SANGKALAN

Beberapa bagian dari salindia perkuliahan ini merupakan materi yang dilindungi oleh HAK CIPTA, dan penggunaannya dalam perkuliahan ini berdasarkan prinsip penggunaan wajar (*fair use*) untuk keperluan edukasi.

Oleh karena itu, mohon untuk membatasi penyebarluasan materi ini secara daring; materi ini hanya untuk penggunaan pribadi mahasiswa peserta mata kuliah ini.

EKOLOGI KOMUNITAS

PREDATOR-PREY INTERACTIONS

Exploitative interactions

- A general terms for one organism makes its living at the expense of another.
- Different forms:
  - Predation
  - Herbivory
  - Parasitism
  - Pathogenism
- Exploitative interactions are dynamics in nature.

Roles of exploitative interactions

- Influence the distribution, abundance, and structure of prey and host populations.
  - Substantially affect the abundance of the organisms they exploit.
- Links between populations.
  - Enhances the fitness of one individual while reducing the fitness of the exploited individual.

TABLE OF CONTENTS

01

PREDATORY INTERACTIONS

Scientific problems

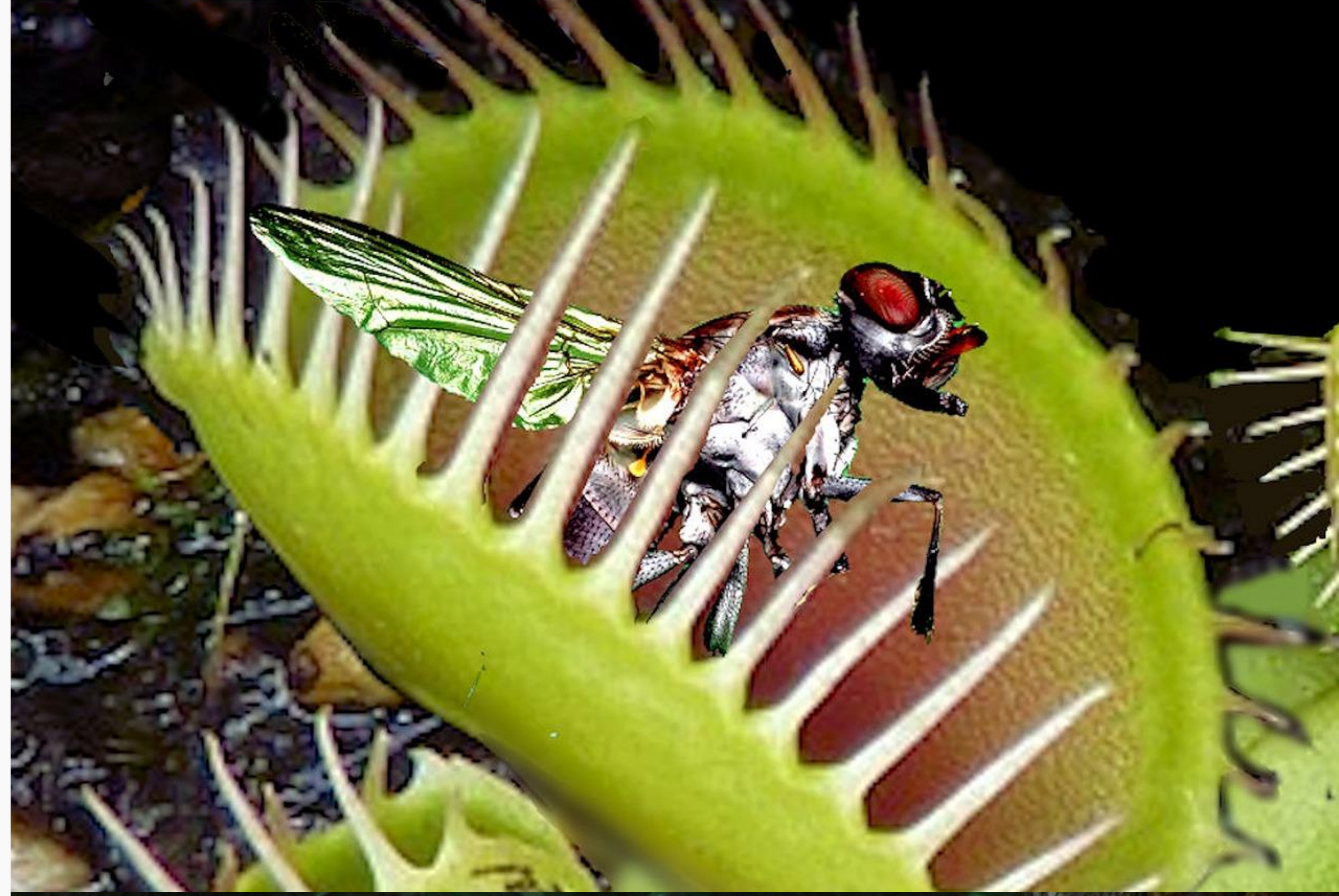
- Do predators reduce the size of prey populations substantially below K?
- Do consumer–resource interactions cause populations to fluctuate independently of variation in the environment?

Scientific problems

- Theory:
  - A predator can drive its prey to extinction.
  - As a consequence, the predator will also become extinct.
- Fact: in many cases, extinction did not happen.
- How do they coexist?

Predation & interspecific competition

- A straight-forward interspecies population interaction.
  - Could extend to herbivory, parasitism, pathogenism (previous lecture).
- Predator can influence prey competition, and vice versa.
  - Predator = density-dependent mortality factor to the prey population.
  - Prey = limiting resource to predators.
- Results in dynamic balance.



Exploitation vs competition

- The distinction between exploitation and competition is blurred when competitors eat each other.
- Case example:
  - *Tribolium* spp. competition result is influenced by the protozoan parasite of *Tribolium*, *Adelina tribolii*.

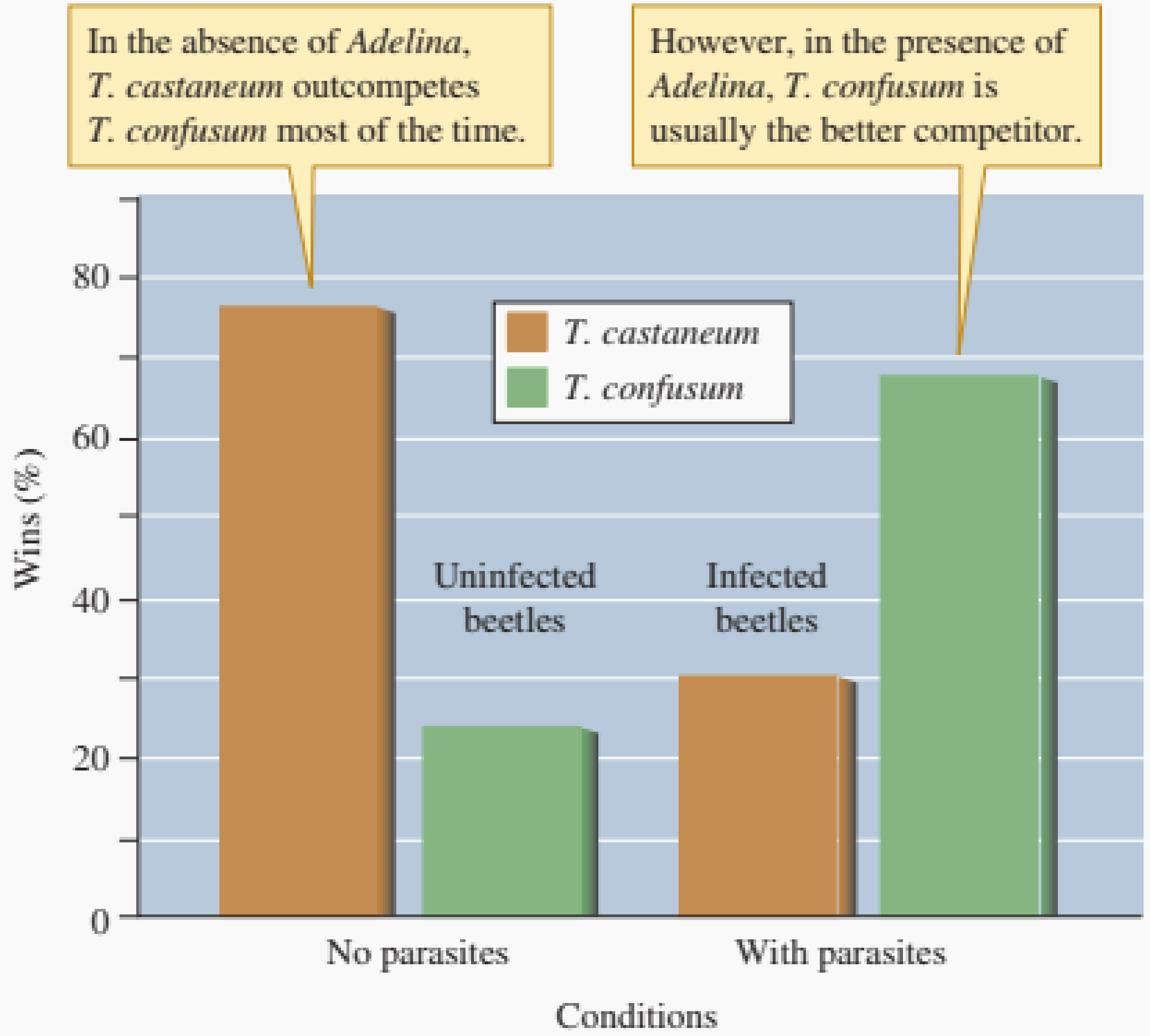
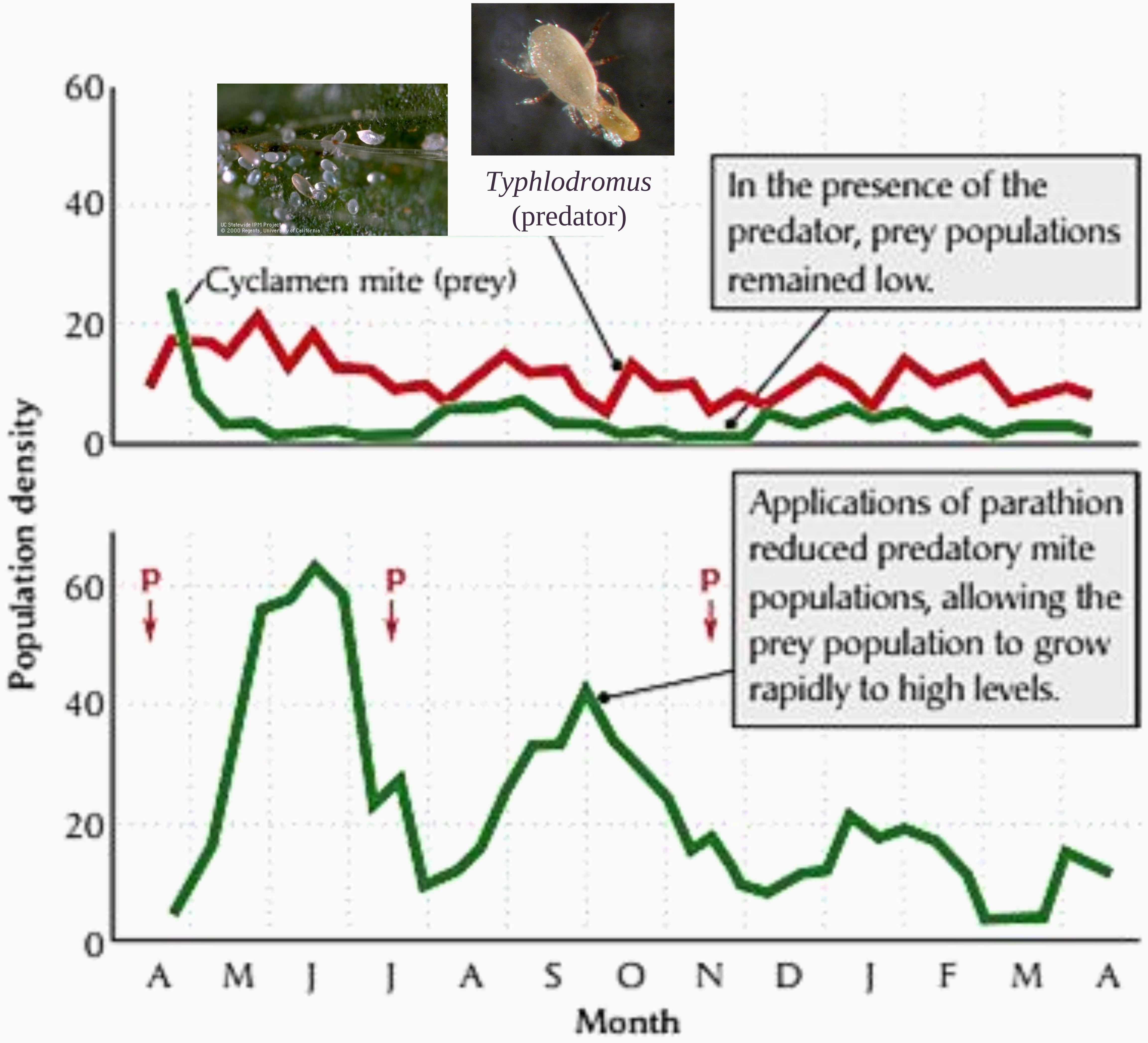


Figure 14.6 The influence of the protozoan parasite *Adelina tribolii* on competition between the flour beetles *Tribolium castaneum* and *T. confusum* (data from Park 1948).

[Figure 14.6], Molles, MC Jr. 2016. Ecology: concepts and applications, 7th edition, NY: McGraw-Hill Education. used under a Fair Use rationale.

Consumers can limit resource populations



- Predators can limit prey populations.
  - This keeps populations below K.
- Populations are regulated from above and below.
  - Predator and prey populations increase and decrease in regular cycles.

Infestations of strawberry plots by cyclamen mites (*Tarsonemus pallidus*) were tracked in the presence (above) and in the absence (below) of the predatory mite *Typhlodromus*. Parathion treatments are indicated by "p." After C. B. Huffaker and C. E. Kennett, *Hilgardia* 26:191–222 (1956).

[Figure 15.3], Ricklefs (2008), The Economy of Nature. 6th ed. NY: W. H. Freeman and Company; [Cyclamen mites], Jack Kelly Clark/UC-IPM, http://ipm.ucanr.edu/PMG/S/I-AC-SPAL-AD.026.html.; [*Typhlodromus occidentalis*], © 2009 Arlo Pelegrin, https://bugguide.net/node/view/352441. Non-commercial license. All images are used under a Fair Use rationale.

Coevolution

- Predator and prey exert natural selection forces on one another.
- Physical coevolution
  - Eyesight of hawks and owls vs earthy-colored prey.
  - Silica substances in grasses vs hard teeth in grazers.
- Chemical coevolution
  - Milkweeds poison vs monarch caterpillars detoxing ability.
  - Infectious microorganisms vs mammalian hosts.
- Behavioral coevolution
  - Mimicry, camouflage, warning coloration, startle coloration.

