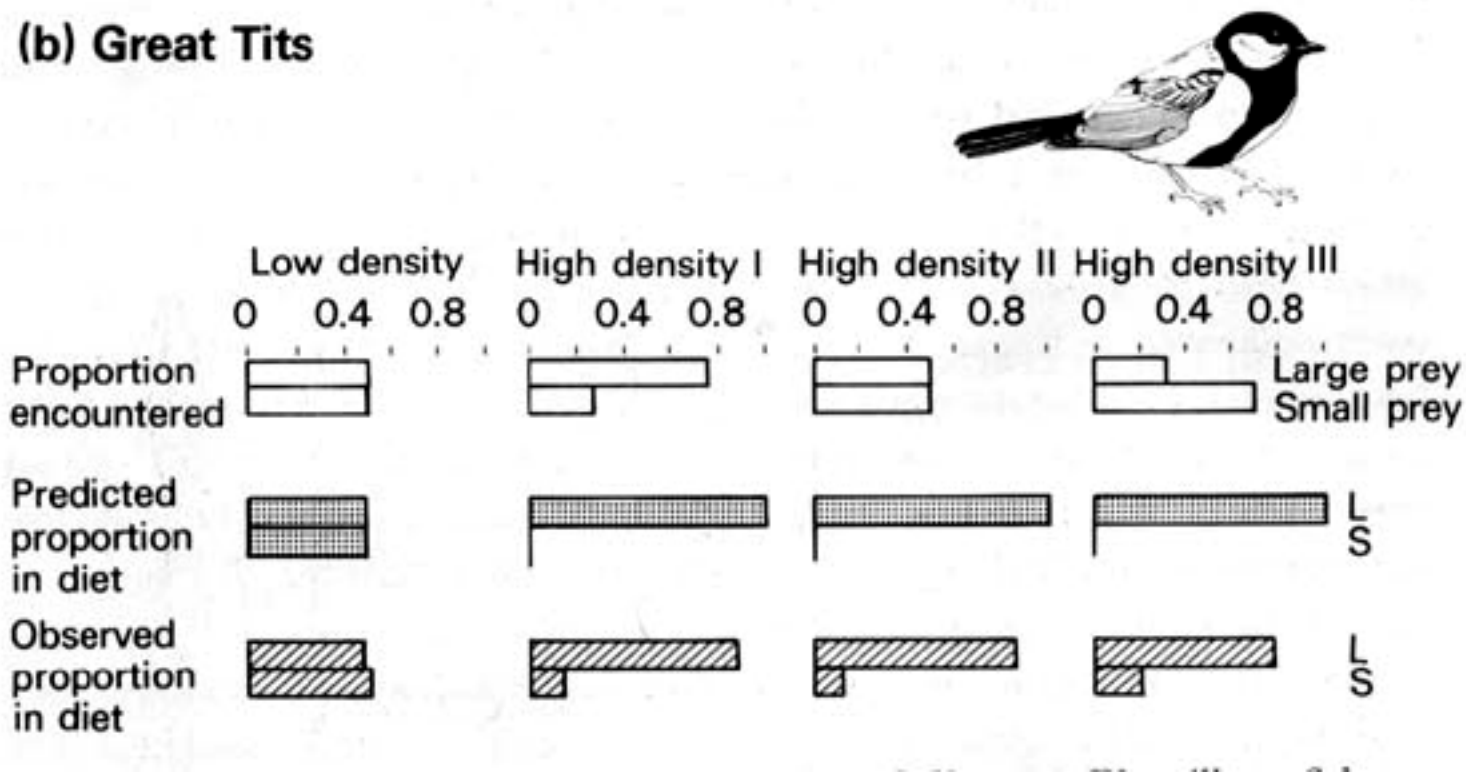
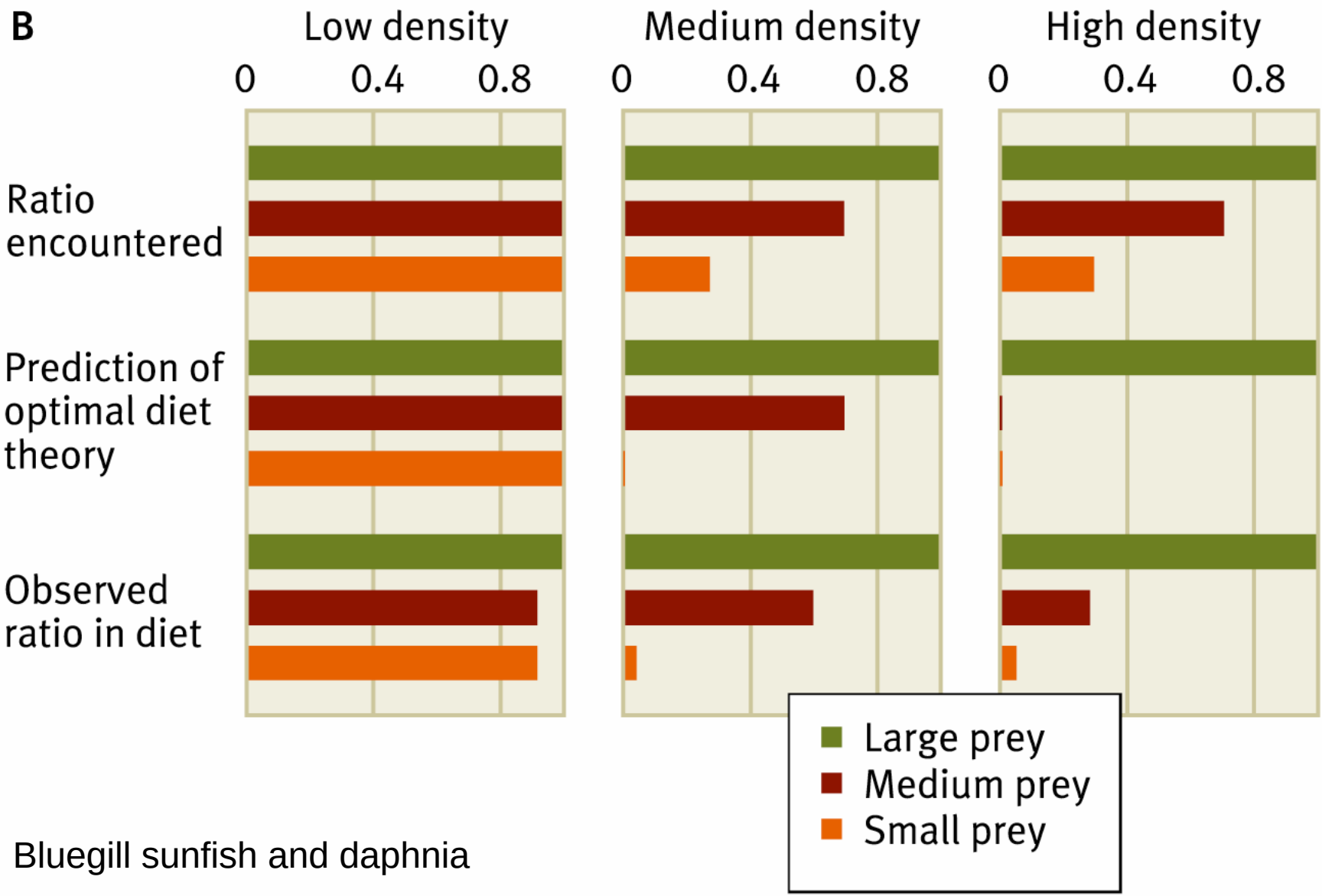


FIGURE 10.6: Great tit foraging



Foragers nearly always take some unprofitable



Bluegill sunfish and daphnia

FIGURE 10.7: Optimal choice of diet

Basic OFT model

- Predictions are generally supported
- BUT the all or nothing rule is not.
- WHY?
  - Sampling
  - Imperfect judgement
  - Other constraints.

For multiple prey items…

- Rank prey items in terms of e/h
- Calculate the gain from a diet containing only the best item.
- Recalculate for diet of items 1 & 2, 1-3, 1-4, etc.
- Find the best solution.

2.- When to move on? Marginal value theorem.

FIGURE 10.8: Patch choice

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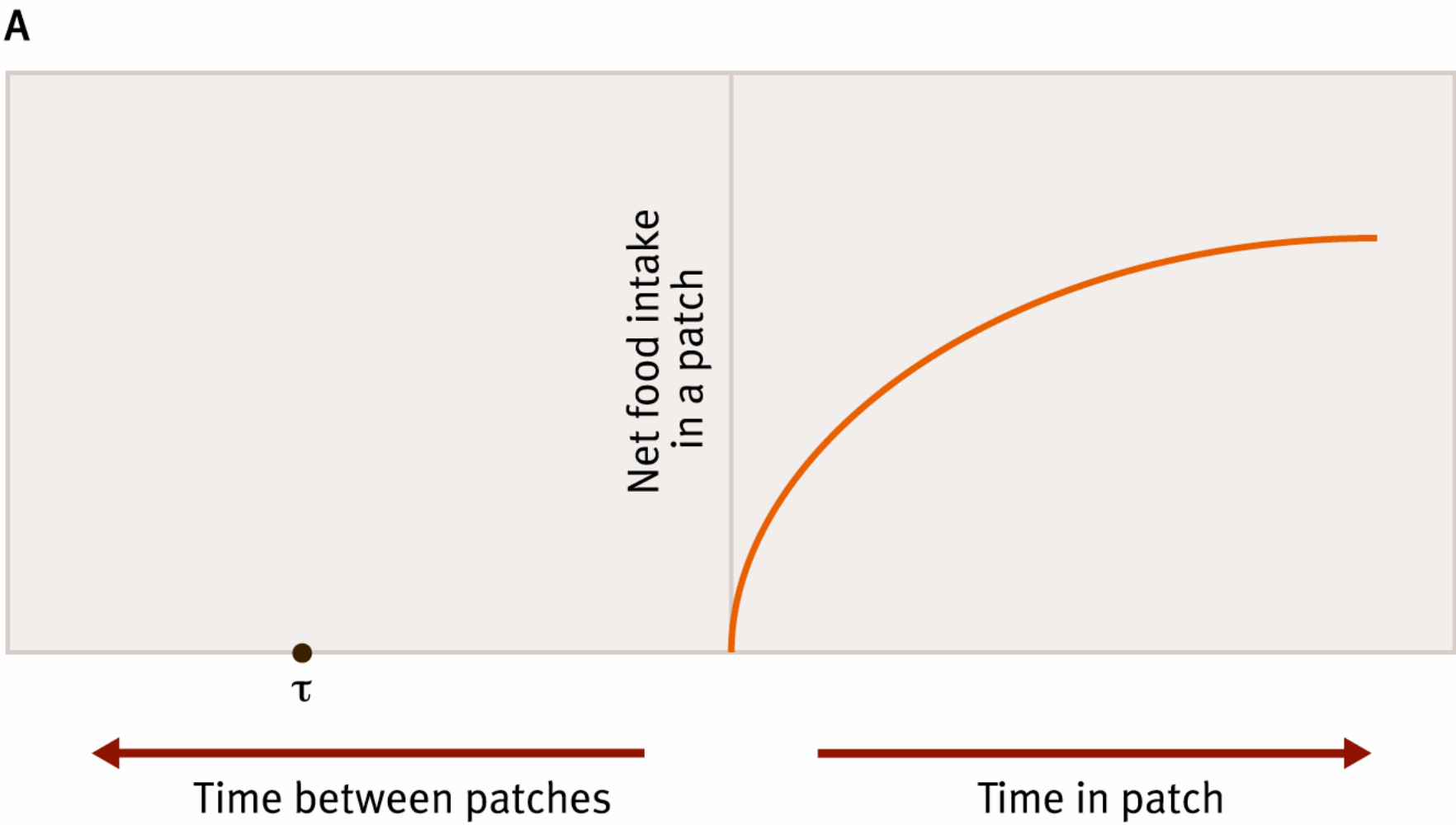


