POPULATION ECOLOGY

ACCEPT OR REJECT

A population subjected to only density-independent factors can not persist over a long period of time – eventually go to extinction

ASSUMPTIONS OF LOGISTIC GROWTH MODEL

- *K* is constant over time
  - does not vary year to year etc.
- *dN* / *Ndt* declines **linearly** with *N*
  - alternative … nonlinear decline
- Effect of density *N* on *dN* / *Ndt* is instantaneous … no delays
  - alternative … density now affects *dN* / *Ndt* some time in the future (**time lag**)
- Continuous overlapping generations

LOGISTIC GROWTH: REAL DATA

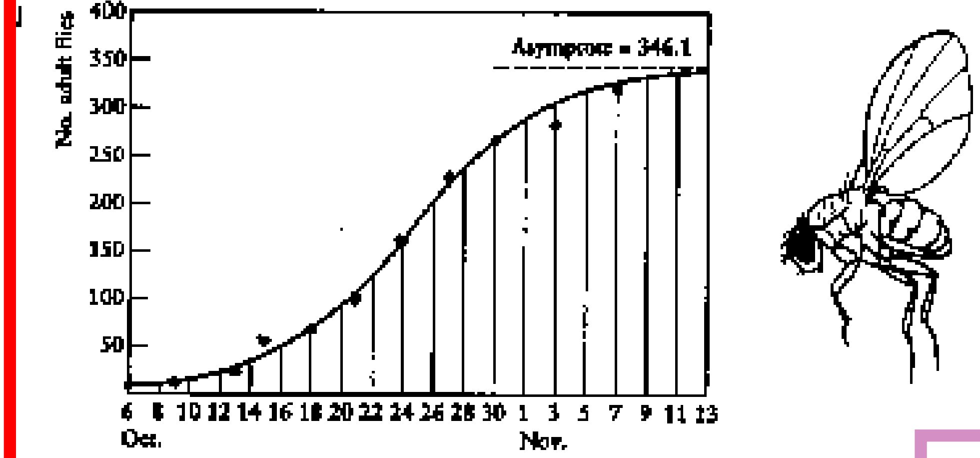
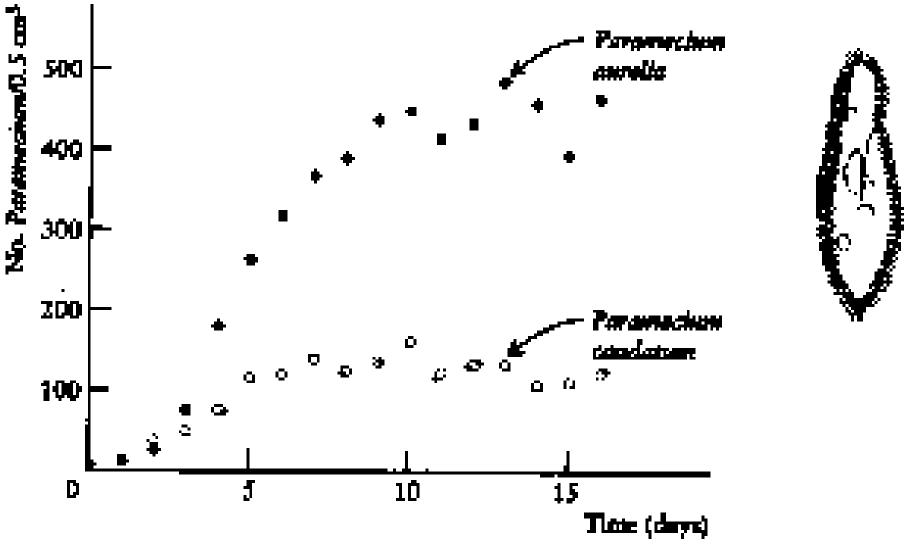


Figure 12.8 Growth of an experimental population of the fruit fly Drosophila melanogaster. *The circles are observed census counts, and the smooth curve is the fitted logistic. (After Pearl 1927.)*