02

PREDATOR-PREY DYNAMICS

Predator-prey cycles

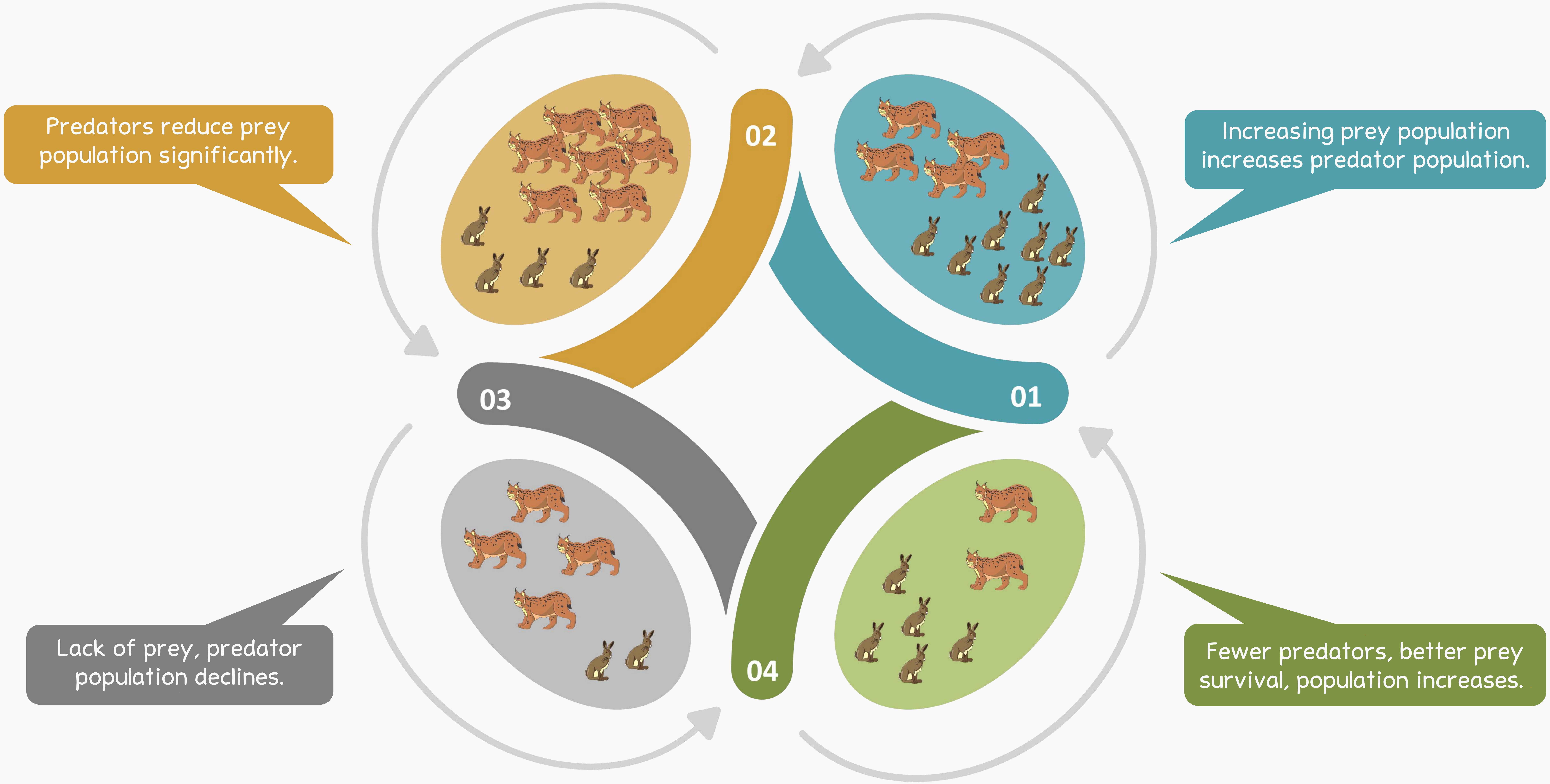


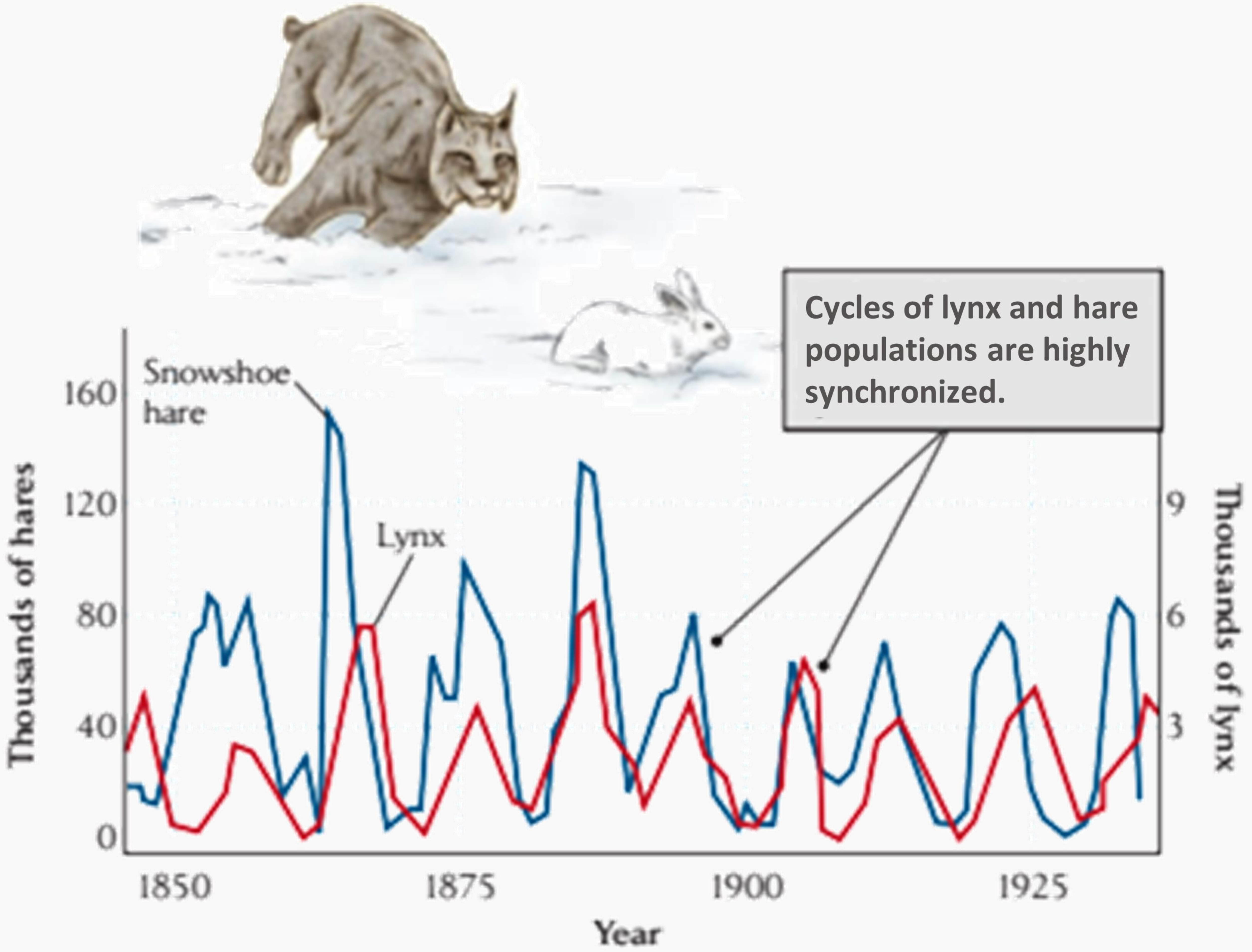
Diagram template "Oval cycle matrix" by PresentationGO.com, with modifications.

Cycles of abundance: snowshoe hares & lynx

- Hare populations in boreal forests fluctuate in a 8–11 year cycle.
- Snowshoe hare is the lynx's primary food.
  - Other prey species often do not meet the lynx's nutritional needs.
- The population cycles of these two species are closely linked.

Lynx canadensis

Lepus americanus



Historical fluctuations in lynx and showshoe hare populations based on the number of pelts purchased by the Hudson Bay Company (MacLulich 1937)

[Figure 15.2], Ricklefs (2008), The Economy of Nature. 6th ed. NY: W. H. Freeman and Company. Used under a Fair Use rationale.

Predator-prey relationships are dynamic

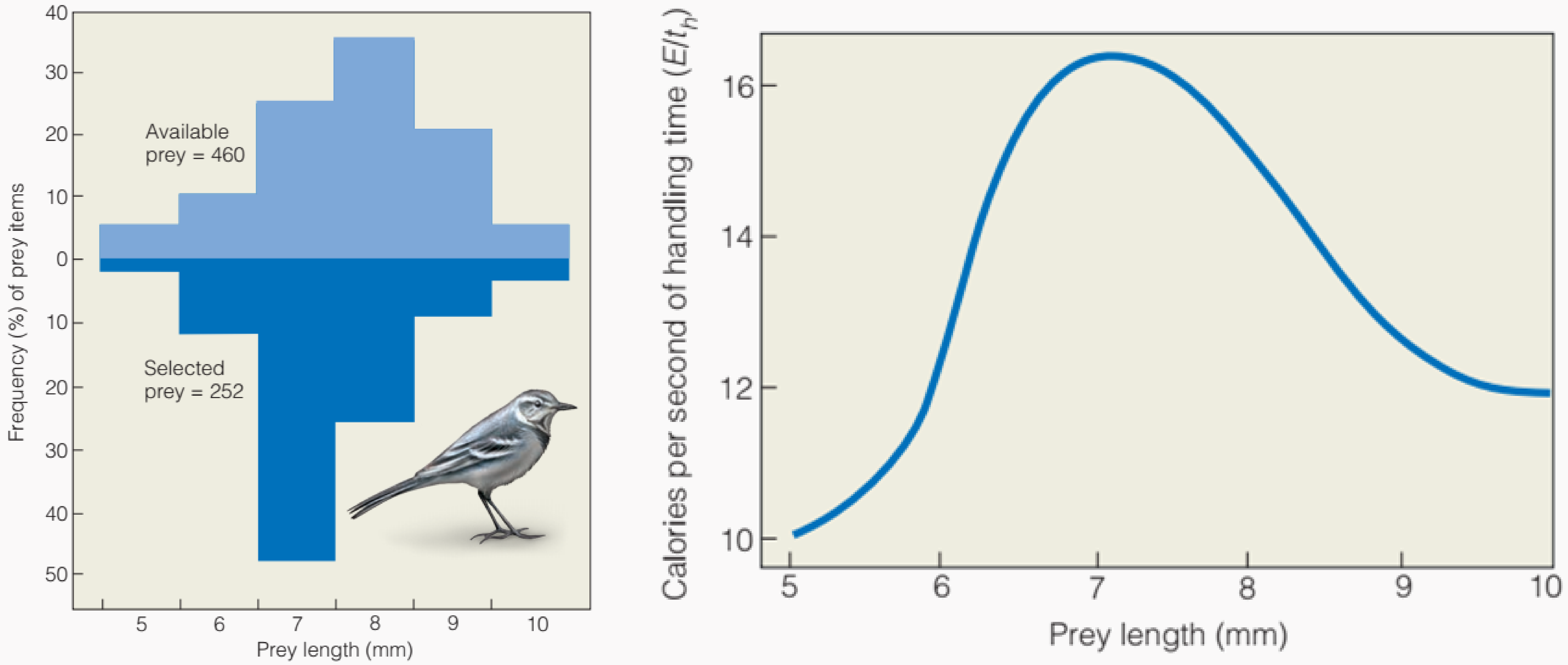
- Influenced by:
  - Climate dynamics;
  - Food availability for the prey species;
  - Other food web dynamics.
- Evolutionary dynamics through an evolutionary “arms race.”
  - A greater hunting efficiency of the predators;
  - Traits that help avoid being eaten in the prey.

Idealized predator-prey coupled dynamics

- Predator-prey relationships are much more complex in real life.
  - Relationships in the food web not only one prey-one predator.
  - The “coupled” nature of the interaction becomes much more vague.
- An increase in prey density OFTEN results in a straight-forward increase in predator population size, **but not always**.
- **REALITY**: prey are variable in value.
  - Choosing prey items that are energetically more “cost-effective” (optimal foraging).

Optimal foraging

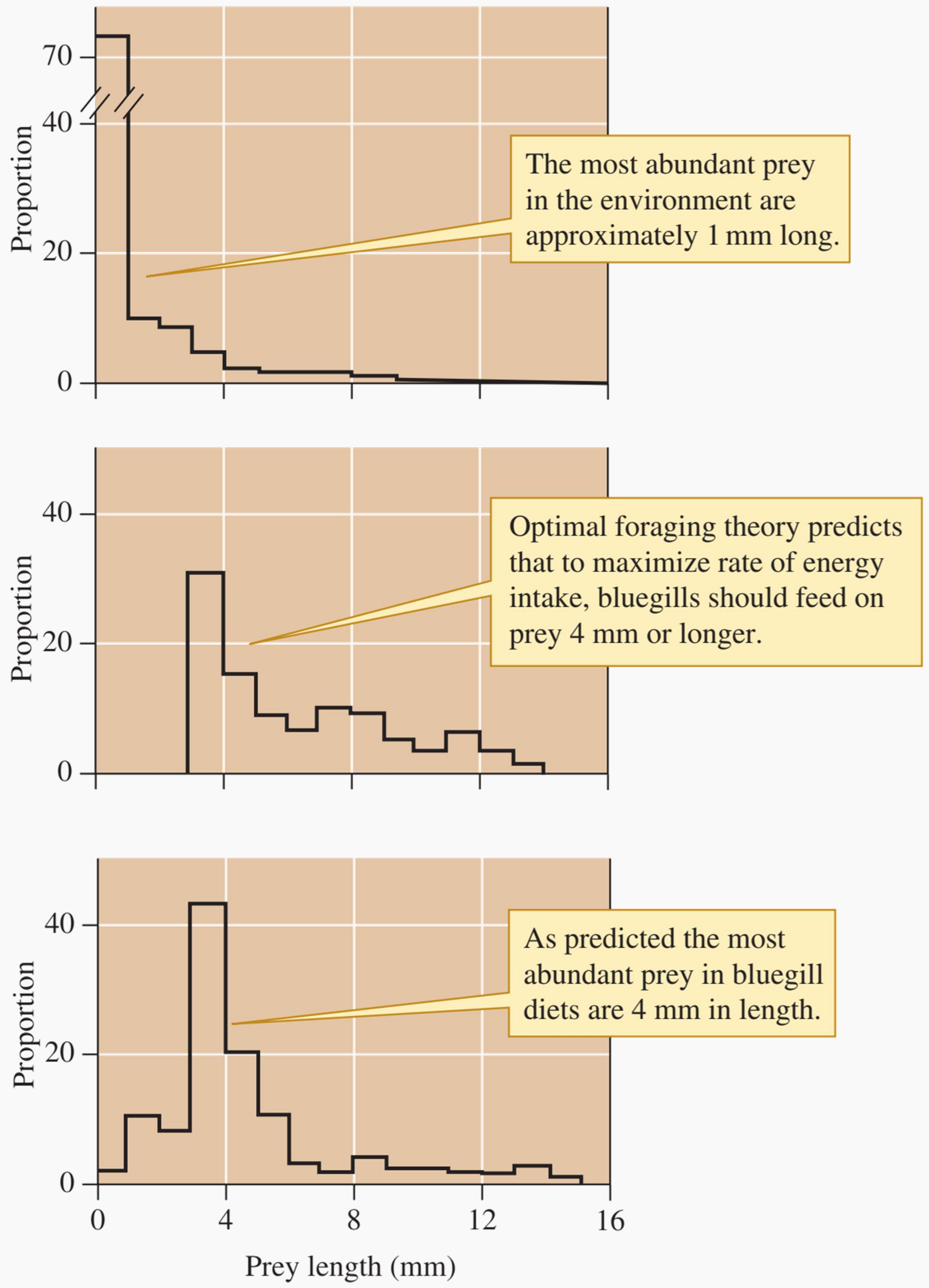
- Foraging involves decisions about the allocation of time and energy.
- Animal adopts a strategy that maximizes fitness,
  - The most energy for the lowest cost.



Medium-sized prey are preferred by pied wagtails.

[Figure 14.14], Smith TM & Smith RL, 2015, Elements of Ecology, 9th ed., Pearson Education Ltd. Used under a Fair Use rationale.

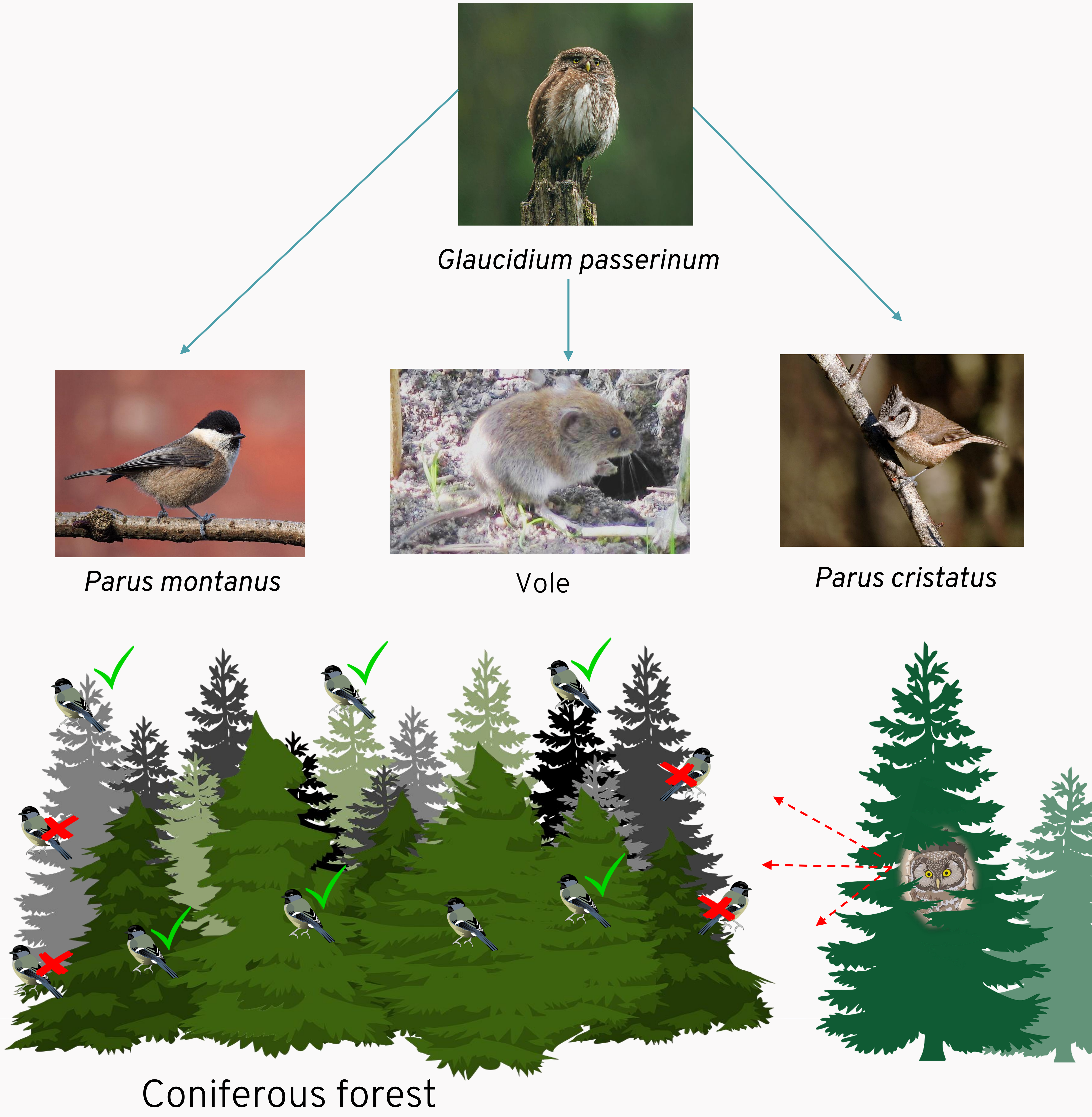
Optimal foraging theory predicts composition of bluegill sunfish diet