FIGURE 10.9: Graphical solution to marginal value problem (top)

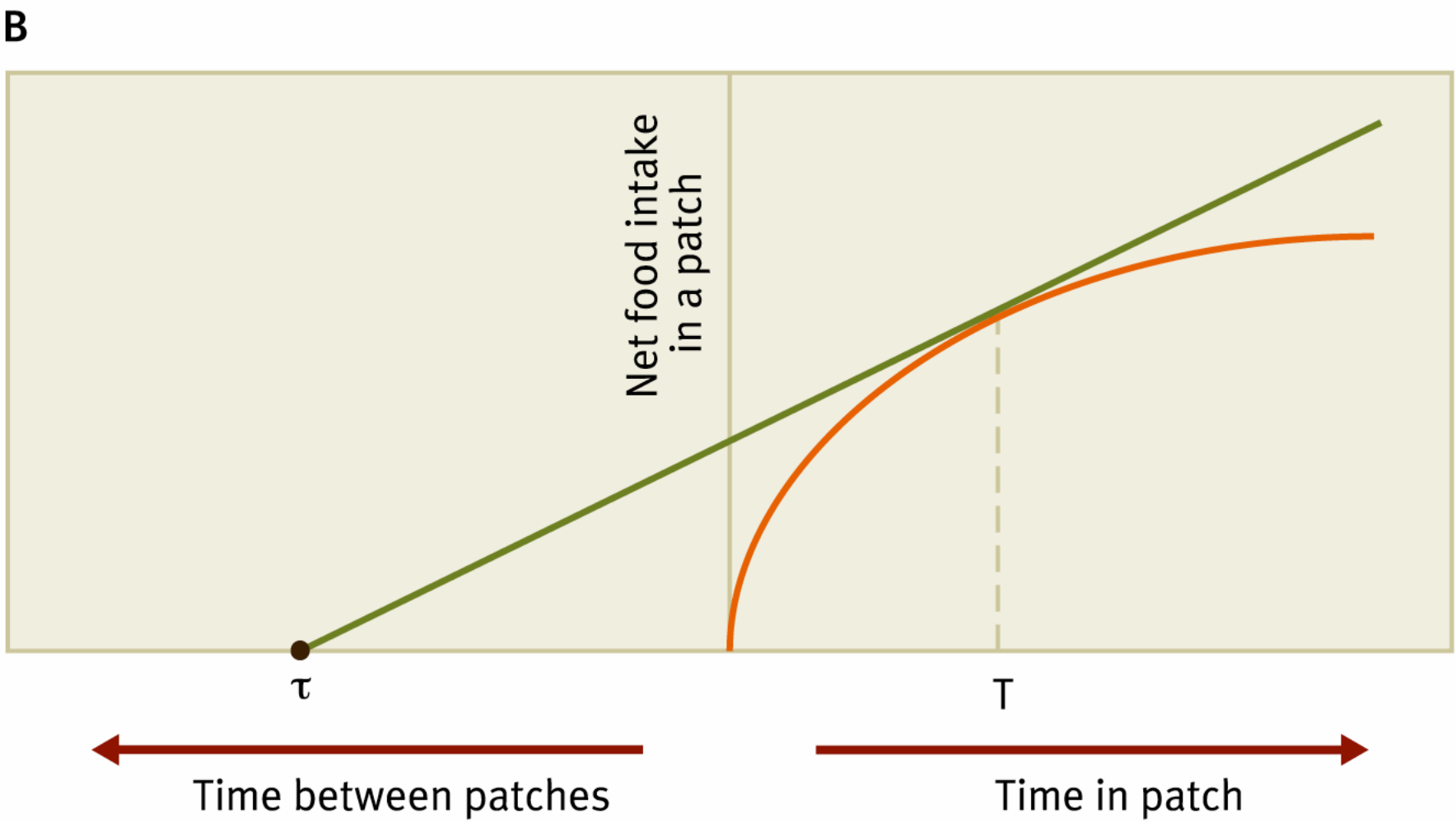
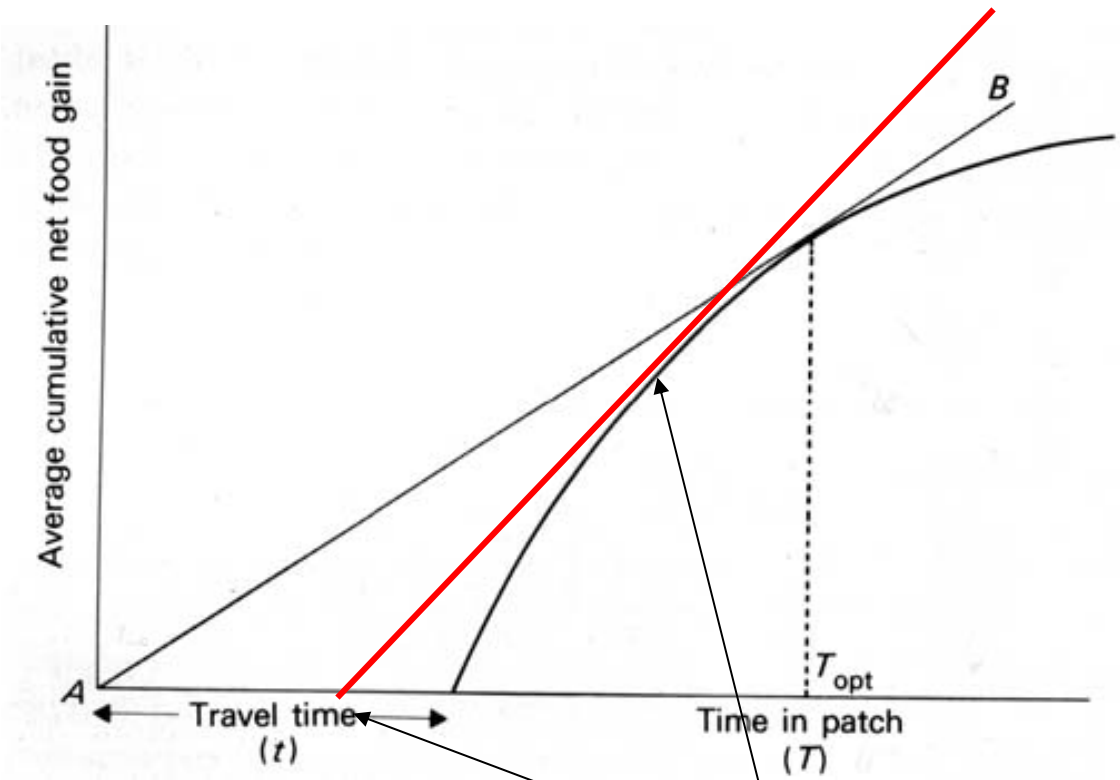
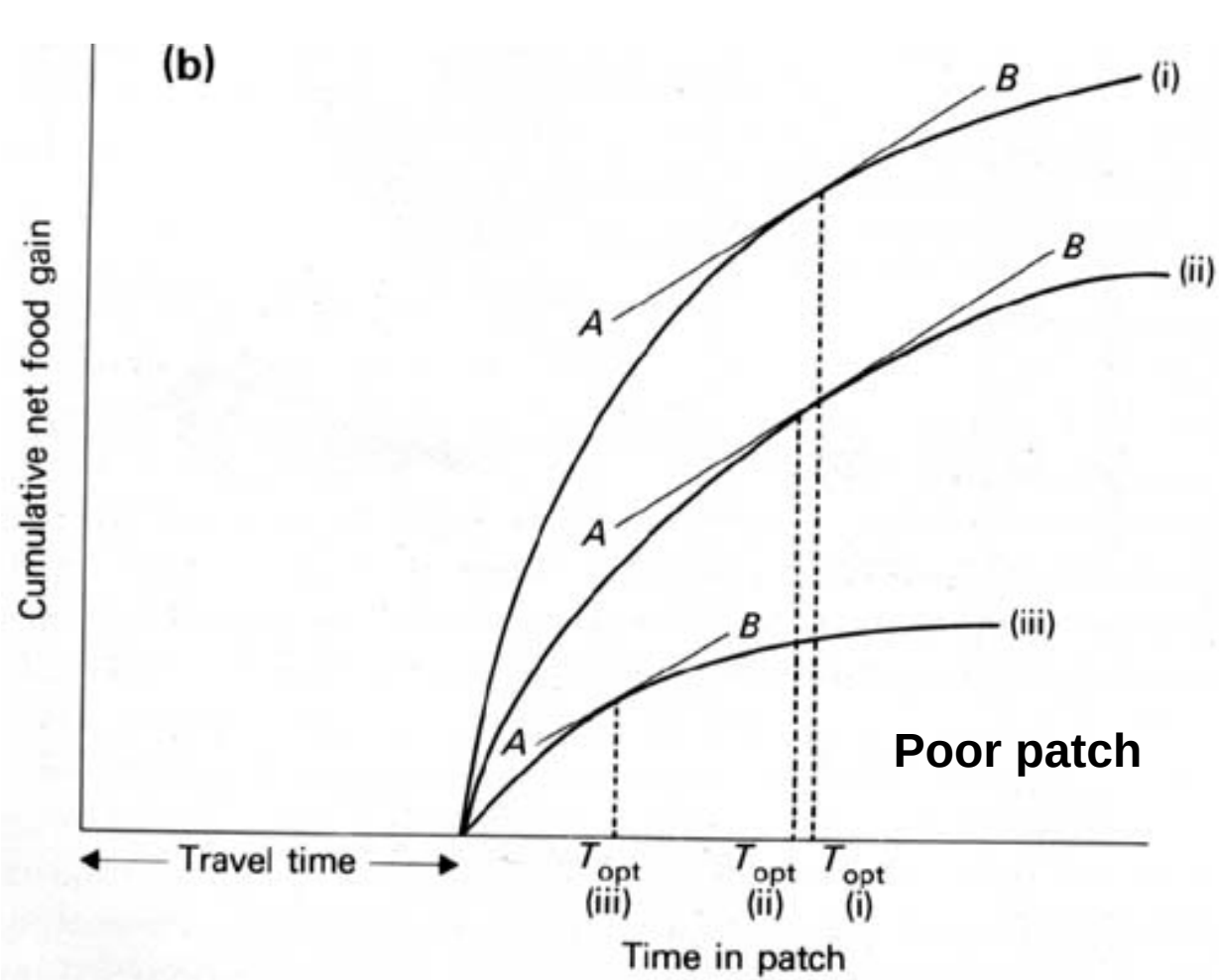