Laboratory populations of Paramecium aurelia
&
Paramecium caudatum

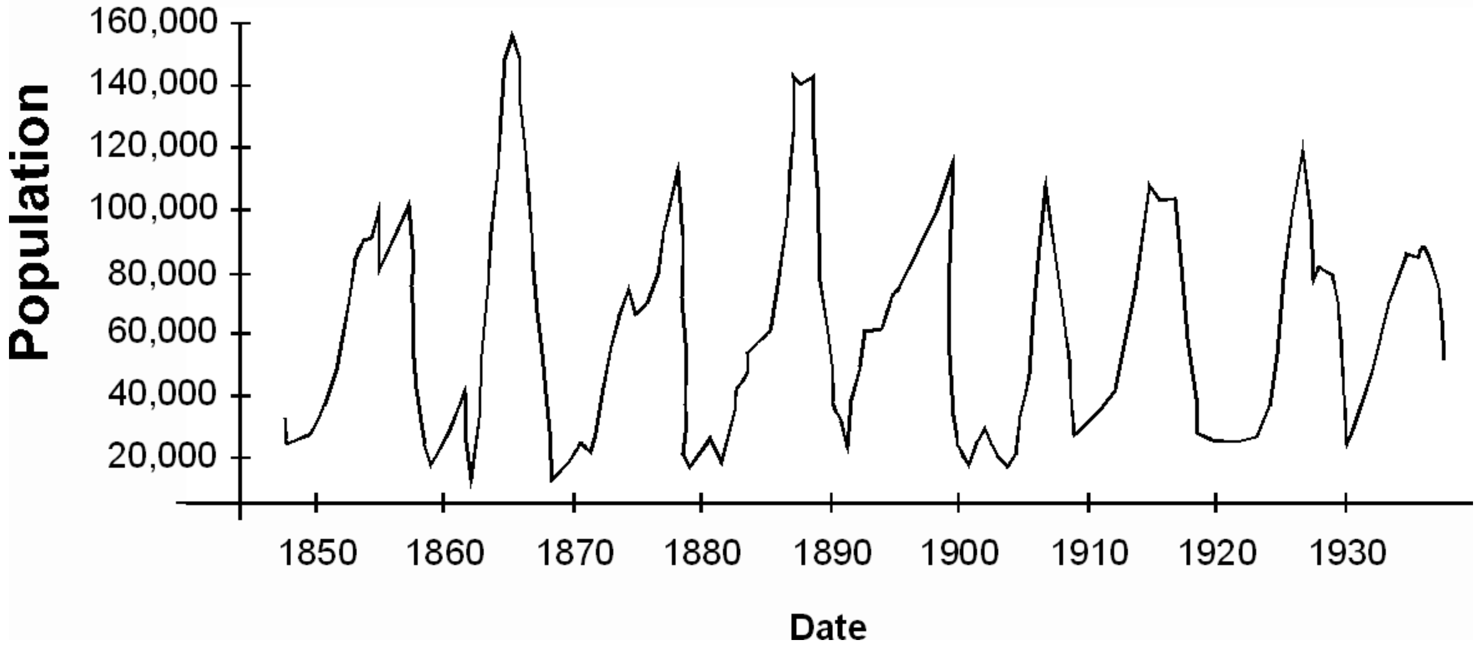
Laboratory population of Drosophila melanogaster



12.5 *Population growth in the protozoans* Paramecium aurelia *and* P. um *at 26°C in buffered Osterhout's medium, pH 8.0, "one-loop" concen- of bacterial food. (Data from Gause 1934.)*

POPULATION CYCLES

Fig. 1.1 Population cycles of the snowshoe hare, based on pelts received by the Hudson Bay Company (after Kormondy, 1969)