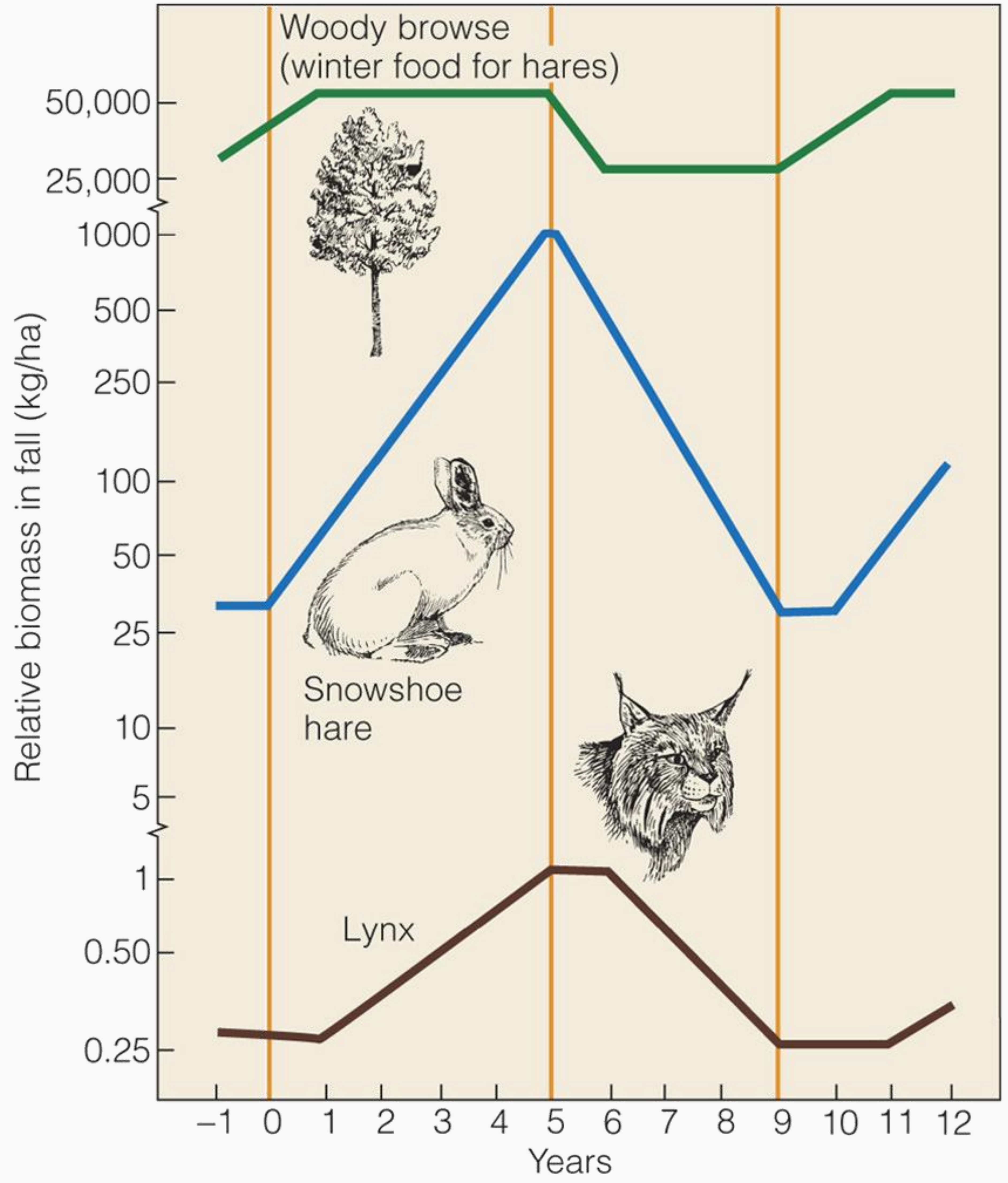
[Figure 7.25], Molles MC Jr., 2016, Ecology: concepts and applications, 7th ed., McGraw-Hill Education. Used under a Fair Use rationale.

Foraging behavior and risk of predation

- The presence of predators affects foraging behavior.
- Predatory species can also face the risk of predation.
  - Foraging profitability and risk of predation vary in different habitats & areas.
- Foraging decision: the balance of a potential energy gains vs predation risk.



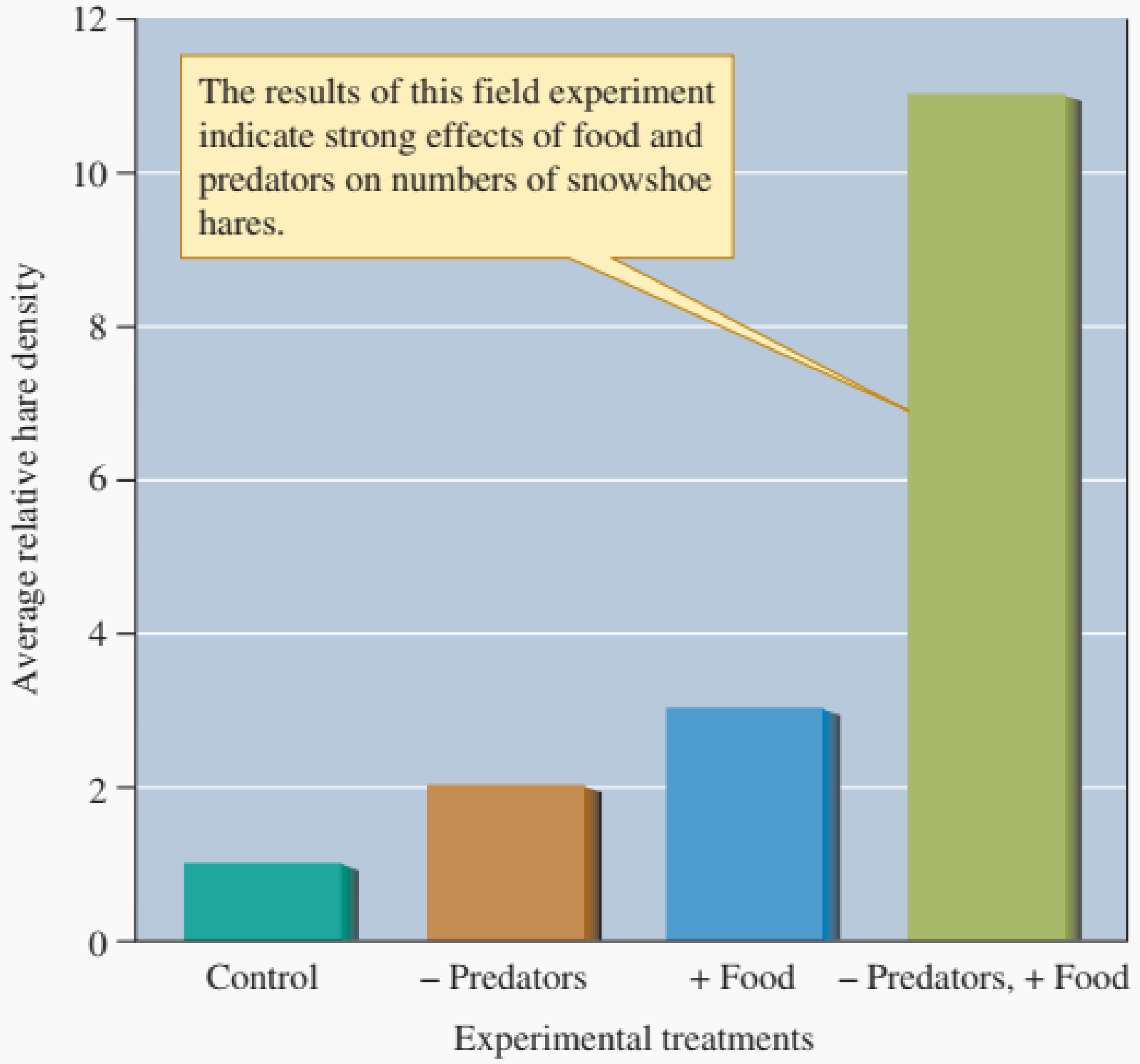
Side impact of predator-prey relationship



- Predator-prey interactions have a wider ecosystem impact.
  - Plants are consumed by herbivores, which in turn are consumed by carnivores.
  - Example: lynx-hares-trees.

The three-way interaction of woody vegetation, snowshoe hare, and lynx.

Krebs et al.'s 8-year experiment (1995) on the impact of food and predation on the densities of snowshoe hares.



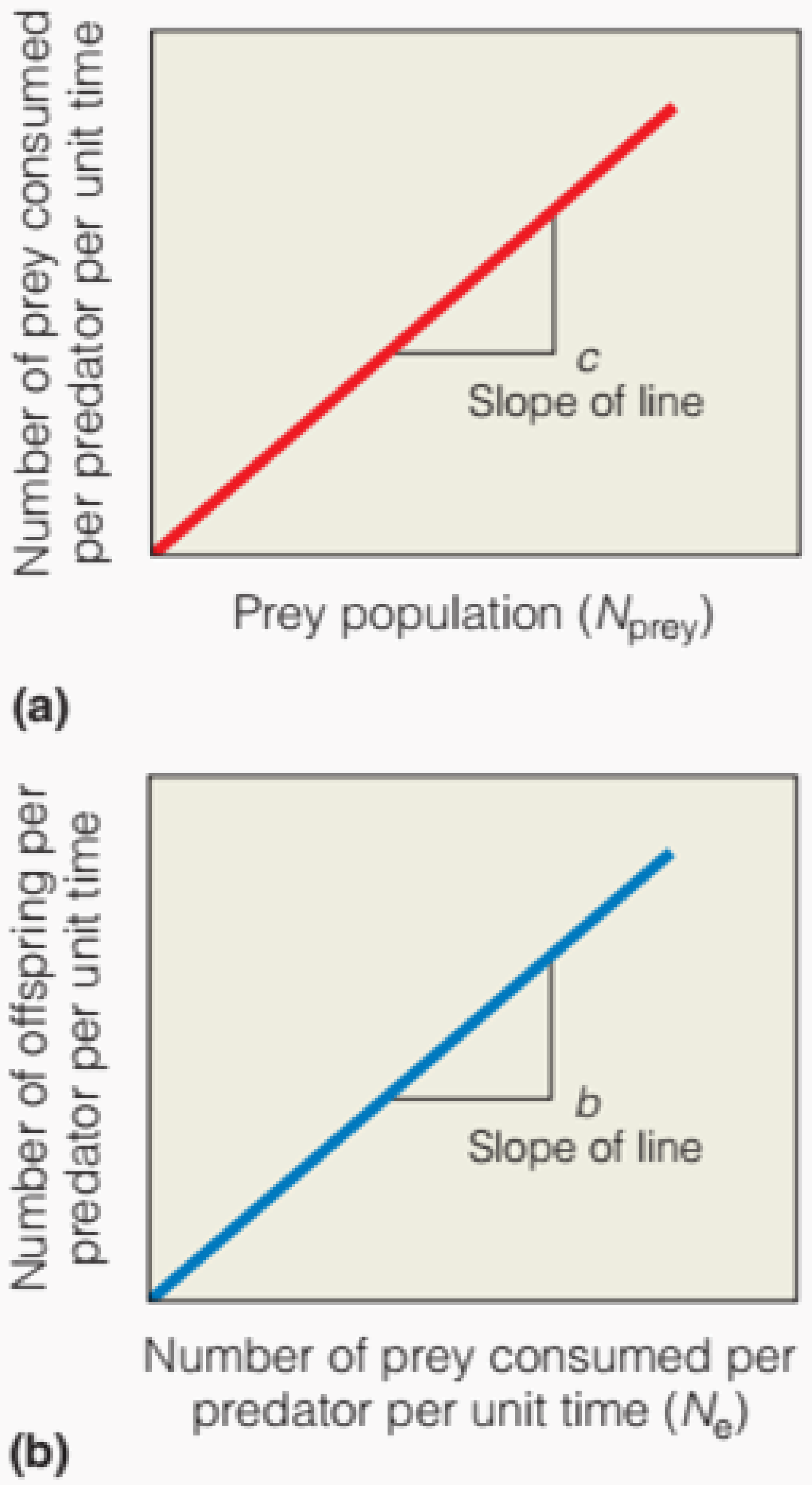
[Figure 14.24], Smith TM & Smith RL, 2015, Elements of Ecology, 9th ed., Pearson Education Ltd. Used under a Fair Use rationale.

[Figure 14.15], Molles MC Jr., 2016, Ecology: concepts and applications, 7th ed., McGraw-Hill Education. Used under a Fair Use rationale.