FIGURE 10.9: Graphical solution to marginal value problem (bottom)



Reducing travel time between patches Reduces leaving time.



Good patch

Average patch

Poor patch

When the rate of gain drops to the average for foraging in all patches.

Note slopes of line AB

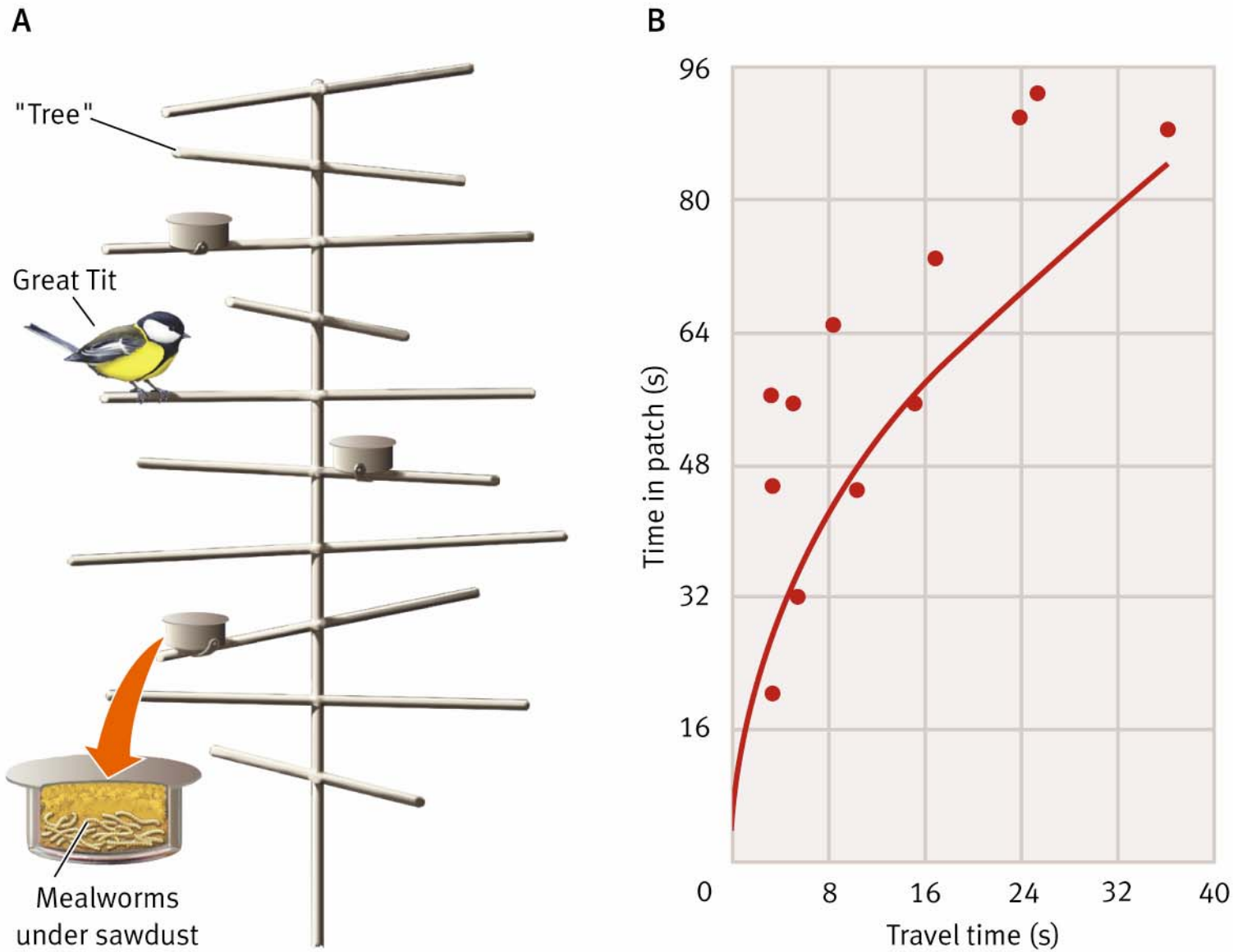
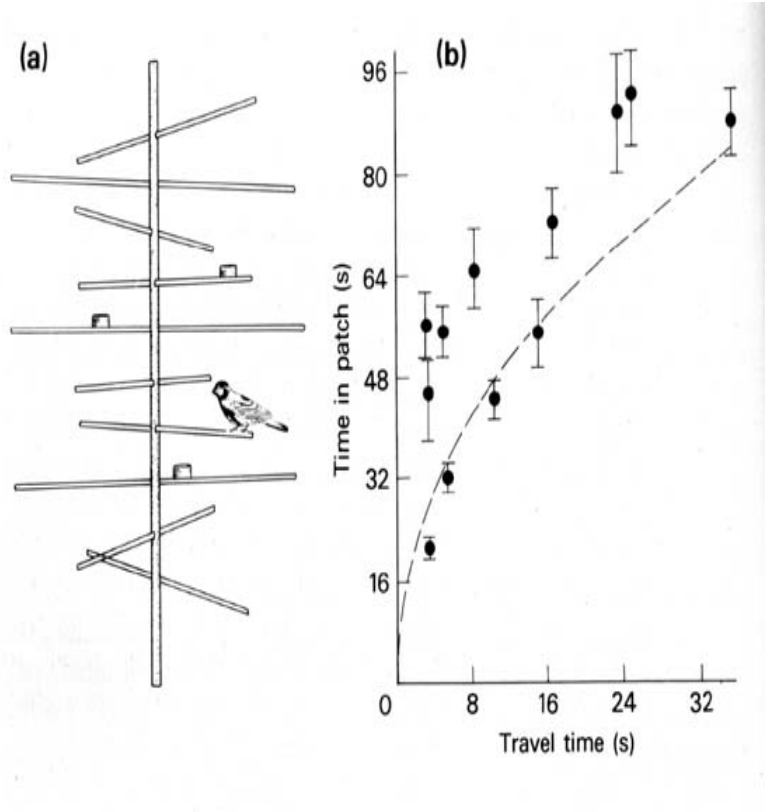
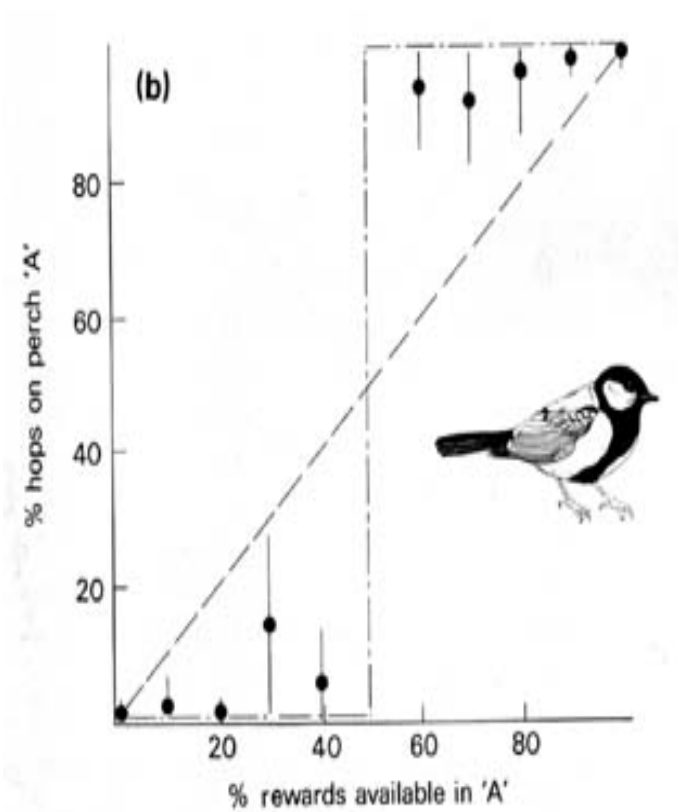