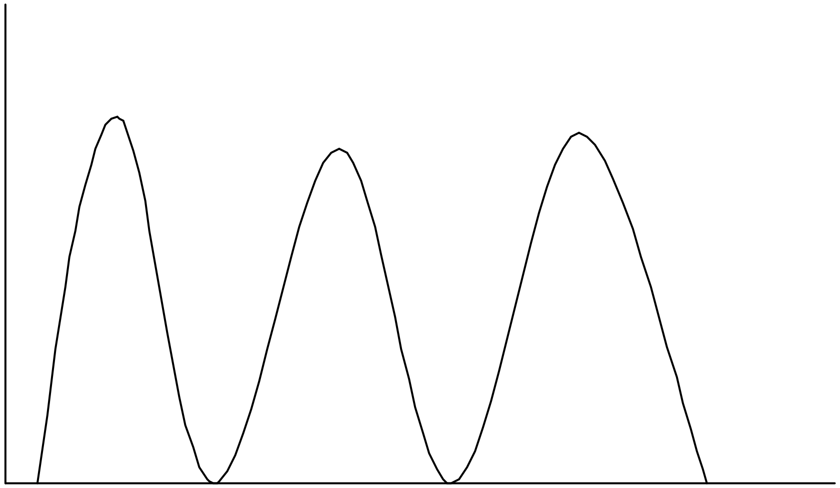
Cycles most common in higher latitudes

Tundra
3-4 year cycles
Predators – Arctic fox, snowy owl, Rough-legged Hawk
Prey – lemmings

Taiga
8-10 year cycles
Predators – Lynx
Prey – Snowshoe Hare, Ruffed Grouse

Temperate Grasslands
3-4 year
Predators - mustelids??
Prey - voles, Prairie Chickens?

Tropics
Probably not ??



2 major cycles identified
voles, lemmings, and grouse –3-4 year period
Snowshoe Hares – 8-10 year

Current research has been concentrated on low phase -

Voles and hares as small mammals have a tremendous capacity for growth during increase phase
Microtines 8-22 fold increase in 6months

What prevents population growth during low phase of cycle?

2 broad categories of hypotheses

1. Classical Model

Something is wrong with the environment

- Food supplies damaged by overgrazing at population peak
- Predators sufficiently abundant to prevent recovery
- Disease or parasites
- Or…interaction

Food Hypothesis

Seems unlikely, numerous food supplement experiments have failed to prevent low cycle