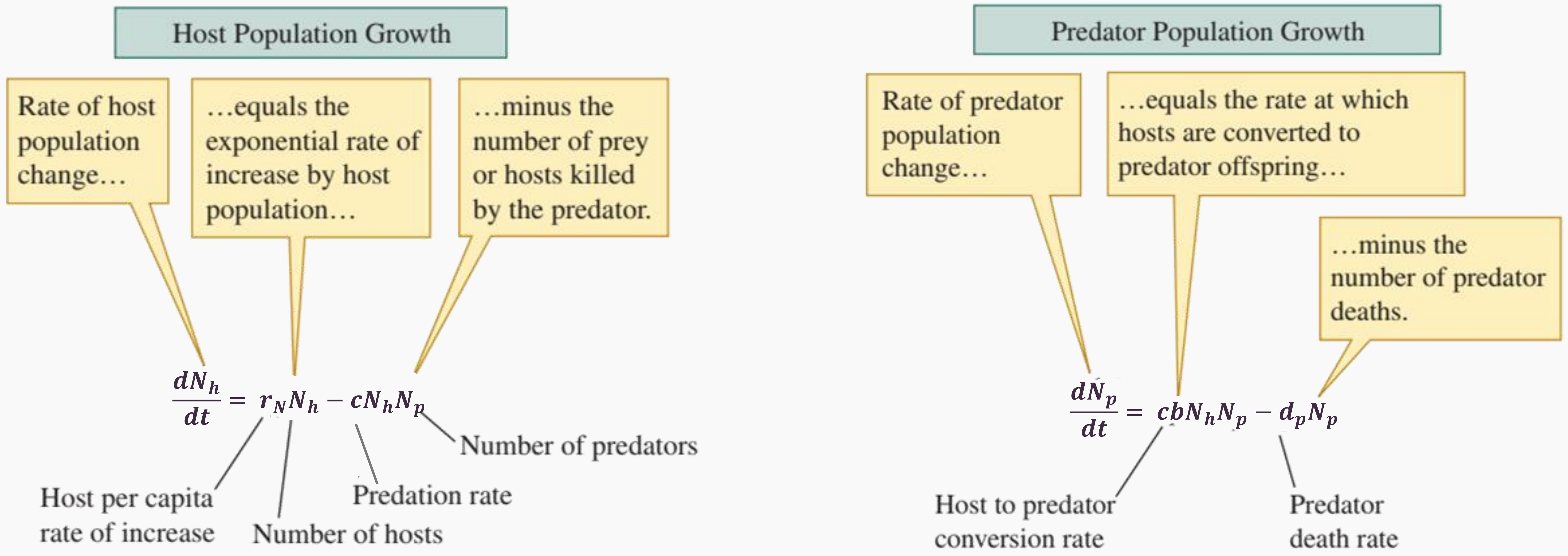
03

PREDATOR-PREY INTERACTION MODELS

Lotka-Volterra predator-prey interaction model

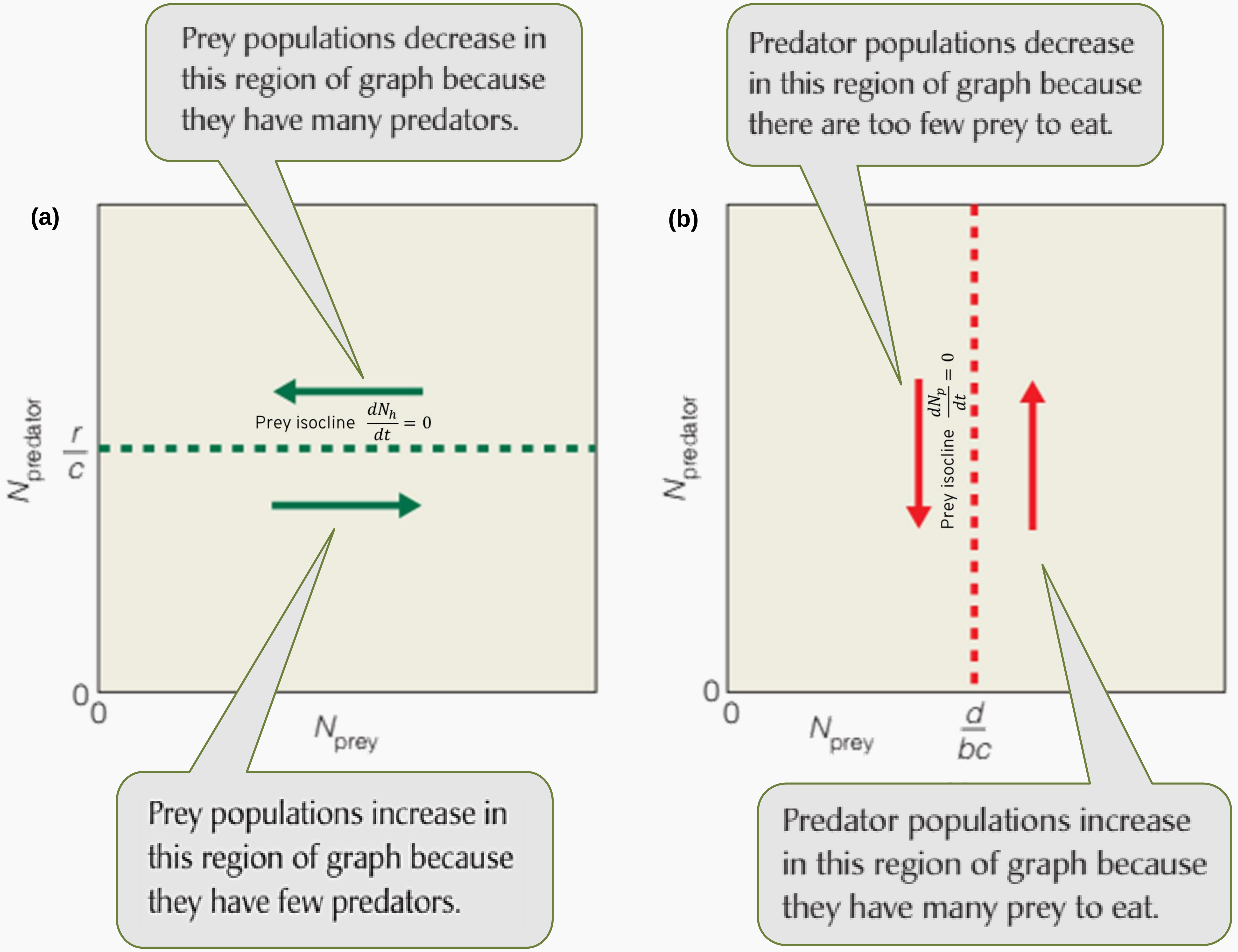


Anatomy of the Lotka-Volterra equations for predator-host population growth ("host" is used in place of "prey" to make meanings of equation terms clear).

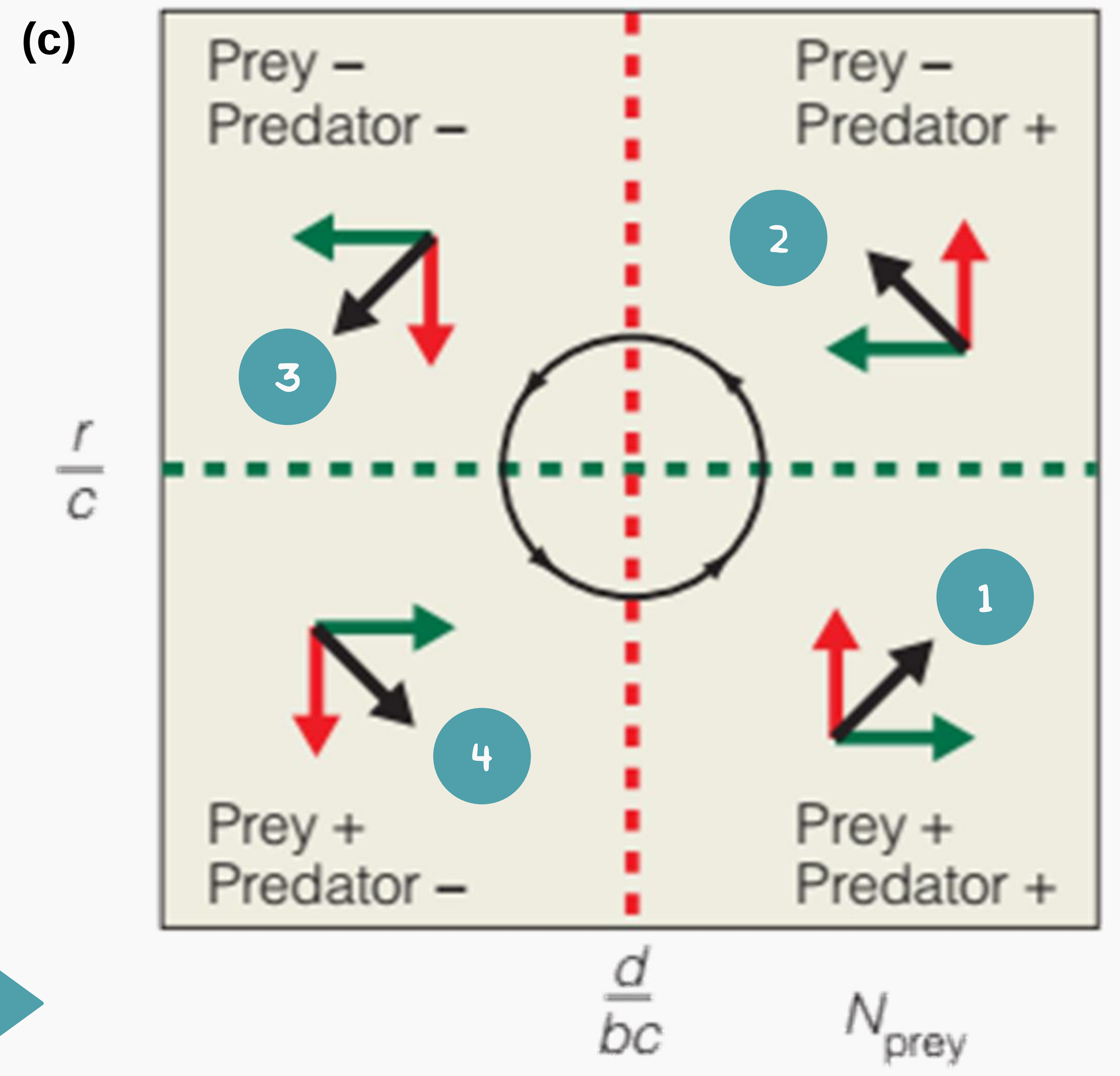


(a) Relationship between prey population and the per capita rate of predation. The slope of the relationship "c" represents the "efficiency of predation." (b) Relationship between the per capita rate of predation and the rate per capita rate or predator reproduction. The slope of the relationship "b" represents the efficiency with which food is converted into predator population growth (reproduction).

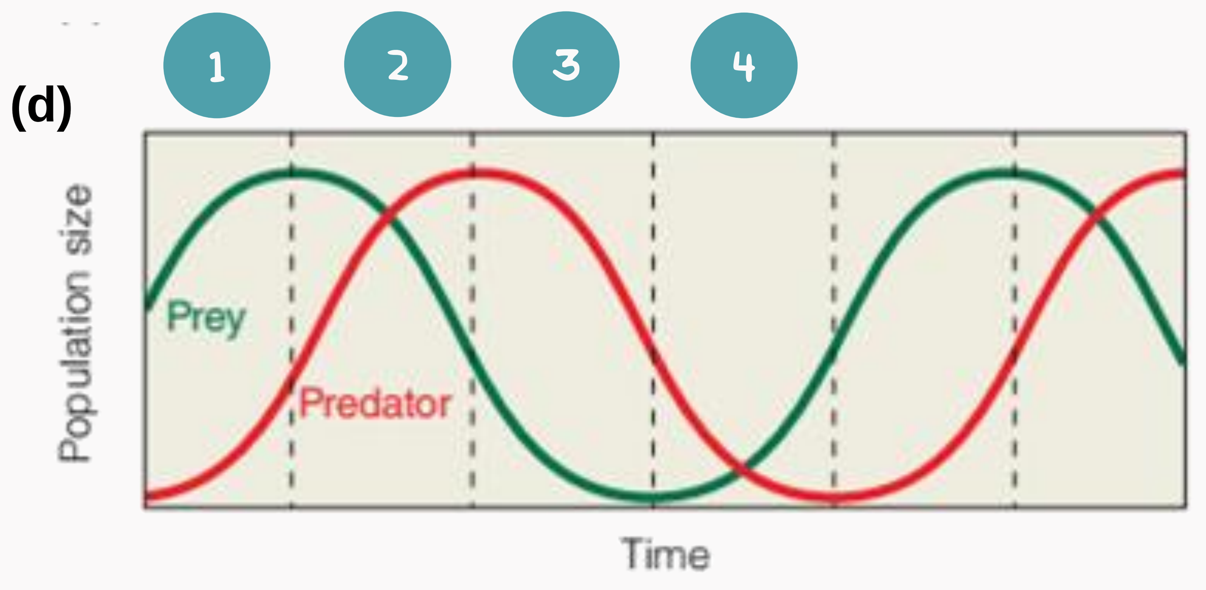
Lotka-Volterra predator-prey interaction model



The equilibrium isoclines for predator and prey populations delineate regions of population increase and decrease. (a) the prey isocline (dN_h/dt = 0 when Np = r/c) separates regions of prey population increase (low predator numbers) and decrease (high predator numbers). (b) the predator isocline (dN_p/dt = 0 when N_h = d/bc) separates regions of predator population increase (high prey numbers) and decrease (low prey numbers).

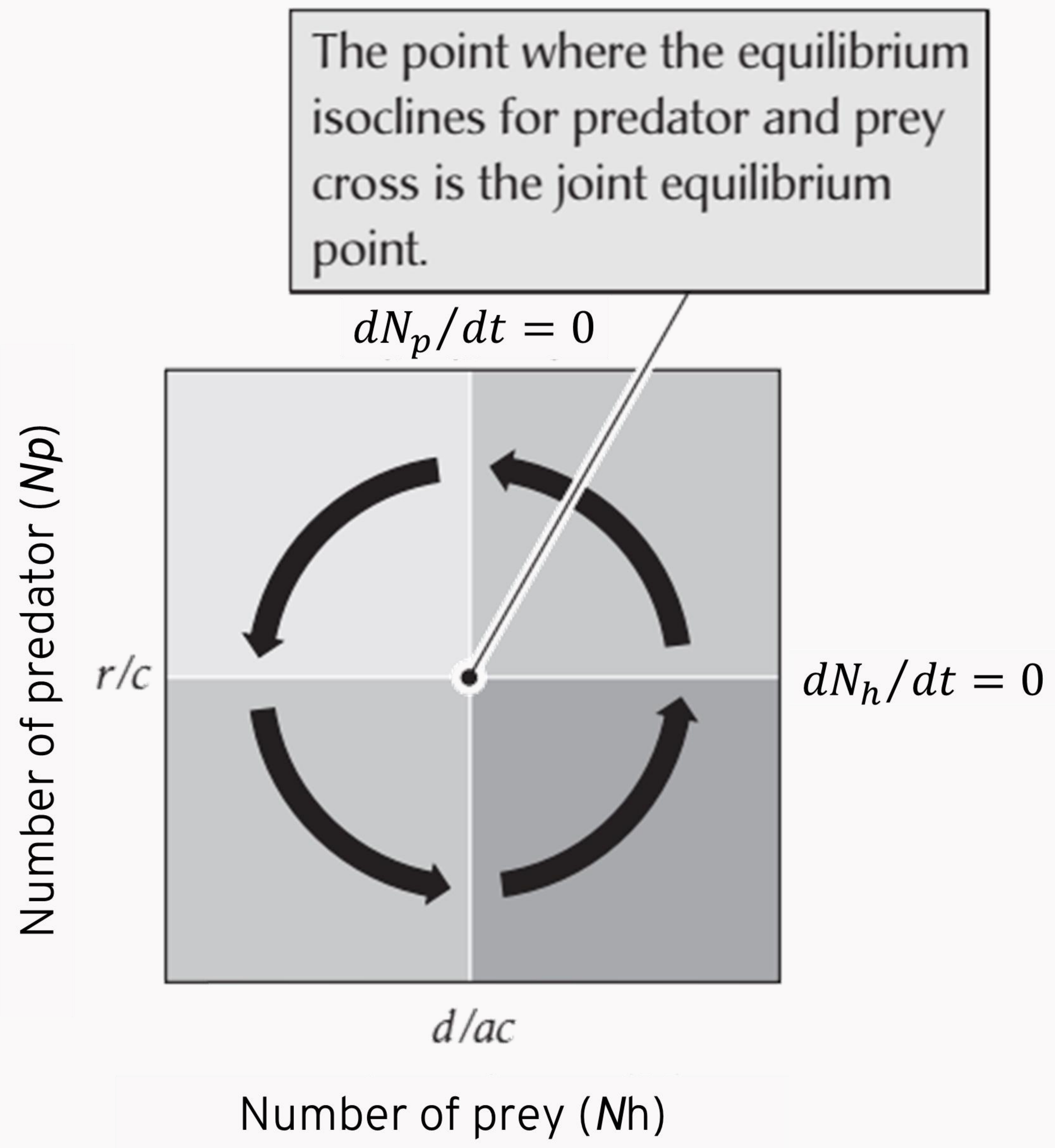


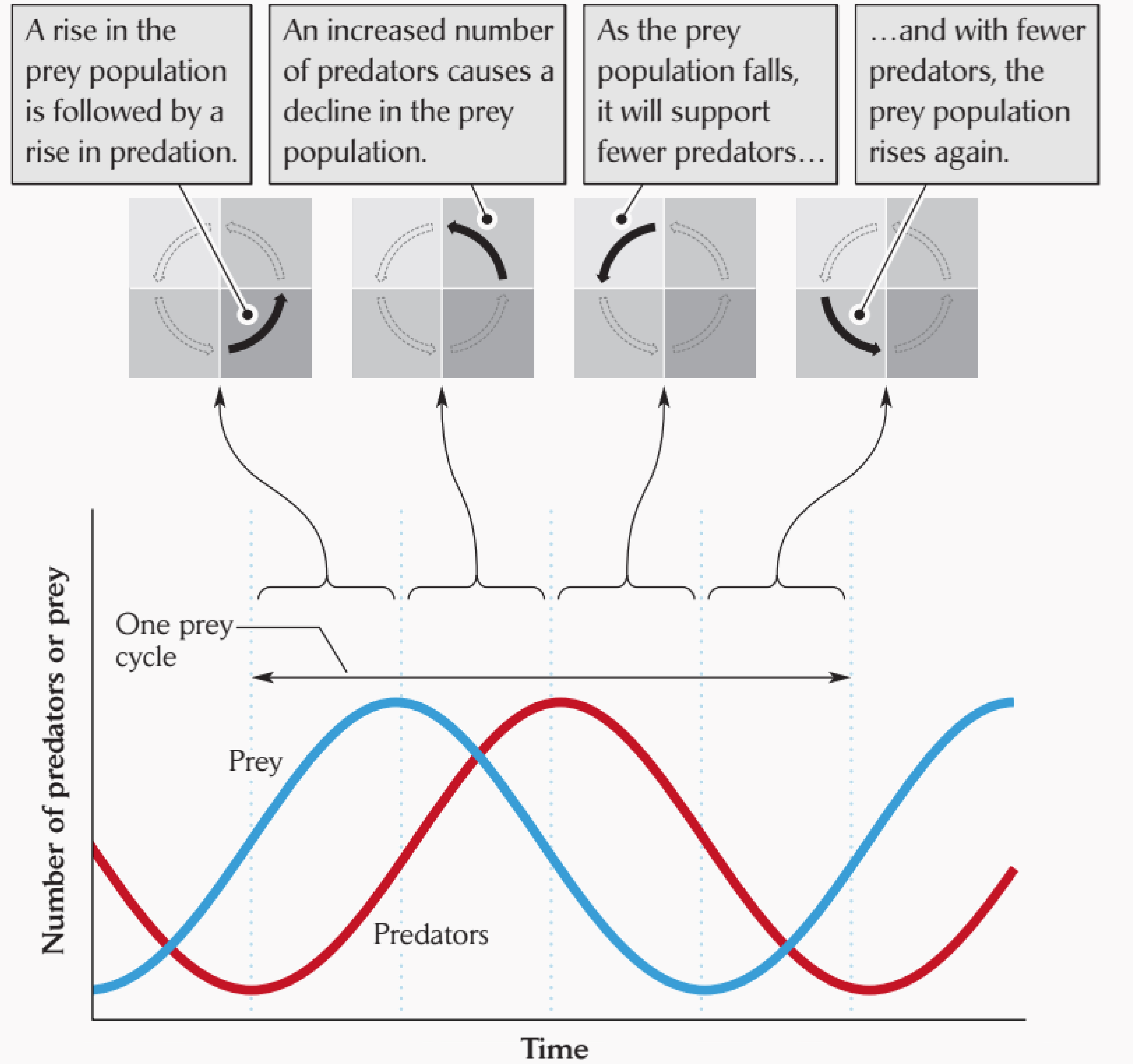
(c) A joint population trajectory combines the individual changes in predator and prey populations. This trajectory shows the cyclic nature of the predator–prey interaction. The black arrows represent the combined population trajectory. A minus sign indicates population decline, and a plus sign indicates population increase. (d) When the changes in size for both the predator and prey populations are plotted through time for each of the four regions of the graph, the two populations continuously cycle out of phase with each other, and the density of predators lags behind that of prey.