FIGURE 10.10: Optimal time in patch and travel time



Time in patch increases with travel time between patches



Tits switch to most profitable patches

3.- CPF

- Must carry food back to central location (nest, storage site).
- Prey carried one at a time.
- Prey types vary in quality
- Aim to maximize E/T.
- round-trips
- More complex model → multiple loads

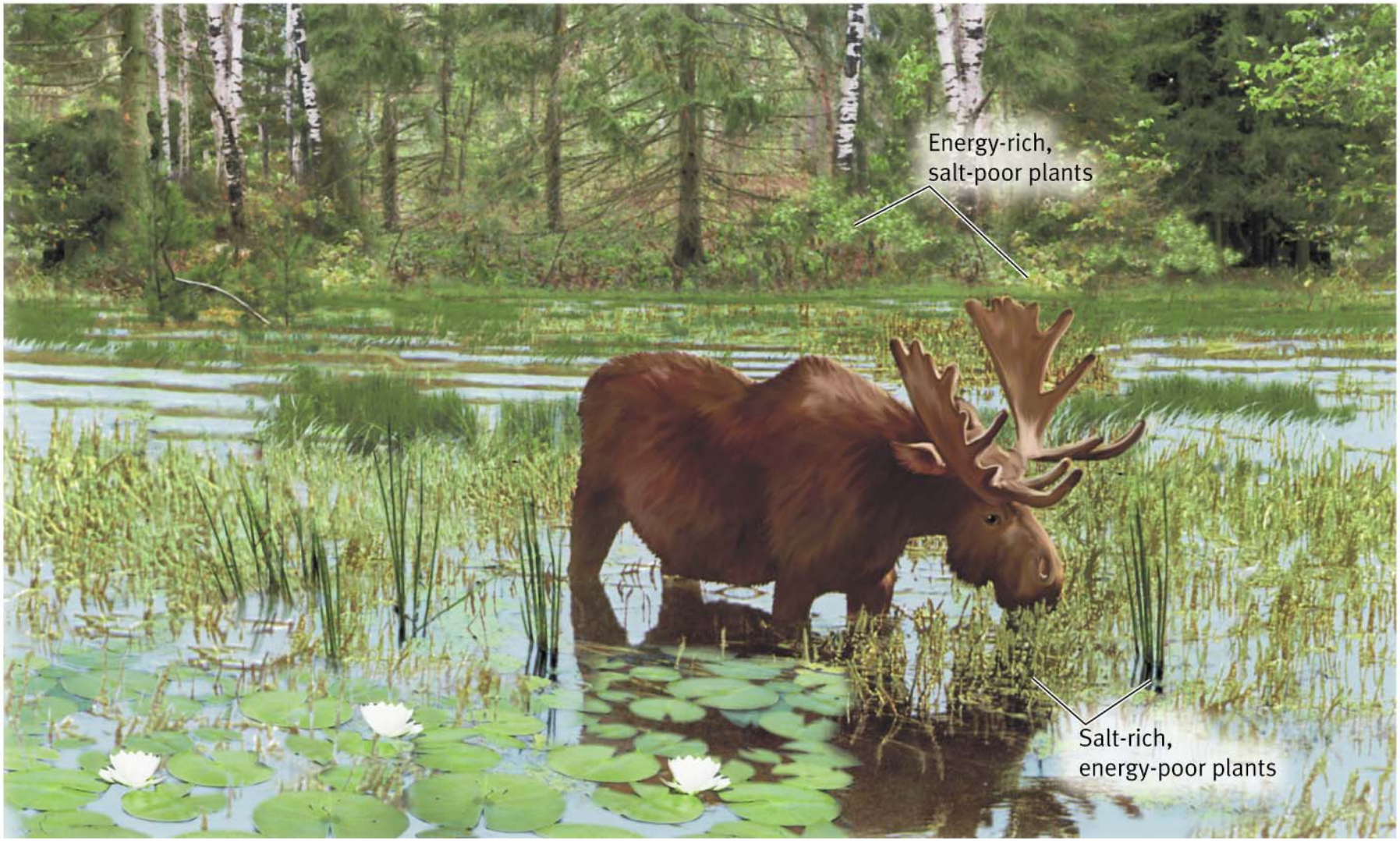


FIGURE 10.12: Specific foraging constraints

5.- Risk-sensitive behaviour

- Take into account means AND variance, and the animal’s need.
- Pulling the goalie
- Safe and risky investing

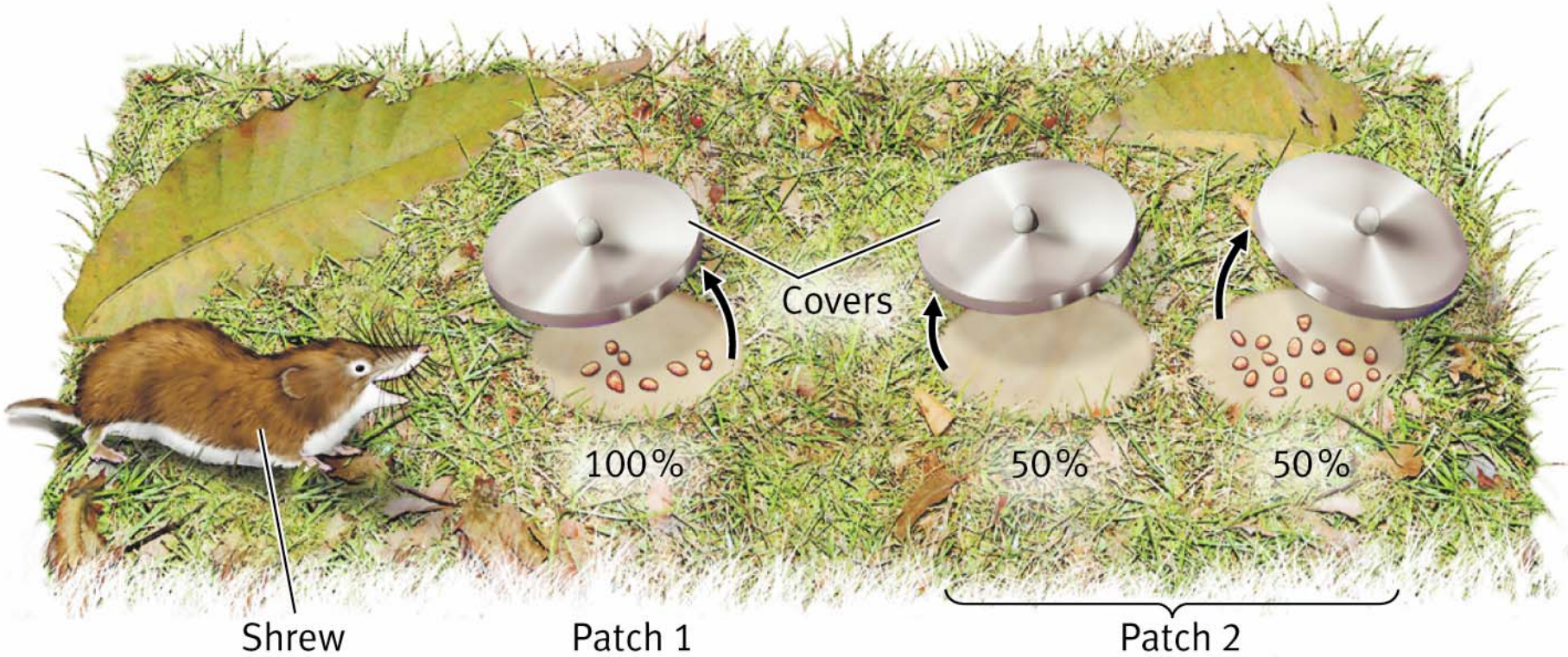


FIGURE 10.13: Risk-sensitive optimal foraging model

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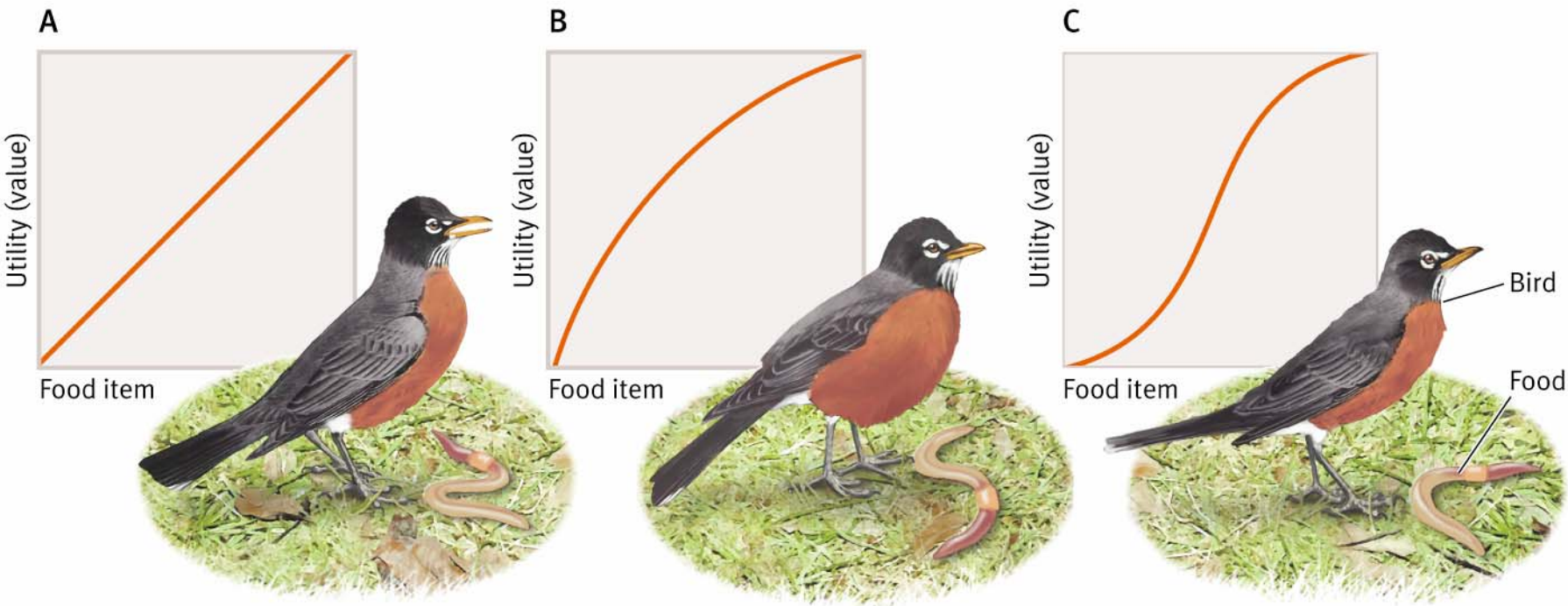

FIGURE 10.14: Utility of food

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In other terms…

- The environment will, on average, yield 6 units or energy.
- If you only need 5 energy units to survive, go for average but predictable reward

- If you need 7 units to survive, playing it safe is pointless.
- Take some risks and go for the big money (or big loss).

Juncos – Caraco 1980

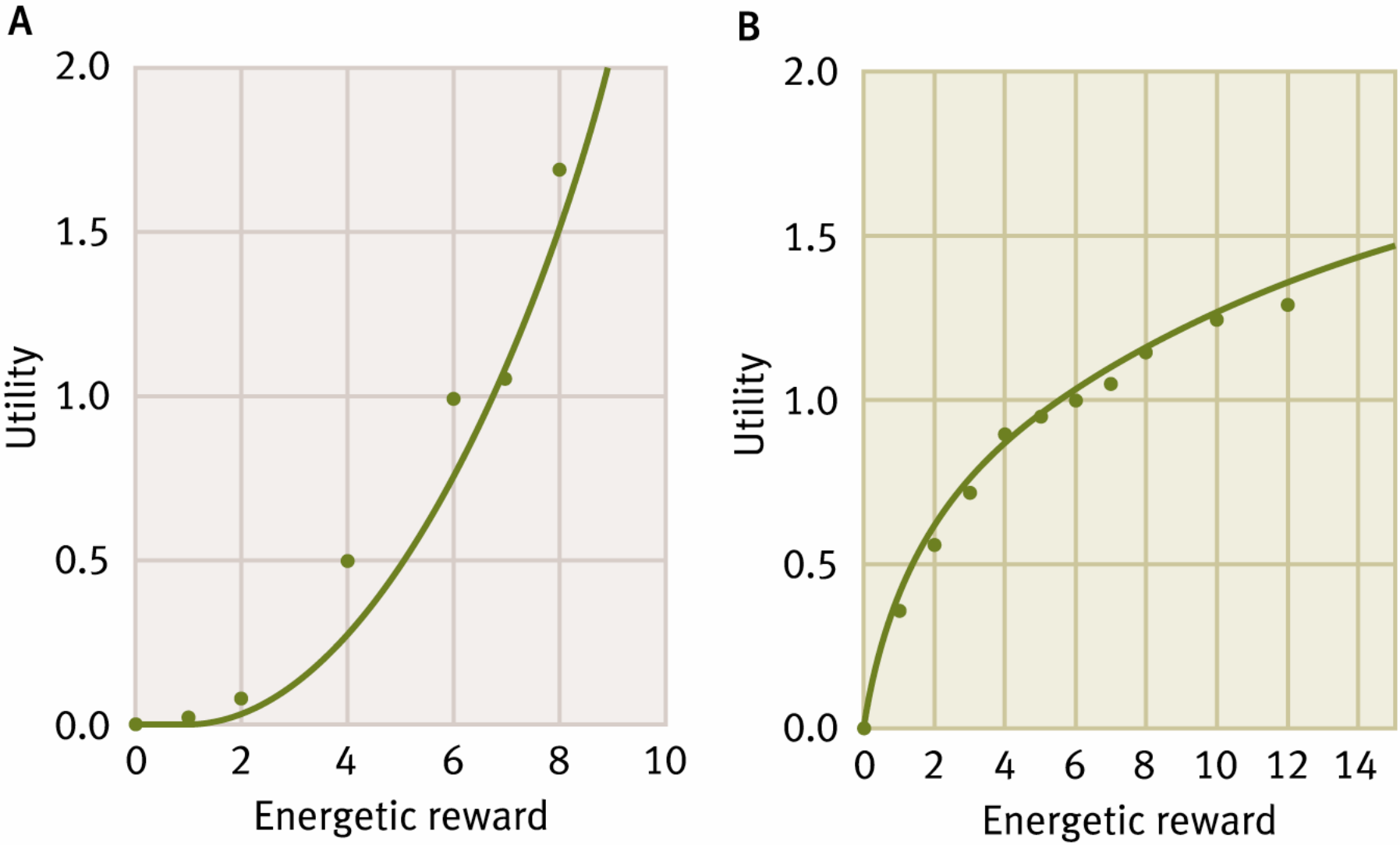

FIGURE 10.16: Utility functions and risk sensitivity

6.- Constraints II: Predators

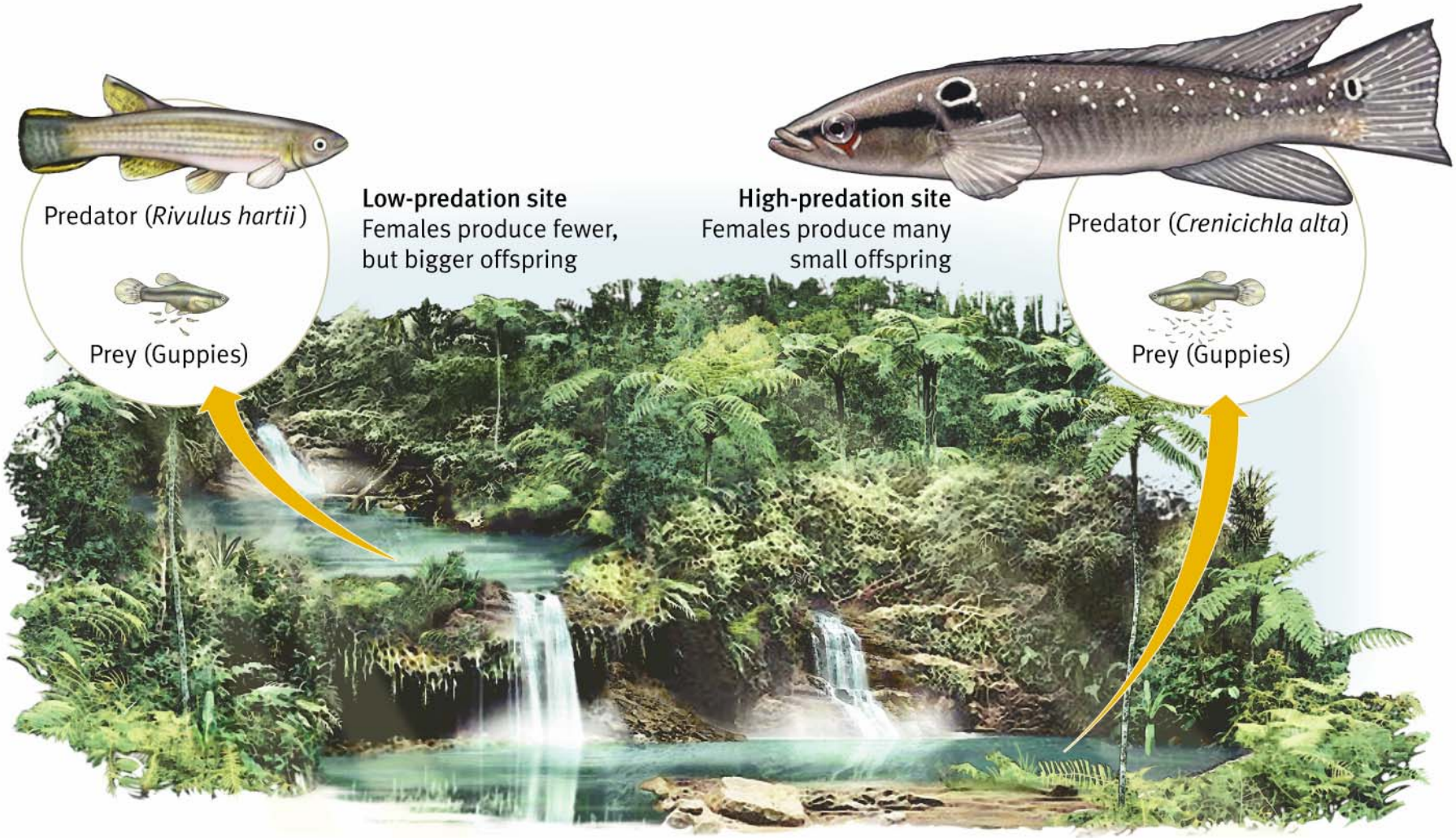

FIGURE 2.18: Natural selection and predation

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7.- Foraging in groups

- Group size effects
  - Local enhancement
  - Social facilitation
  - Predator monitoring
- Cooperation
- Social learning
  - Conducive conditions
  - Producer-scrounger
  - Diet choice in children
  - Public information

Bluegill sunfish – capt/min/ind.