Variables: **Np** = number of predators or consumers; **Nh** = number of prey or host; **t** = time; **r** = growth rate of prey; **c** = predator's efficiency at turning food into offspring (conversion efficiency); **b** = the efficiency with which food is converted into predator population growth (reproduction); **d** = predator per capita death rate.

Regular cycling of predator–prey populations





- The Lotka–Volterra model predicts a regular cycling of predator and prey populations.
- The curves show how predator and prey populations continually *cycle out of phase* with each other.

[Figure 15.14 and 15.15, with modifications], Ricklefs RE, 2008, The Economy of Nature. 6th ed. NY: W. H. Freeman and Company. Used under a Fair Use rationale.

Assumptions of the Lotka-Volterra model

- A mutual regulation of predator and prey populations.
- The growth of predator and prey populations is described by $\mathbf{cN_hN_p}$.
  - Regulation of prey's population growth through mortality.
  - Regulation of predator's population growth through reproduction.
- Predator populations do not increase at the same time as the prey, because:
  - Prey grow exponentially in the absence of predators.
  - Predation is directly proportional to the product of prey and predator abundances (random encounters).
  - Predator populations grow based on the number of prey, but death rates are independent of prey abundance.

Simplified assumptions of the model

- No refuges or different habitats for the prey.
- One predator species eating one prey species.
- All predators respond to prey in the same fashion regardless of density.

Neutral stability in the Lotka-Volterra model

- The Lotka–Volterra model is said to exhibit neutral stability.
  - The system stays where it is, until it is perturbed.
  - The model has no intrinsic stabilizing force.
- The model is a set of differential (continuous-time) equations,
  - The populations' responses to change are immediate.
  - Unable to return the system exactly to the joint equilibrium point.
- If written in a difference (discrete-time) equation, introducing response time delays, population cycles would be unstable.

Criticisms of the Lotka-Volterra model

- The model greatly oversimplifies nature.
  - No time delays in the model.
  - No intrinsic stabilizing force.
  - Lack of adequacy in the model (the predation term).
    - The rate at which prey are captured (cN_hN_p) increases in direct proportion to prey density (N_h), implying that predators cannot be satiated.
  - Overemphasizing the mutual regulation of predator and prey populations.
- Predator satiation can stabilize the Lotka-Volterra model.

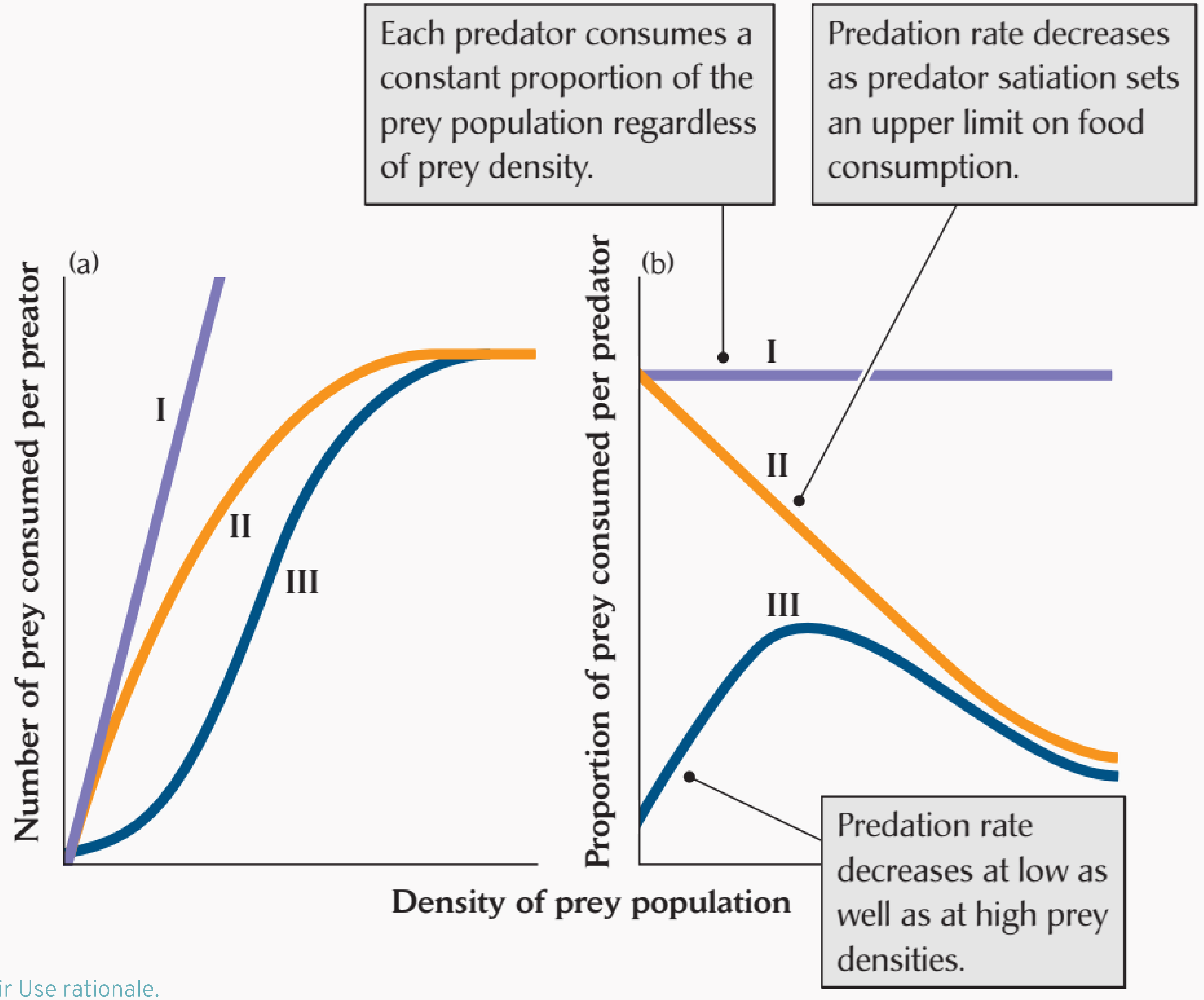
Regulation of the predator population growth

Two responses by the predator to changes in prey population:

1. **Functional response**
   - The relationship between the per capita rate of consumption and the number of prey.
   - Predator population growth depends on the per capita rate at which prey are captured (cN_h).
   - The greater the number of prey, the more the predator eats.
2. **Numerical response**
   - The relationship between the consumption of prey and the predator reproduction.
   - The increased consumption of prey results in an increase in predator reproduction $b(cN_h)$.

Predator's functional response

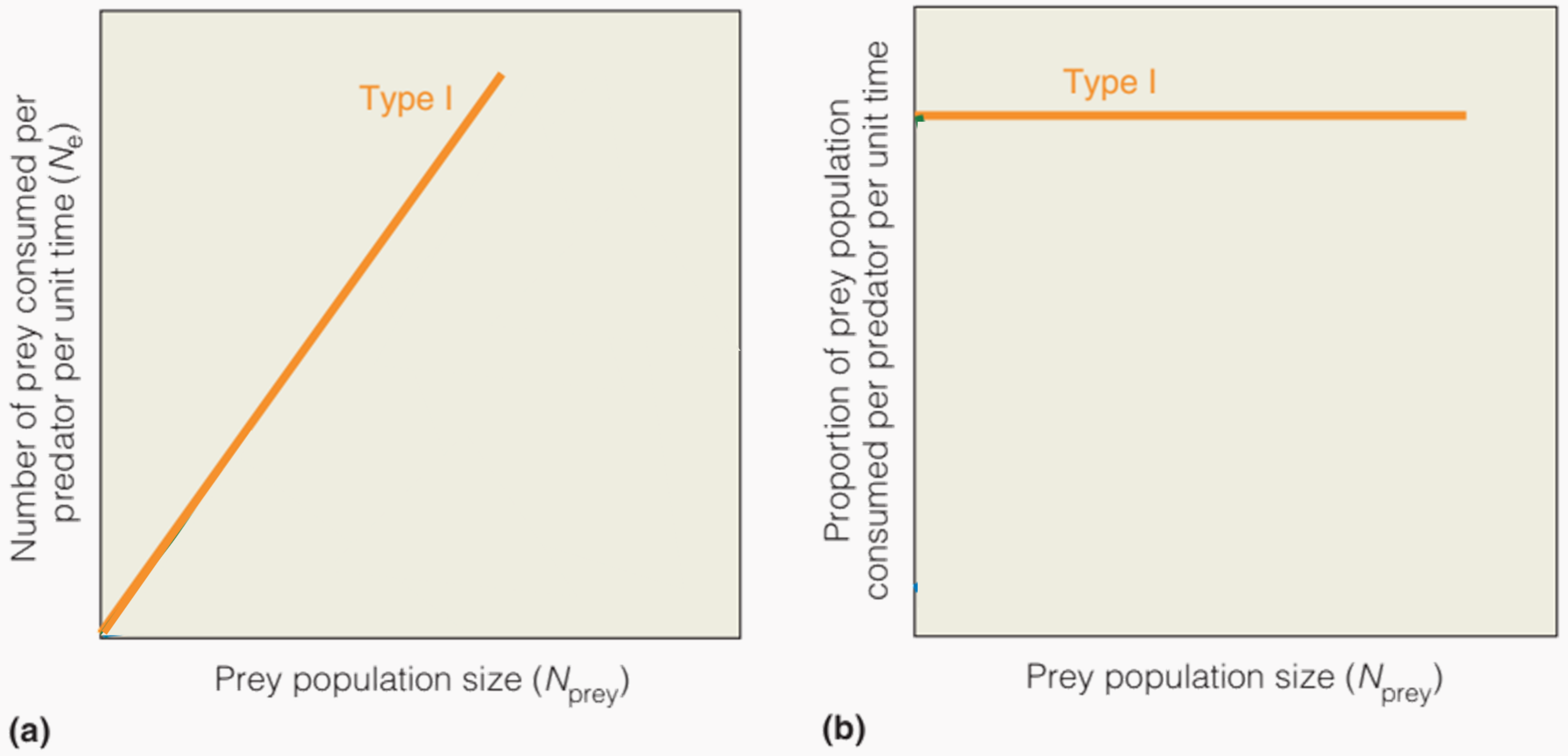
- Three types of functional responses to increasing prey density (developed by C.S. Holling).
  - Type I (Lotka-Volterra model).
  - Type II (modification of type I).
  - Type III (similar to type II).



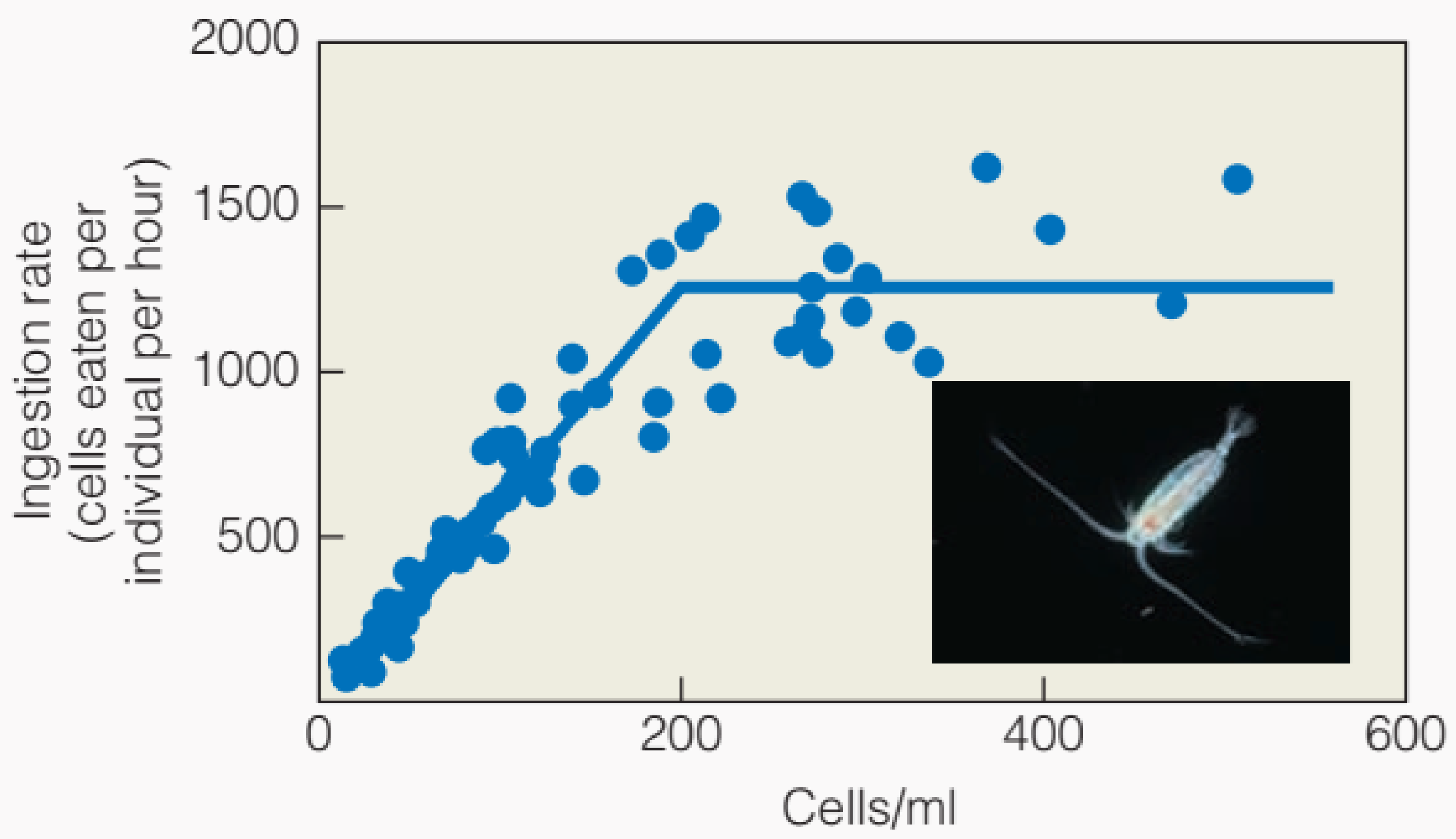
[Figure 15.21], Ricklefs RE, 2008, The Economy of Nature. 6th ed. NY: W. H. Freeman and Company. Used under a Fair Use rationale.

Type I functional response

- N_e increases linearly with increasing N_{prey}.
- The rate of prey mortality as a result of predation is constant, equal to c.
- Limitations:
  - Predators never become satiated.
  - Predators will be limited by the handling time.



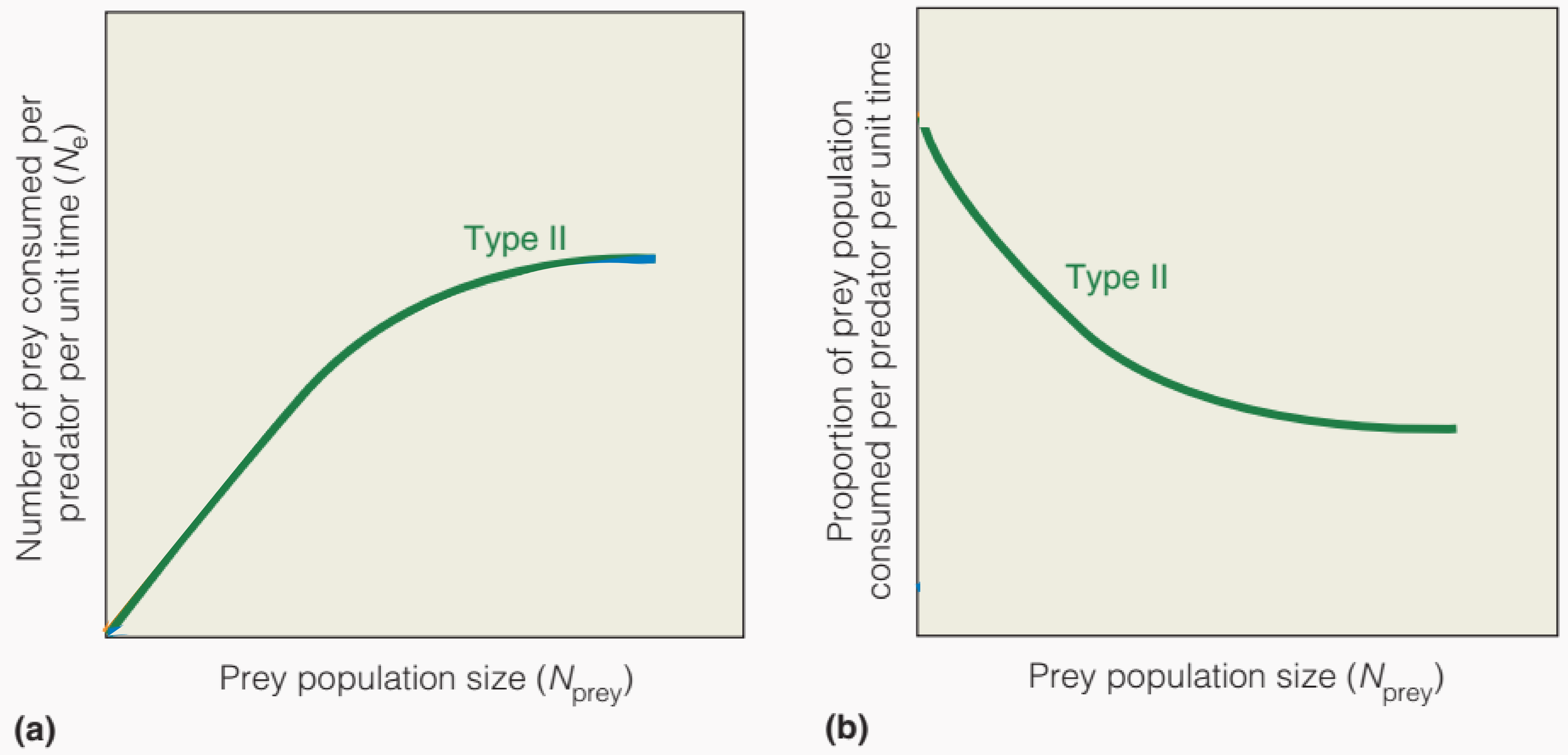
Type I functional response of the marine copepod *Calanus* (zooplankton filter feeder) feeding on *Coscinodiscus angstii*



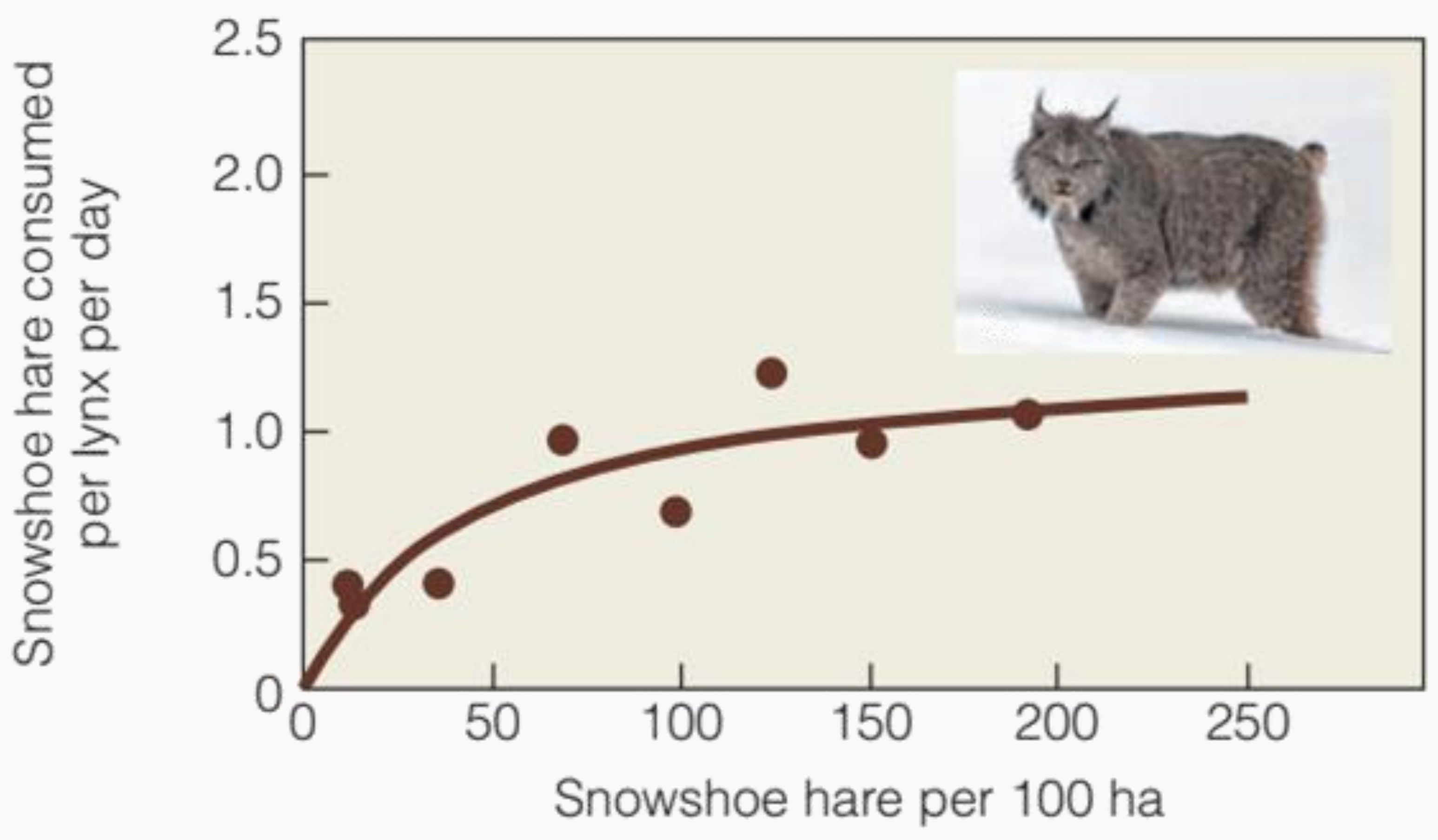
[Figure 14.6 (modified) and 14.7a], Smith TM & Smith RL, 2015, Elements of Ecology, 9th ed., Pearson Education Ltd. Used under a Fair Use rationale.

Type II functional response

- Adding the constraint of handling time.
- Ne increases in a decelerating fashion.
- Declining mortality rate of prey with increasing prey density.
- Related to the predator's time budget.
  - At high prey density, the search time ~0, using all of time handling prey.



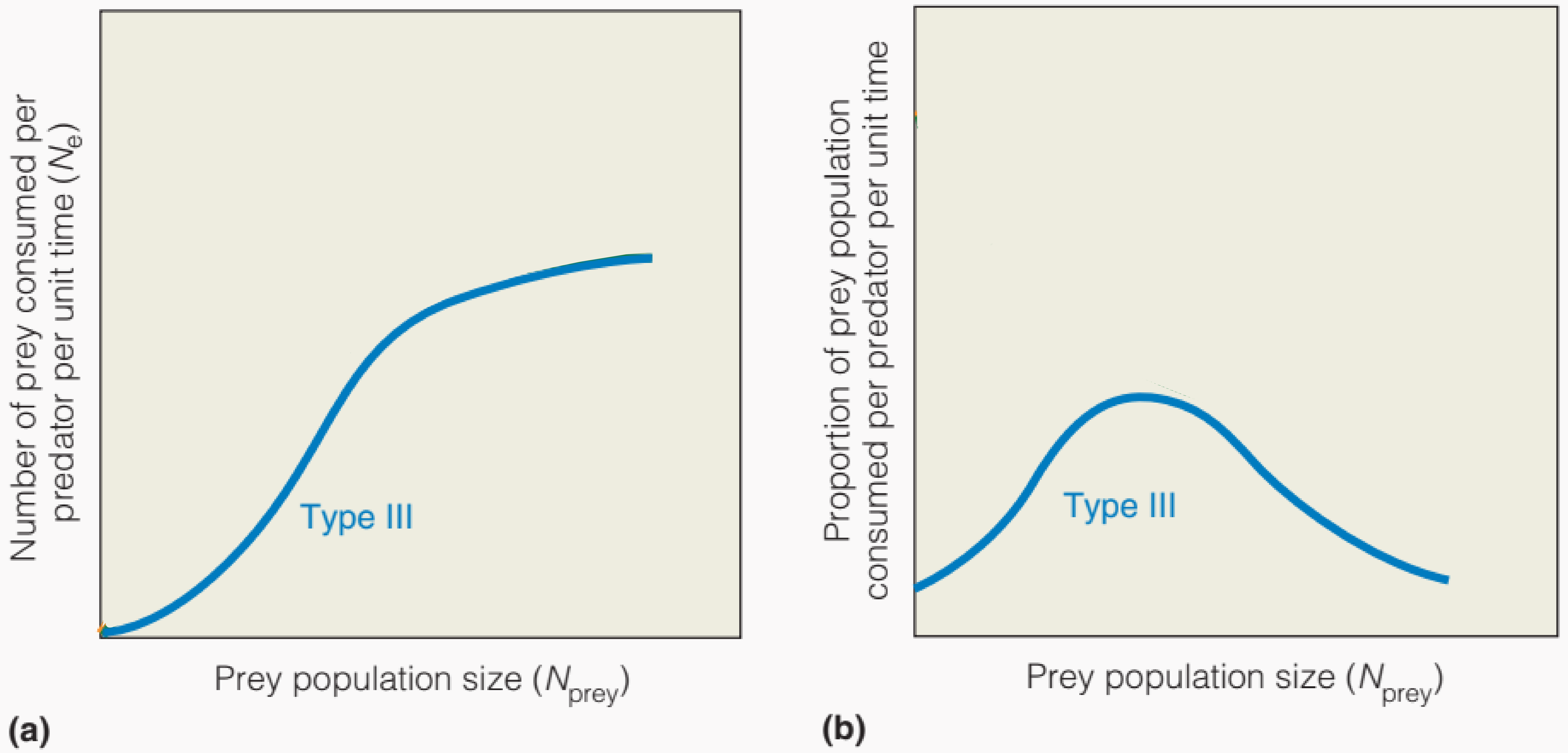
Type II functional response of Canadian lynx (*Lynx canadensis*) feeding on snowshoe hare (*Lepus americanus*) at a site in the southwest Yukon Territory, Canada



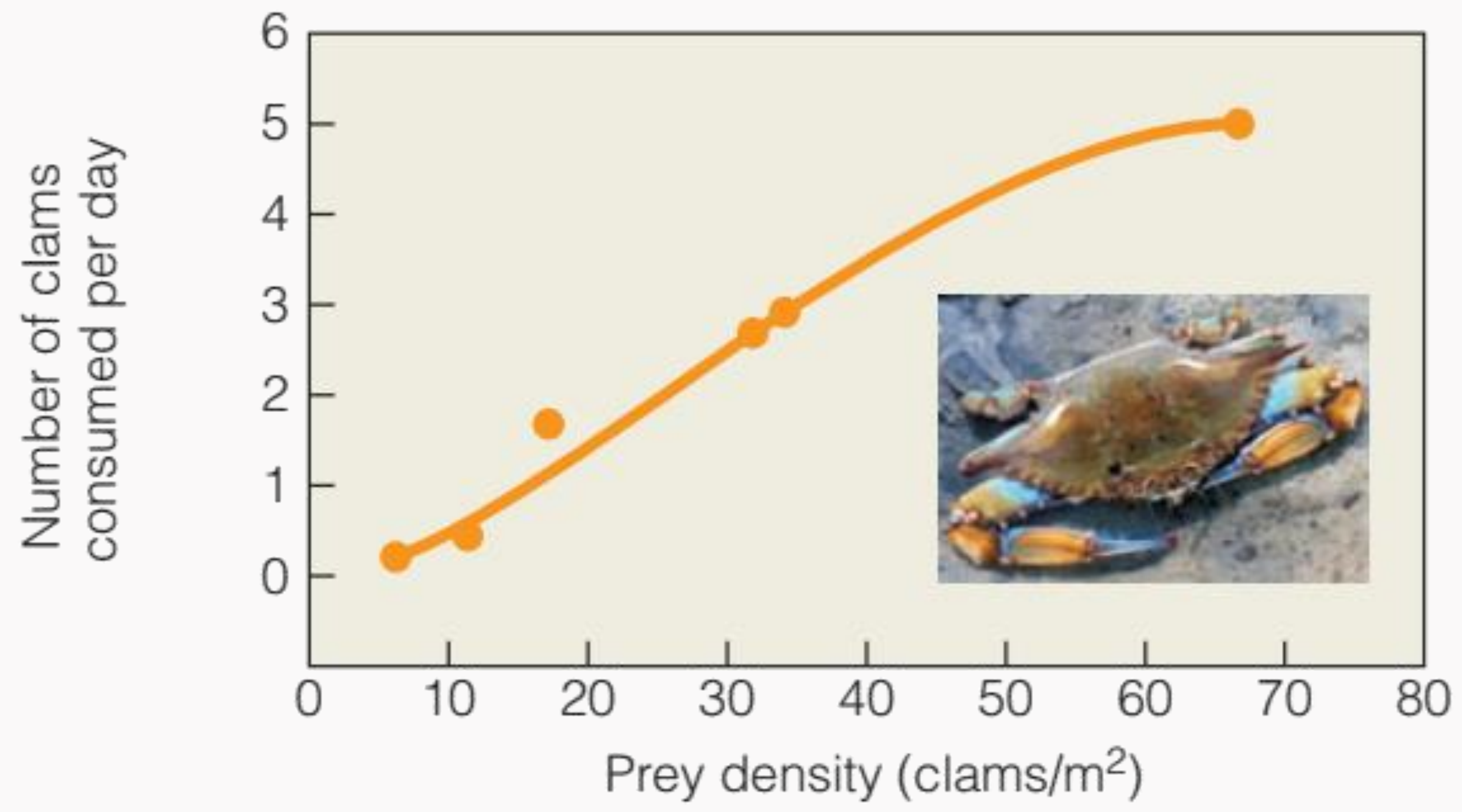
[Figure 14.6 (modified) and 14.7b], Smith TM & Smith RL, 2015, Elements of Ecology, 9th ed., Pearson Education Ltd. Used under a Fair Use rationale.

Type III functional response

- Similar to Type II, but prey consumption rate is low at first, increasing in an S-shape.
- Mortality of the prey is low at low prey abundance, increases as the prey population increases (density dependent).
- Factors caused the S-shape response
  1. Availability of cover to escape the predators.
  2. Prey switching.
  3. Predator's search image



Type III functional response of blue crabs (*Callinectes sapidus*) feeding on the clam (*Mya arenaria*)



[Figure 14.6 (modified) and 14.7c], Smith TM & Smith RL, 2015, Elements of Ecology, 9th ed., Pearson Education Ltd. Used under a Fair Use rationale.

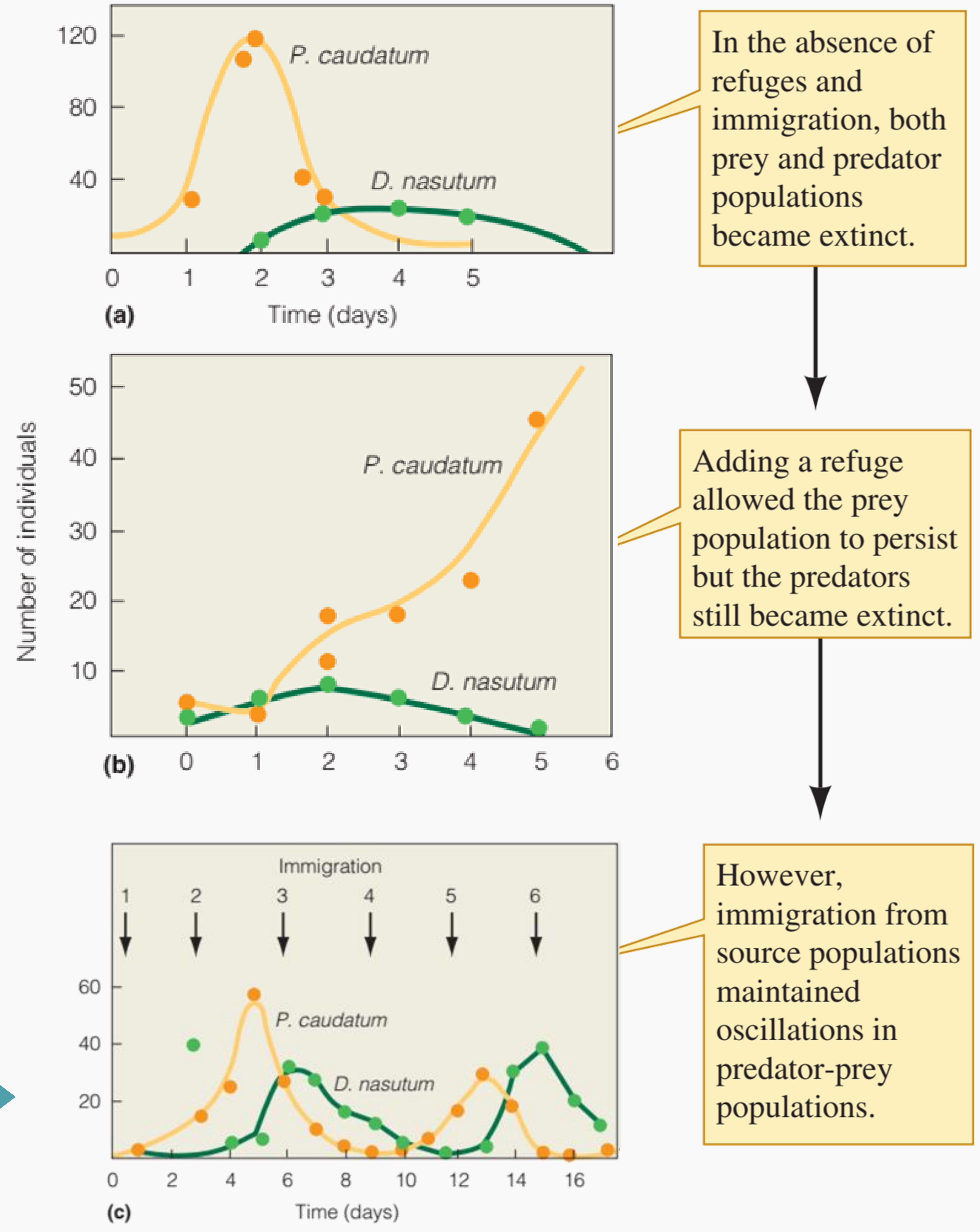
Refugia and dispersal: Gause's experiment

- Experiment on population cycles between *Paramecium* (prey) and *Didinium* (predator) in a microcosm experiment.
  - **Phase 1:** *Didinium* quickly consumed all the *Paramecium* and then went extinct.
  - **Phase 2:** Addition of sediment in the bottom, acting as a refugium.
    - *Paramecium* was able to hide; *Didinium* went extinct and *Paramecium* population recovered.
- Dispersal of prey away from predators can prevent prey extinction.