Amphipod prey

lab

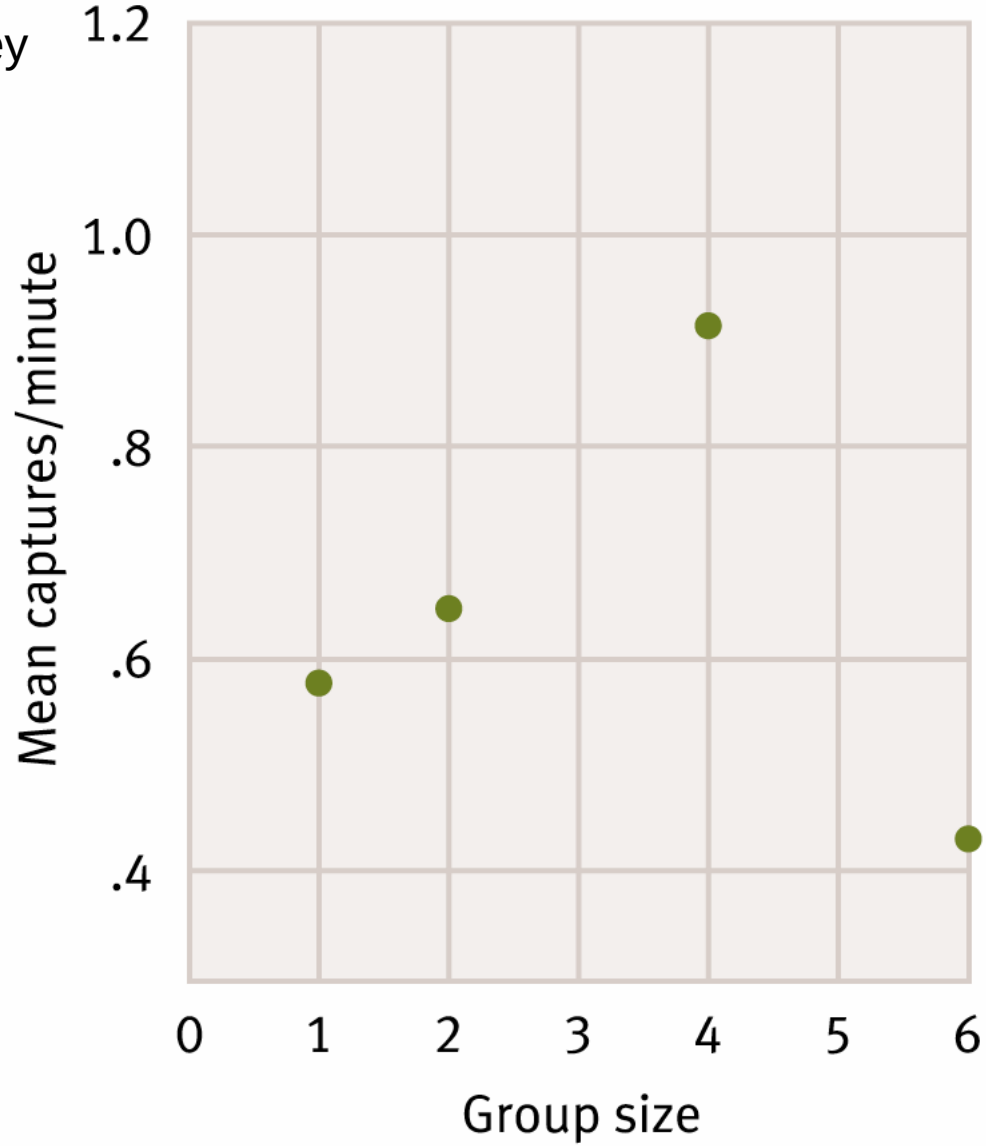

FIGURE 10.19: Group size and foraging success

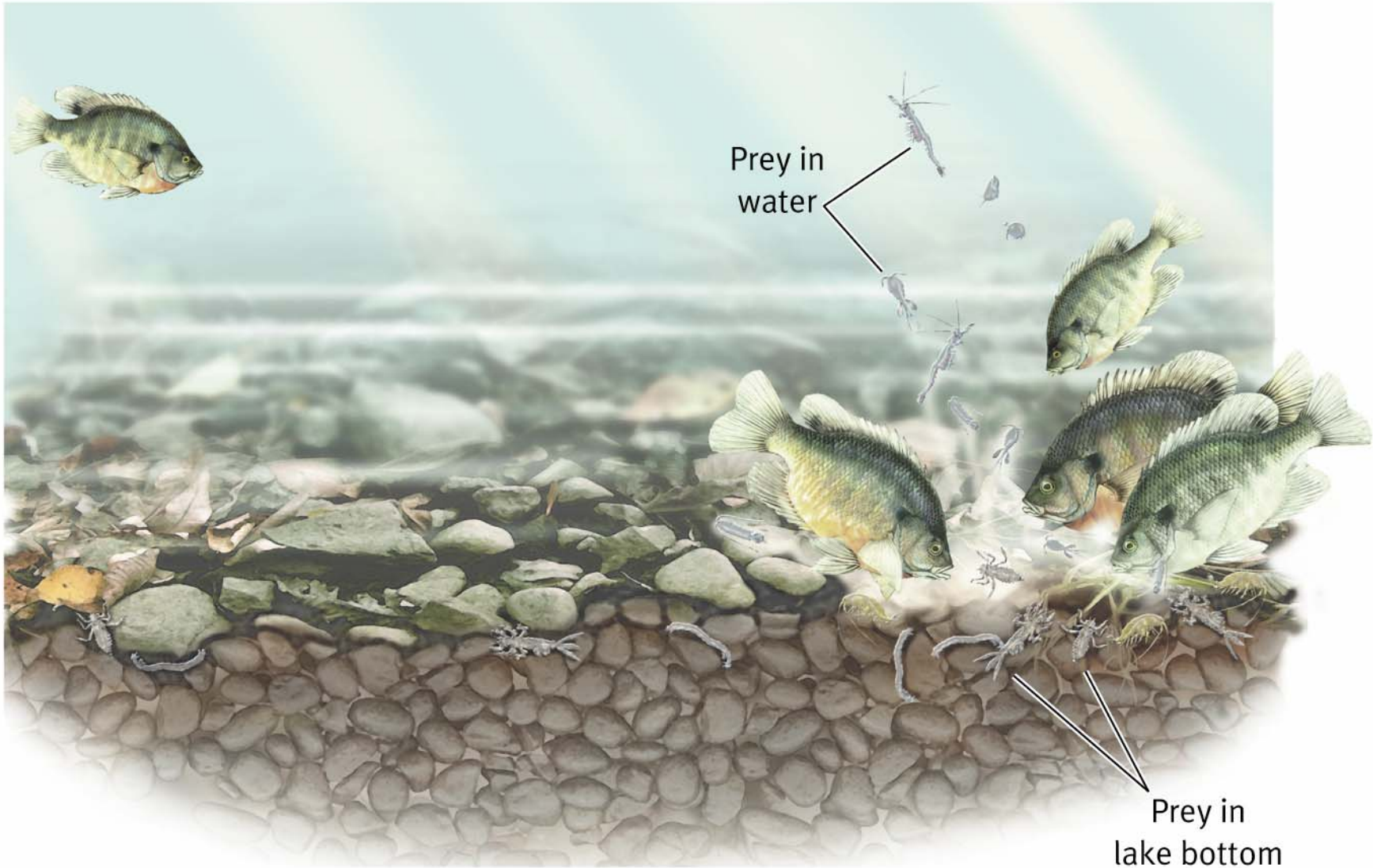

FIGURE 10.20: Bluegill group foraging

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A

FIGURE 10.21: Cooperative hunting in wild dogs

7.- Foraging in groups

- Group size effects
  - Local enhancement
  - Social facilitation
  - Predator monitoring
- Cooperation
- Social learning
  - **Conducive conditions**
  - **Producer-scrounger**
  - **Diet choice in children**
  - **Public information**