Gause's experiment:
Didinium vs *Paramaecium*

- *Didinium nasutum* (Ciliata) as the predator, *Paramaecium caudatum* as the prey.
- Predator-prey oscillations could only be maintained, when the microcosm was periodically restocked with both species.
- The system had to include a refuge for the prey and a reservoir for the predator.

Outcome of Gause's experiments of predator–prey interactions between the protozoans *Paramecium caudatum* and *Didinium nasutum* in three microcosms: (a) oat medium without sediment, (b) oat medium with sediment, and (c) with immigration. (Data from Gause 1934.)



Combination and modification of:
[Figure 14.19], Molles MC Jr., 2016, Ecology: concepts and applications, 7th ed., McGraw-Hill Education.
[Figure 14.4], Smith TM & Smith RL, 2015, Elements of Ecology, 9th ed., Pearson Education Ltd.
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Refugia and dispersal: Huffaker's experiment

- Reproduction of Gause's experiment, without restocking.
  - The predator and prey are responsible for their own immigration and emigration.
- Prey species: the sixspotted mite *Eotetranychus sexmaculatus.*
- Predator: predatory mite *Typhlodromus occidentalis.*

Eotetranychus sexmaculatus (© DPIRD), Fair Use.

Typhlodromus occidentalis (© Arlo Pelegrin), NC.

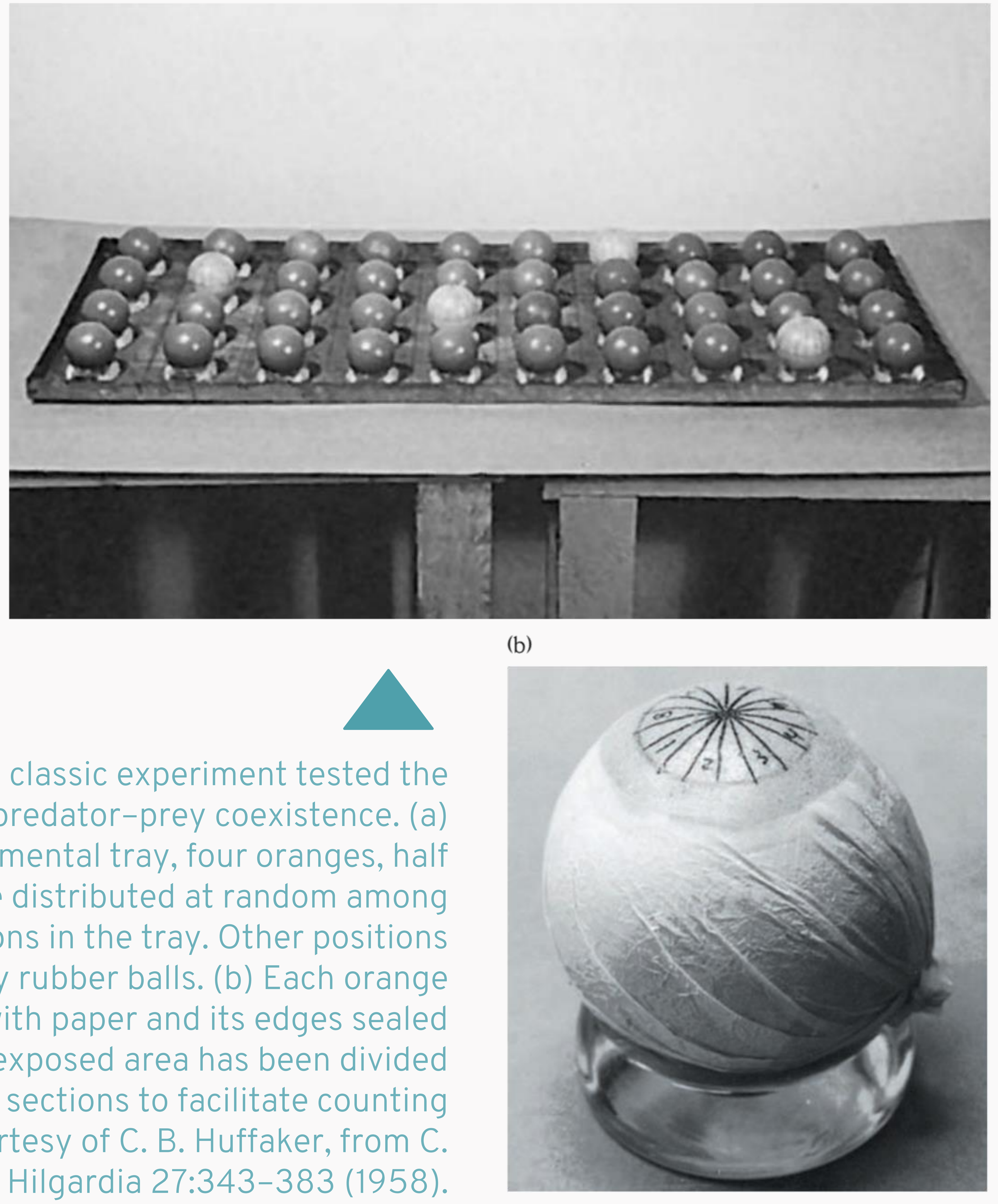
Huffaker's initial experiments results

Universe: 40-oranges tray setup

- Did not produce predator-prey oscillations.
- Predators drove prey extinct then went extinct themselves.
- However, the distribution of the exposed areas of the oranges influenced the course of extinction.
- The survival of the prey could be prolonged by providing it with remote areas of suitable habitat.

(a)

(b)



C. B. Huffaker's classic experiment tested the parameters of predator–prey coexistence. (a) In each experimental tray, four oranges, half exposed, are distributed at random among the 40 positions in the tray. Other positions are occupied by rubber balls. (b) Each orange is wrapped with paper and its edges sealed with wax. the exposed area has been divided into numbered sections to facilitate counting the mites. Courtesy of C. B. Huffaker, from C. B. Huffaker, Hilgardia 27:343–383 (1958).

[Figure 15.11], Ricklefs RE, 2008, The Economy of Nature. 6th ed. NY: W. H. Freeman and Company. Used under a Fair Use rationale.

Huffaker's subsequent experiments results

The Huffaker's 120-oranges tray experiments. The environment was more spatially complex and barriers (petroleum jelly around oranges) were introduced to slow the predator's dispersal. The shaded boxes show the positions and relative densities of Huffaker's mites in the trays at the eight times indicated. From C. B. Huffaker, Hilgardia 27:343–383 (1958).

[Figure 15.12], Ricklefs RE, 2008, The Economy of Nature. 6th ed. NY: W. H. Freeman and Company. Used under a Fair Use rationale..

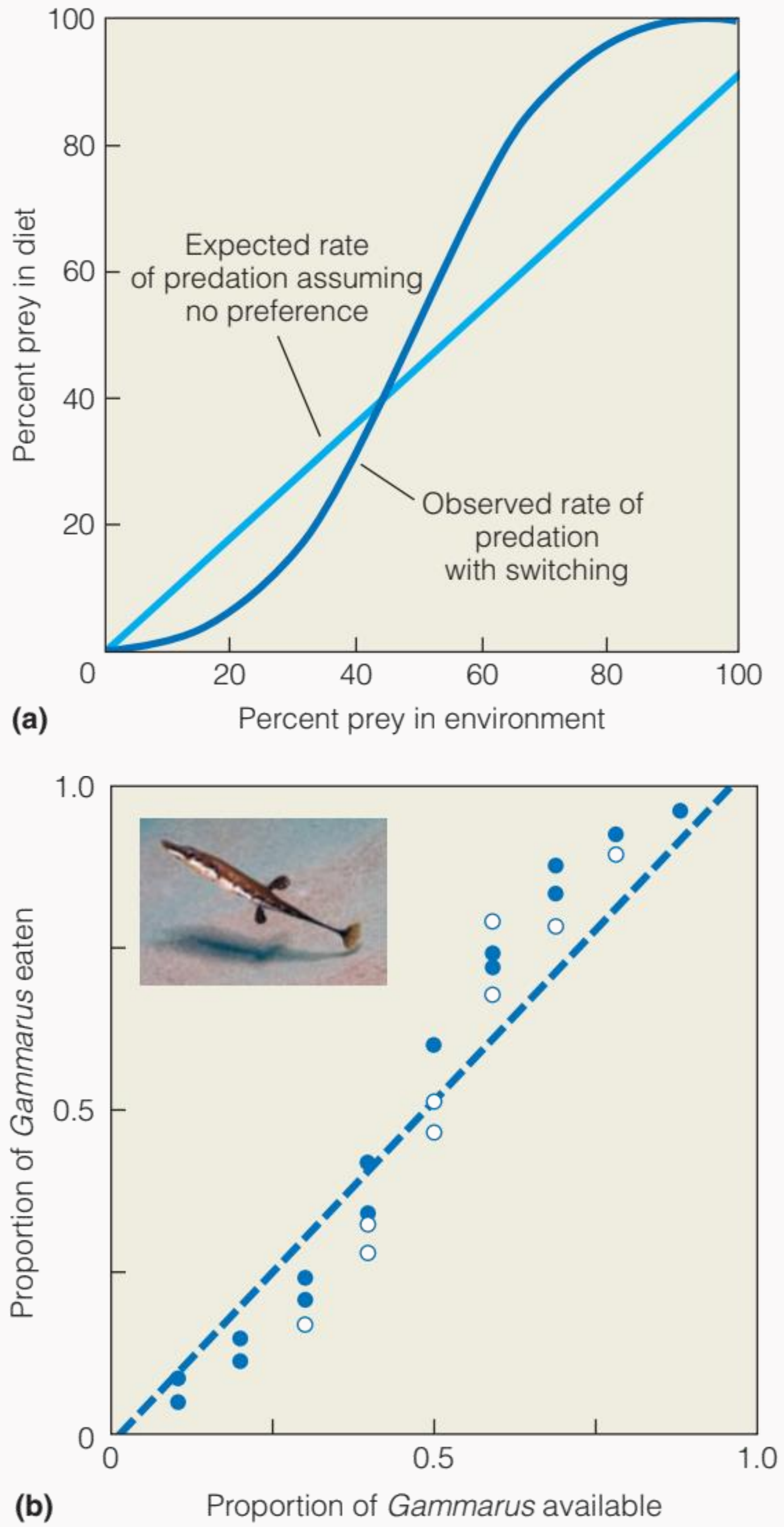
Huffaker's subsequent experiments results

Universe: 120-oranges tray setup

- Three predator-prey oscillations occurred over the 8-months experiment.
  - Maintained by the dispersal of predator and prey among oranges as "refugia".
- Refuges from predation allow predator and prey to coexist.
  - A spatial mosaic of suitable habitats could enable predator and prey populations to coexist through time.
- Two kinds of time delays:
  - Slow dispersal of predators between food patches.
  - Time needed for predator numbers to increase.

Prey switching

- Predator feeds heavily on the more abundant species, less attention to the less ones.
- Switching when the relative abundance of the second prey species increases, and vice versa.
- When does a predator switch prey?
  - Depends considerably on the predator's food preference (palatability vs quantity).

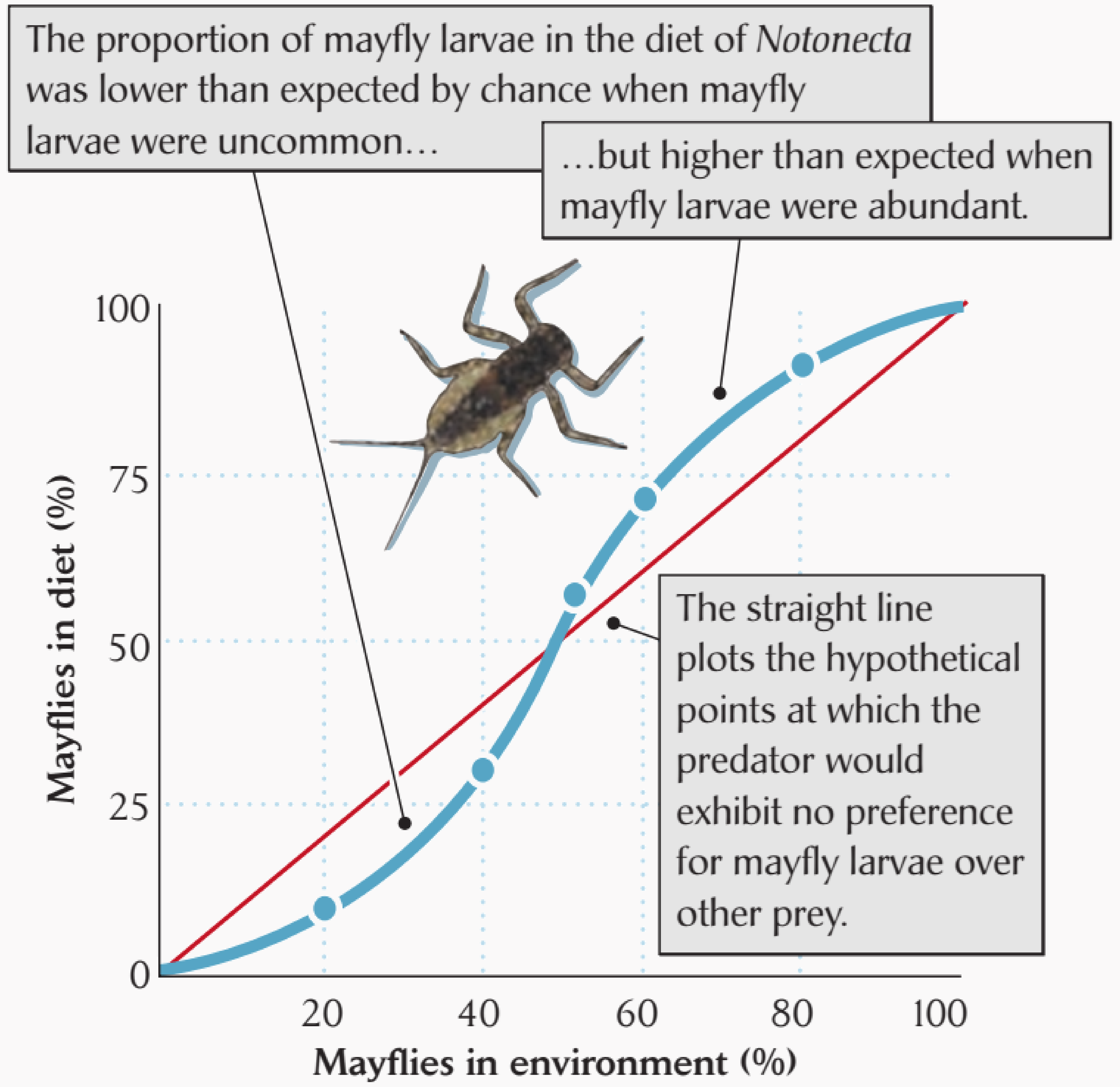


(a) A model of prey switching. The straight line represents the expected rate of predation assuming no preference by the predator. The prey are eaten in a fixed proportion to their relative availability (percentage of total prey available to predator in environment). The habit of prey switching results in a Type III functional response between a predator and its prey species. (b) Example of frequency-dependent predation (prey switching) by sticklebacks (Spinachia spinachia) fed on mixtures of Gammarus and Artemia. Proportion of Gammarus in the diet is plotted as a function of the proportion available. Dotted line represents frequency-independent predation. Closed symbols denote trials with increasing availability of Gammarus, open symbols decreasing availability of Gammarus prey. (Hughes and Croy 1993.)