Conducive conditions – LL and LAG - axes

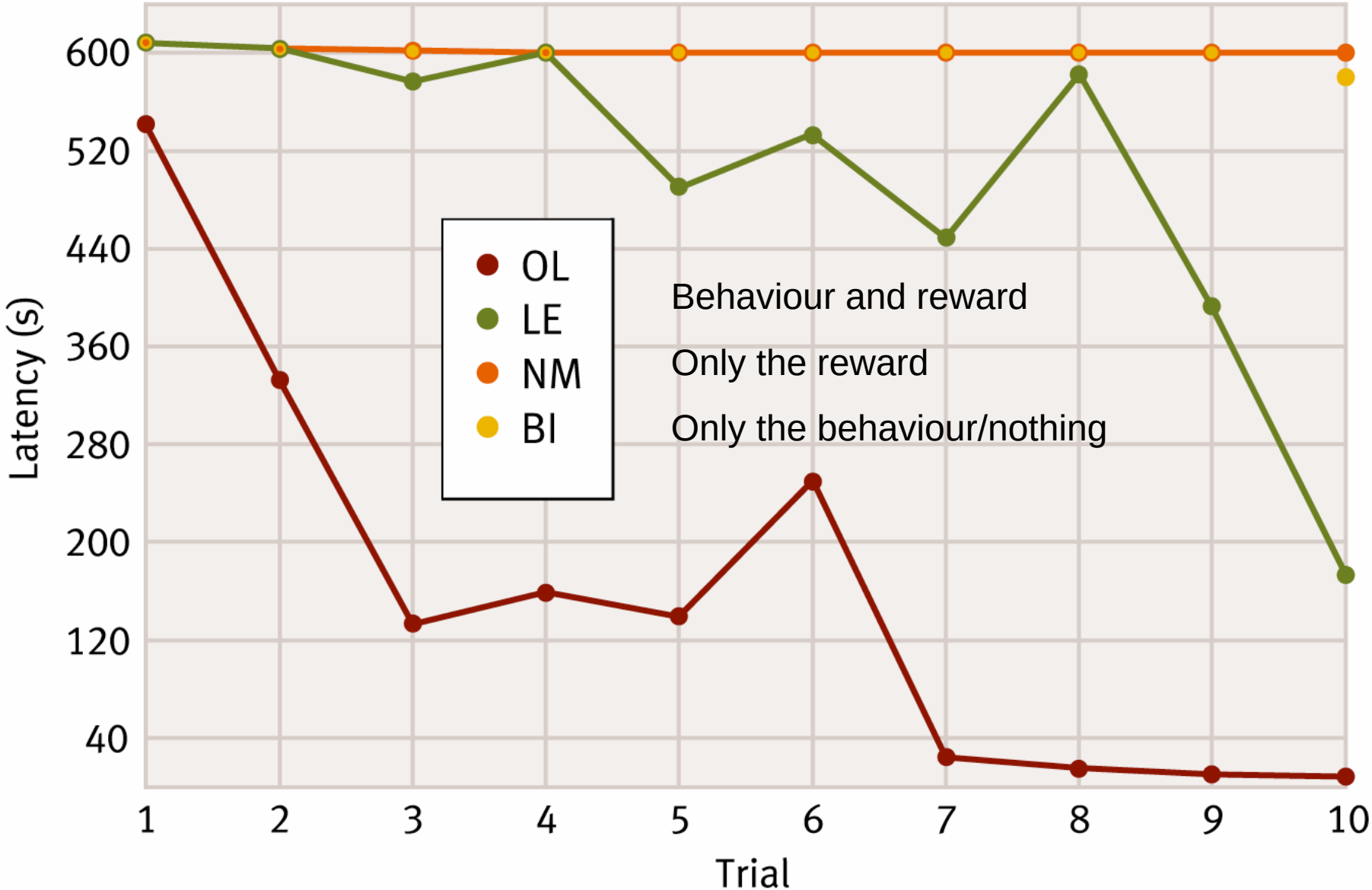

FIGURE 10.24: Social learning and foraging in pigeons

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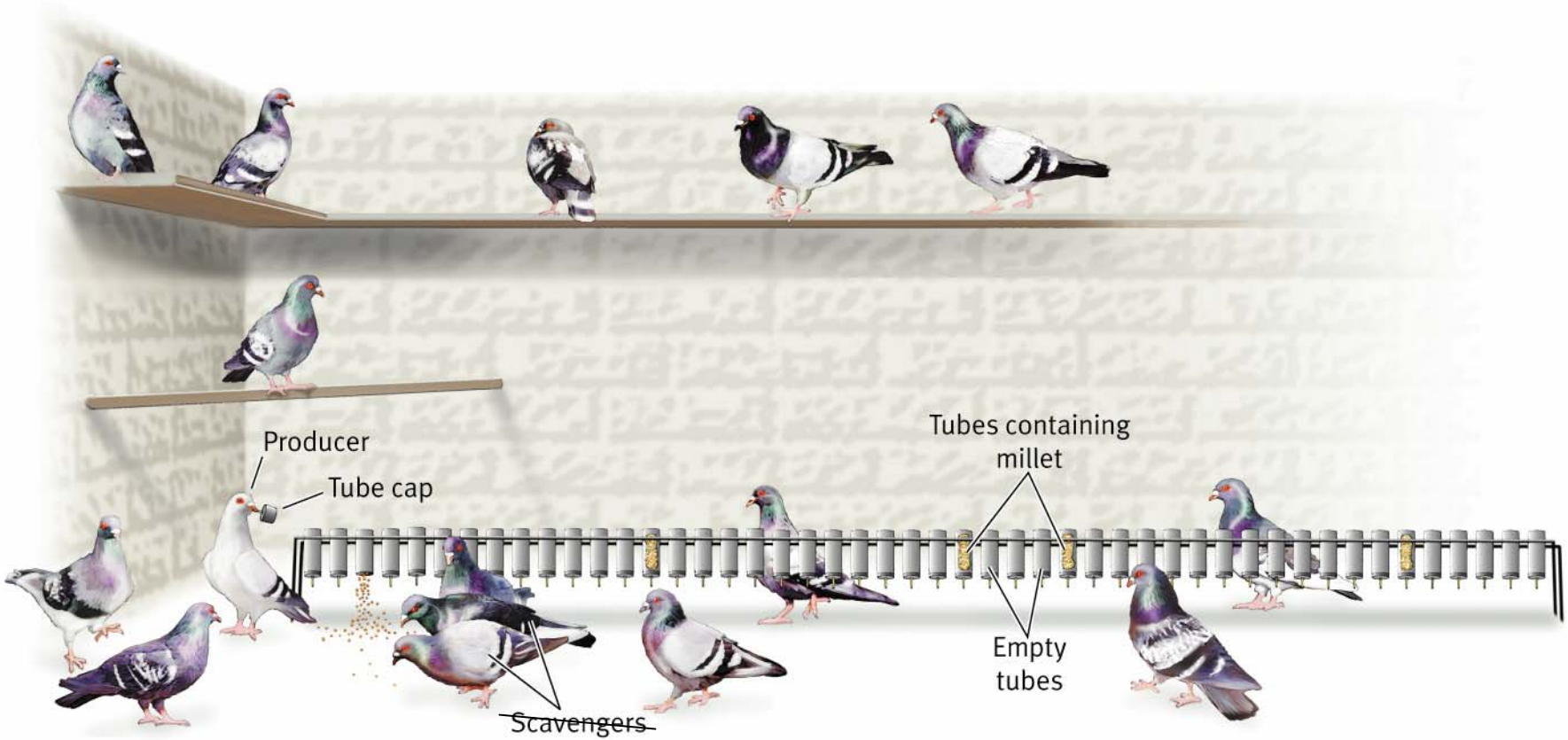
LL and LAG : only 2 producers. When removed…



scroungers

FIGURE 10.25: Producing and scrounging

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LL and LAG
Obs. saw model' s behaviour and its reward.

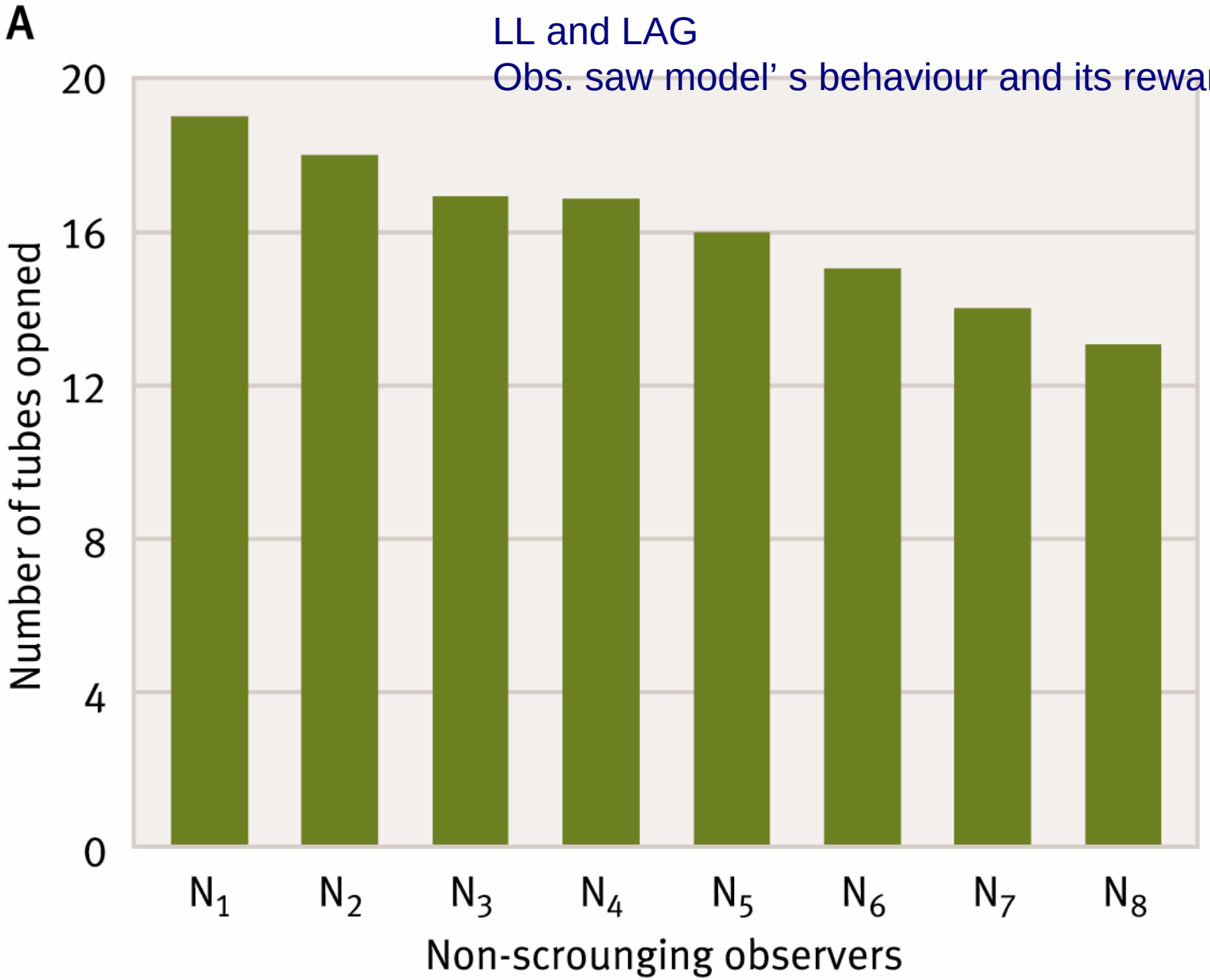

FIGURE 10.26: Scrounging prevents social learning (top)

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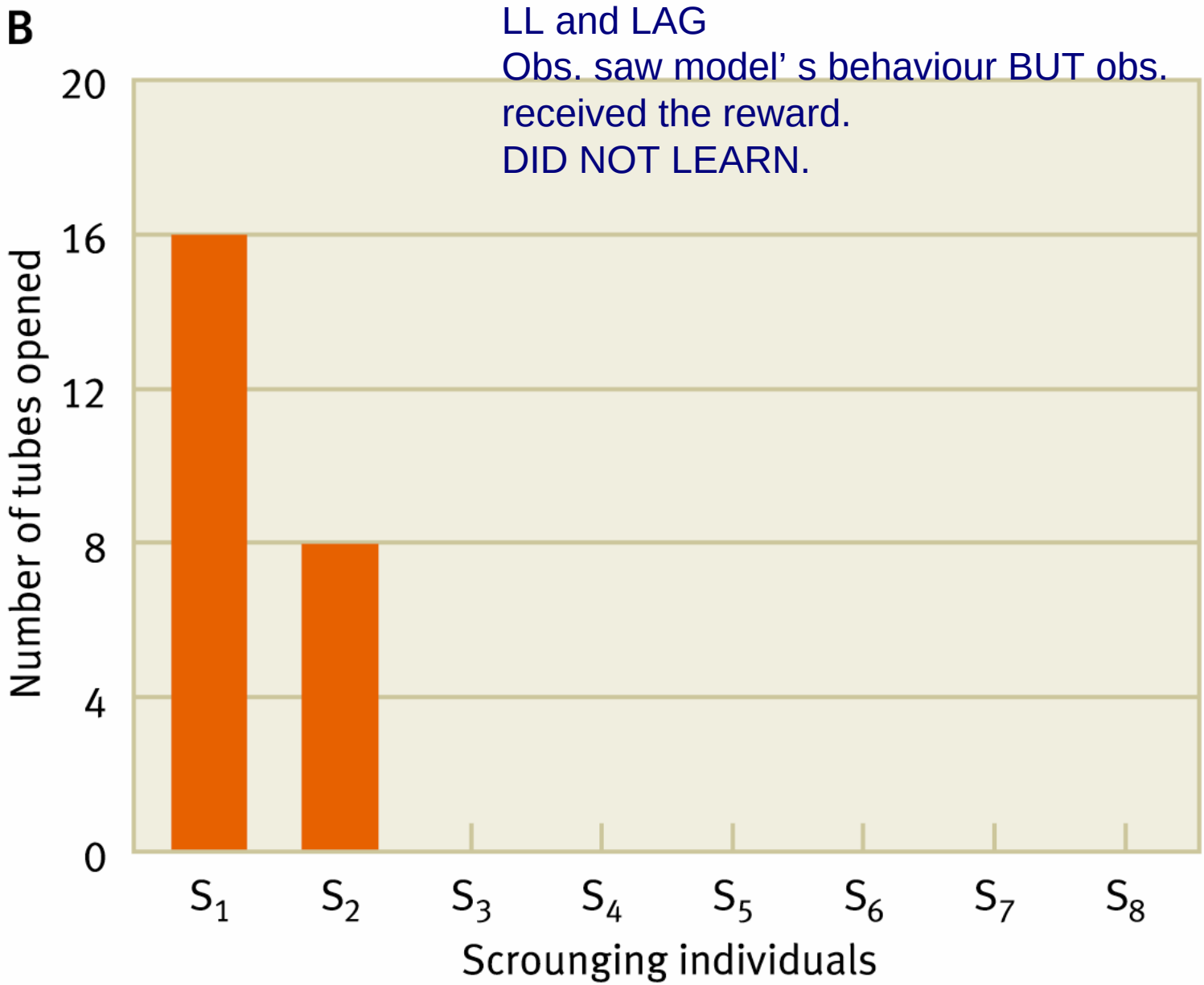

FIGURE 10.26: Scrounging prevents social learning (bottom)

FIGURE 10.28: Public information Templeton + LAG

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Public info.

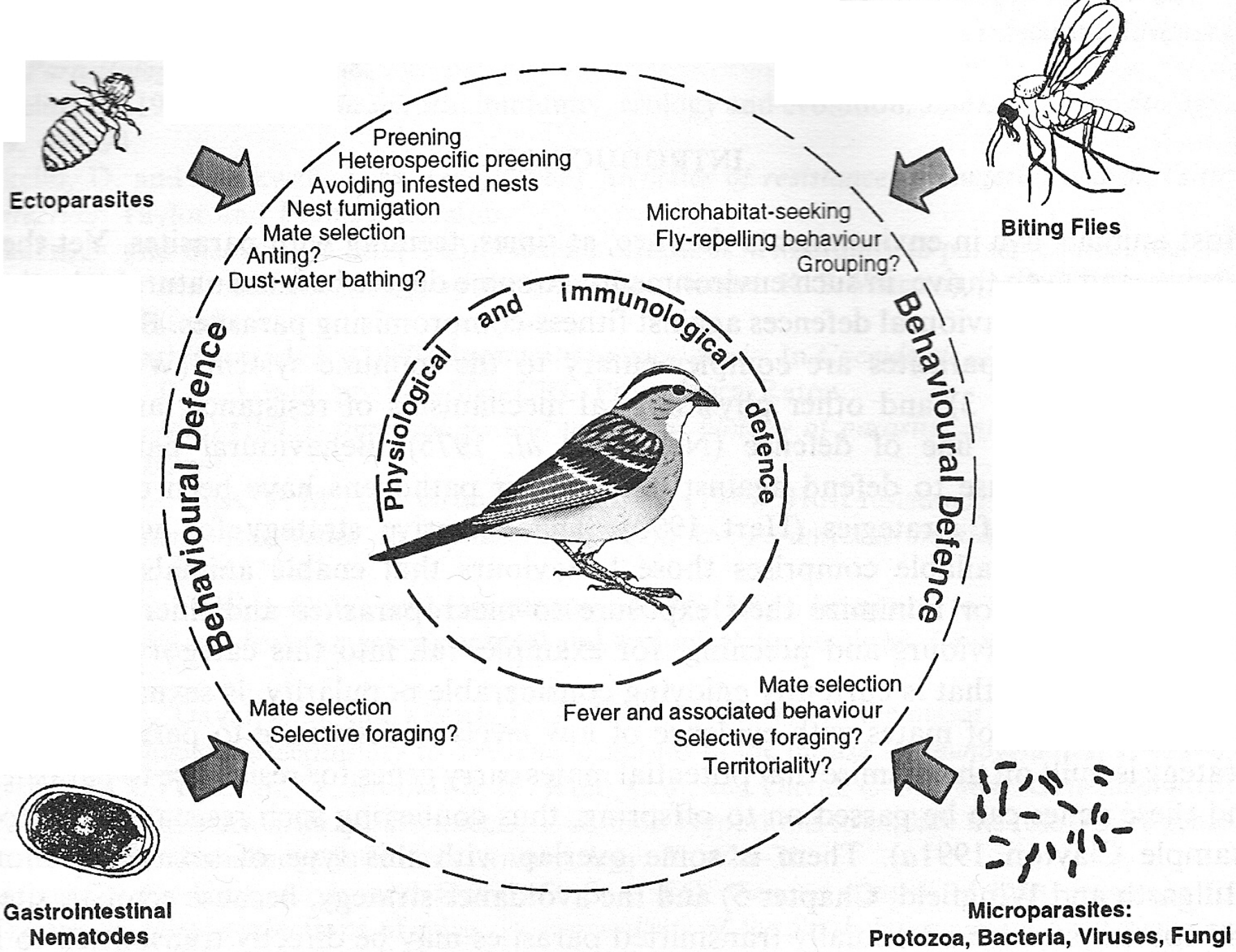
- Use of conspecifics to assess the value of an area.
- Two birds (1 and 2), foraging alone or not

8.- Constraints III: parasites.

- By definition, parasites are or can be detrimental to their hosts
- What can hosts do?
- Avoidance behaviours
- Changes in foraging behaviour

Same paper?

- Hart, B. L. 1990. Behavioral adaptations to parasites an pathogens: five strategies. Neuroscience and Biobehavioral Reviews 14: 273-294.
- --- 1992. Behavioral adaptations to parasites: an ethological approach. J. of Parasitology. 78: 256-265.
- --- 1994. Behavioral defenses against parasites: interactions with parasite evasiveness. Parasitology 109: 139-151.
- --- 1997. Behavioral defense In: Host-parasite evolution: general principles and avian models. (D. H. Clayton and J. Moore, eds.) Ch 4. pp 59-77.


Ectoparasites
Preening
Heterospecific preening
Avoiding infested nests
Nest fumigation
Mate selection
Anting?
Dust-water bathing?
Behavioural Defence
Biting Flies
Microhabitat-seeking
Fly-repelling behaviour
Grouping?
Behavioural Defence
Physiological and immunological defence
Gastrointestinal Nematodes
Mate selection
Selective foraging?
Microparasites:
Protozoa, Bacteria, Viruses, Fungi
Mate selection
Fever and associated behaviour
Selective foraging?
Territoriality?

Parasites' Effects on Foraging Behaviour

- Why foraging?

- Avoidance of potential parasite sources
- Prophylactic self-medication
- Therapeutic self-medication

Parasite Avoidance - Foraging

- Avoidance of areas or food items because of the risk of parasitism.
- E.g., Waterfowl diets
- Herbivorous during the winter
- More invertebrates during the breeding season
- More so for females – Ca
- Problem: Snails → ??
- Result more parasitism in females and when invert. diet is higher.

Parasite Avoidance - Foraging

- Foraging behaviour takes into account the risk of parasitism,
- NOT just energy or nutritional requirements
- Particularly a problem for herbivores (at least that is where most of the work has been done).

Effects on Foraging Behaviour

Prophylactic	**Therapeutic**
Risk of parasitism	Actual presence
infective stage	established stage
seasonal changes?	individual changes
possibly genetic	learned
interpop diffs	interindivid. diffs
part of the usual diet	specifically to deal with illness

Prophylactic . .

- Geophagia in primates
  - Macaques, gorillas, chimps
  - Antidiarrheal clays – only mineral analyses so far
- Antischistosomal drugs use in baboons
  - 2 habitats fast upstream, slow downstream
  - IH absent where??
  - Baboon diet differed up/down
  - Shrub balanites – antischitosomal?? NO

…prophylactic

- Antibacterial foliage in starlings
  - Probably not
- Anting and fur rubbing
  - Birds:Ants, centipedes, lime, mothballs
  - Mammals: citrous fruits, resins, etc
  - Much annecdotal evidence, seems to work

Therapeutic

- Supposedly occurs in chimpanzees, but very difficult to clearly demonstrate.
- Chemical or physical removal of intestinal parasites.
- Manipulative experiments unethical.
- Follow and observe, but difficult to make a definite connection.

…..therapeutic self-medication

- Learning mechanisms (individual or social) required would be extremely complex and have not been demonstrated.

- The bottom line… really interesting story, but it seems unlikely.

Next-→ foraging for mates