[Figure 14.9], Smith TM & Smith RL, 2015, Elements of Ecology, 9th ed., Pearson Education Ltd. Used under a Fair Use rationale.

Prey switching

- Predatory water bug *Notonecta glauca* vs two types of prey, isopods and mayfly larvae.
- No innate preference for either type of prey, only a preference for the more abundant one.
- Attack success higher in prey greater densities.

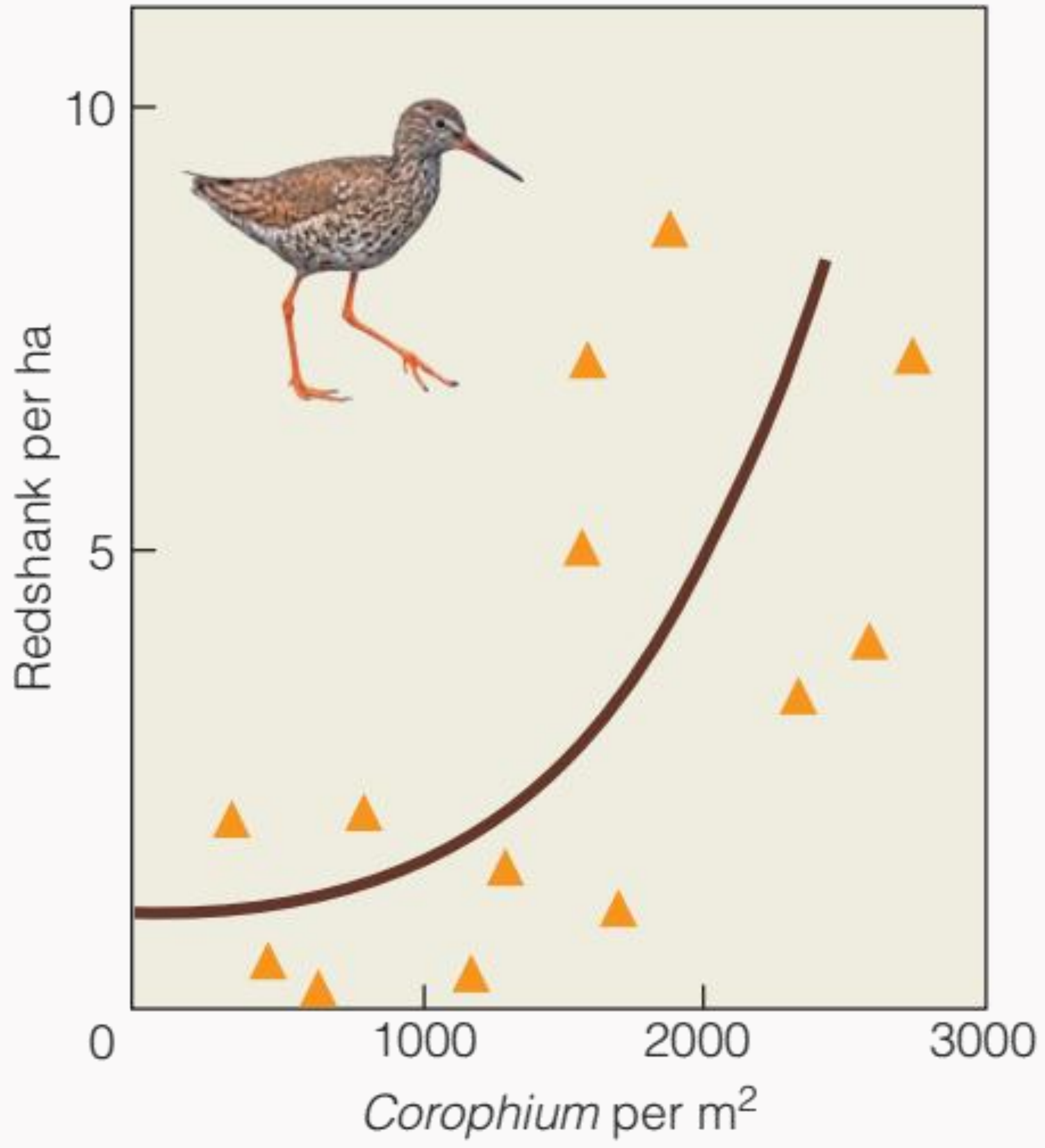


The predatory water bug *Notonecta glauca* switches to different prey in response to fluctuations in prey density (isopods or mayfly larvae).

[Figure 15.22], Ricklefs RE, 2008, The Economy of Nature. 6th ed. NY: W. H. Freeman and Company. Used under a Fair Use rationale.

Predator's numerical response

- Predators can increase their consumption only to the point of satiation.
- Afterwards, predators respond numerically with a population increase.
  - By immigration ("aggregative response").
  - By population growth (slower than prey).



Aggregative response in the redshank (*Tringa totanus*). The curve plots the density of the redshank in relation to the average density of its arthropod prey (*Corophium* spp.). (Data from Hassel and May 1974.)

[Figure 14.10], Smith TM & Smith RL, 2015, Elements of Ecology, 9th ed., Pearson Education Ltd.
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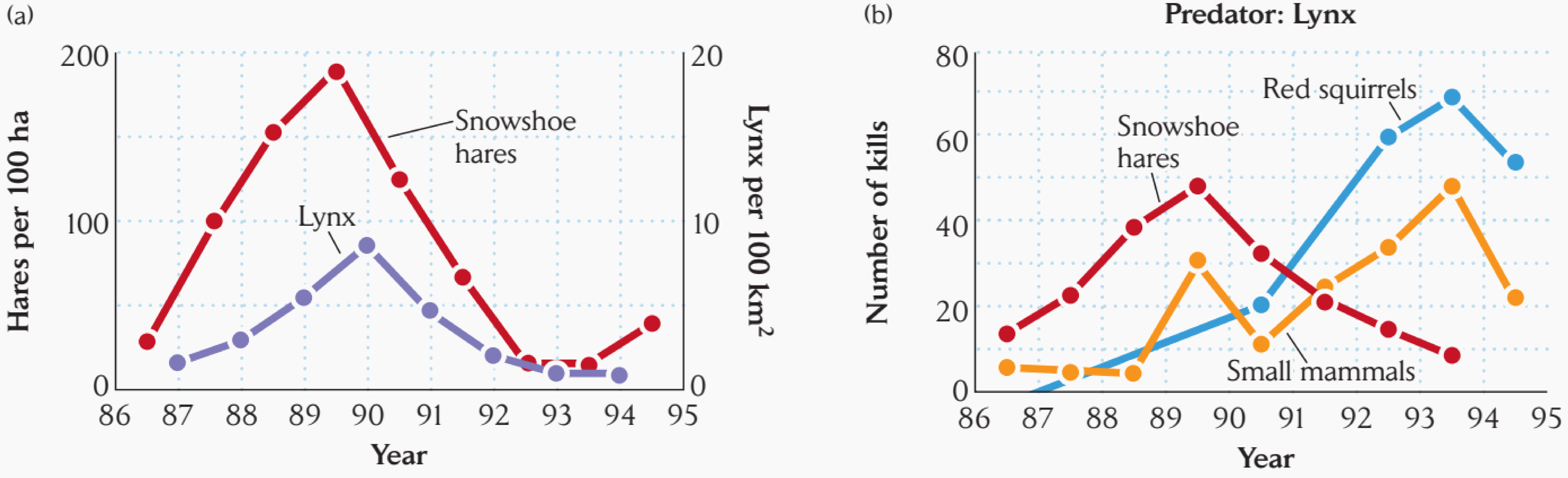
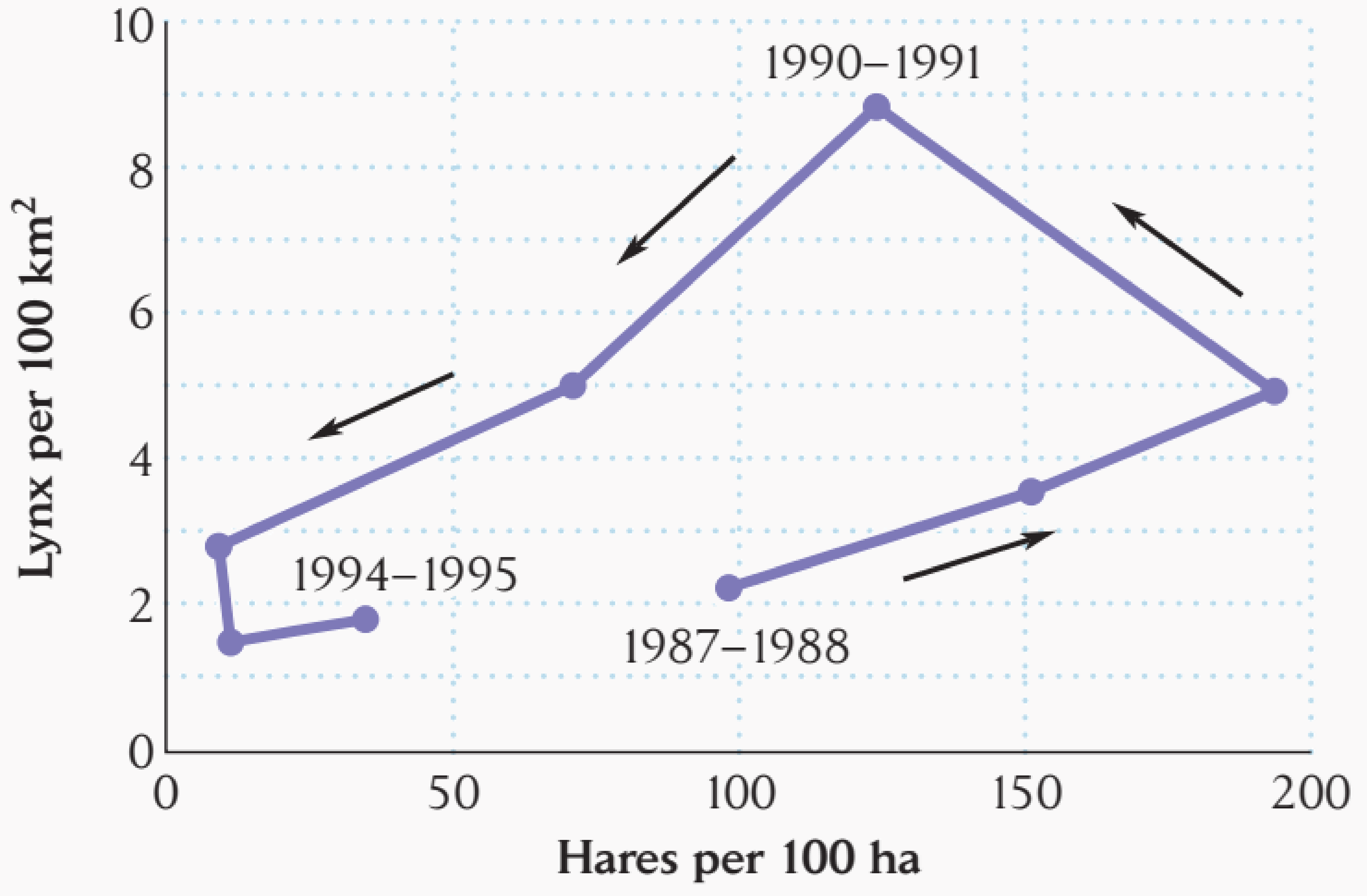
Numerical response: Lynx and snowshoe hare.



Numerical response to changes in prey density. (a) In southern Yukon, the population densities of lynx closely tracked those of their preferred prey, snowshoe hares, through a hare population cycle. (b) Red squirrels and other small mammals were eaten by lynx in large numbers only after the densities of hares fell to a low level. After M. S. O'Donoghue et al., Oikos 82:169–183 (1998).



The numerical response of a predator population lags behind changes in prey density. The lynx population shown in the above figure responded to changes in the hare population following the counterclockwise joint population trajectory predicted by the Lotka–Volterra model. Data from M. S. O'Donoghue et al., Oikos 82: 169–183 (1998)

[Figure 15.23 and 15.24], Ricklefs RE, 2008, The Economy of Nature. 6th ed. NY: W. H. Freeman and Company. Used under a Fair Use rationale.

Predator-prey cycles can be unstable

- Efficient predators can drive prey to extinction.
- Reduction in the number of predators can lead to an outbreak of prey.
- If the population moves away from the equilibrium, there is no force pulling the populations back to equilibrium.
- Eventually random oscillations will drive one or both species to extinction.

Factors promoting stability

1. Inefficient predators (prey escaping).
    - Less efficient predators (lower c) allow more prey to survive.
    - More living prey support more predators.
2. Outside factors limit populations.
    - Higher d for predators, lower r for prey.
3. Alternative food sources for the predator.
    - Less pressure on prey populations.
4. Refuges from predation at low prey densities.
    - Prevents prey populations from falling too low.
5. Rapid numeric response of predators to changes in prey population.

Multiple stable states in predator-prey systems

- Alternative stable states:
  - A population may have two or more stable equilibrium points, only one of which may be occupied at a given time.
  - Alternative stable states can arise when different factors limit populations at low and at high densities.
- Types of the stable state:
  1. Consumer-imposed equilibrium.
  2. resource-imposed equilibrium

Credits

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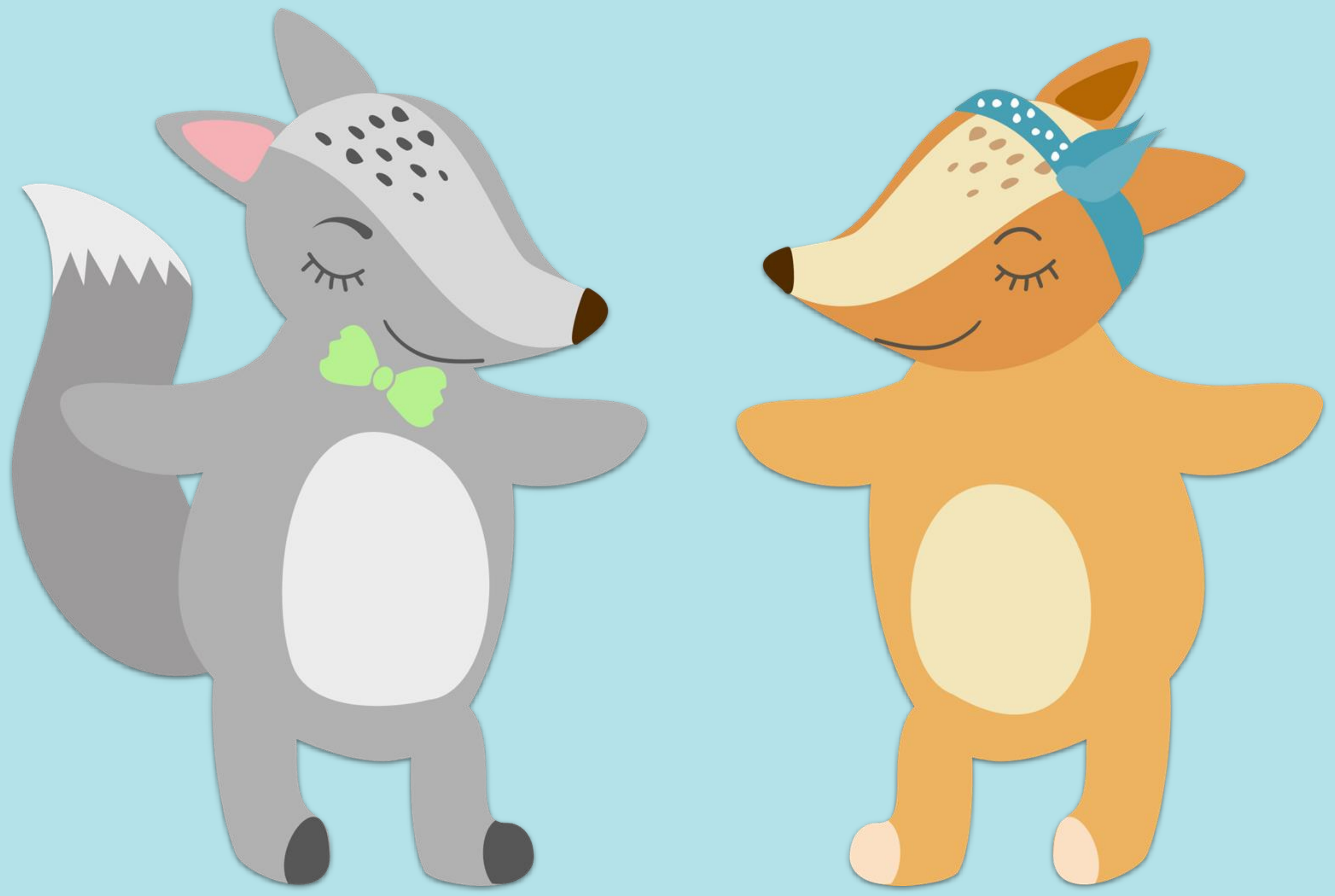

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