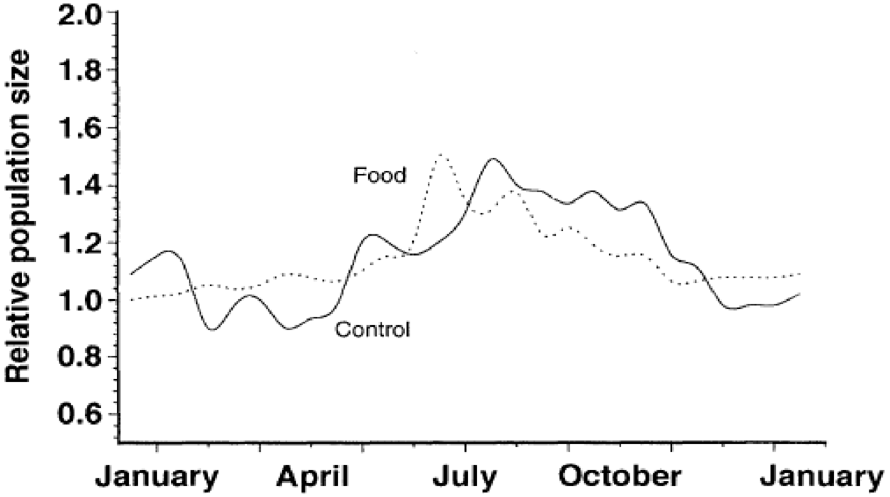
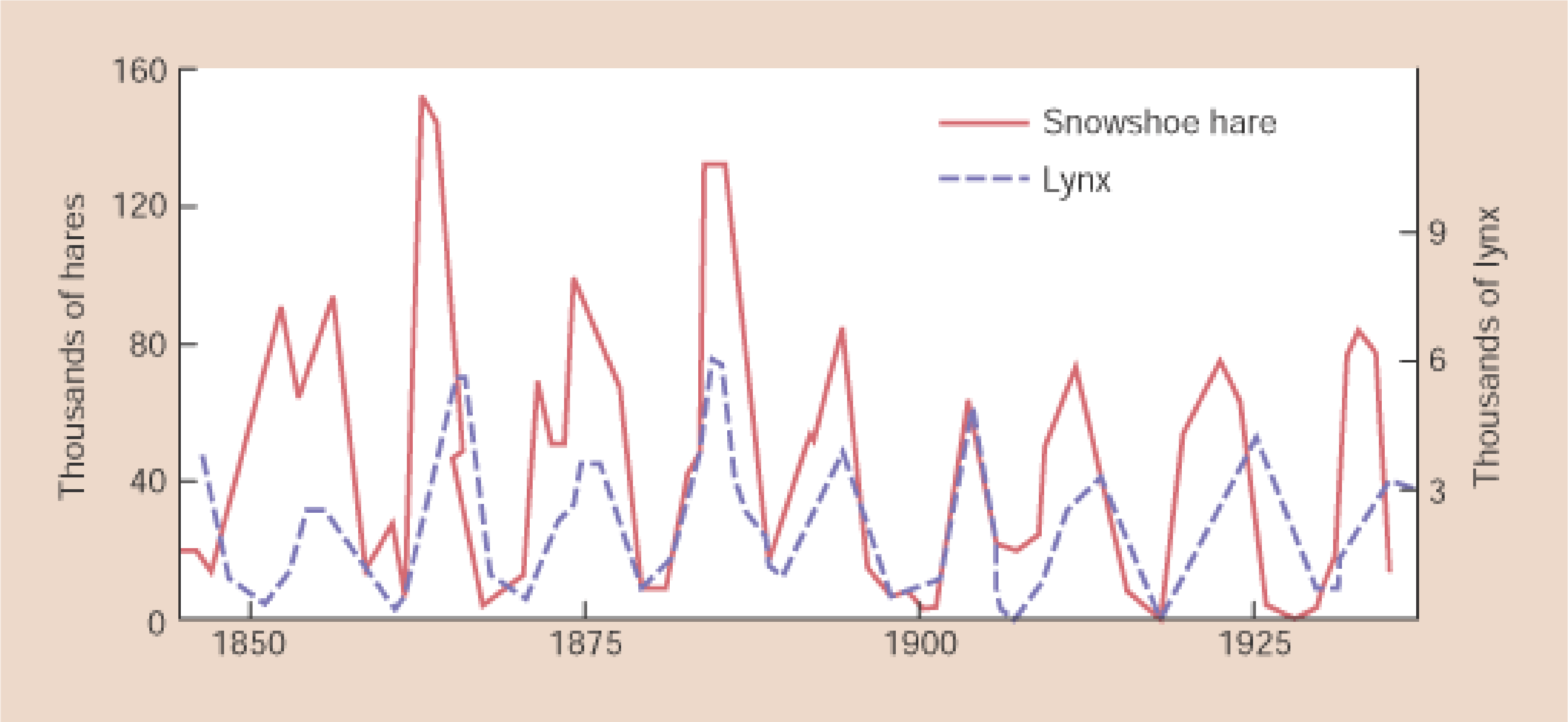


FIG. 4. Population estimates for Townsend's vole (*Microtus townsendii*) in a low-density period during which a feeding experiment was performed in 1973 (Taitt and Krebs 1981). Relative population size is calculated by standardizing densities to 1.0, using the density of each area for the period January–March 1973 before the food was added at the end of March 1973. Food-supplemented populations did not increase more than control populations, suggesting that food was not a resource in short supply.

Predators

Difficult to tease apart cause and effect



2 Possibilites

a. predators simply follow changes in prey abundance and thus have little consequence on prey demography

b. predators drive cycles and are cause of cycles
Lows would be caused by predators that keep prey # depressed for extended period following the decline

Snowshoe hares – decline directly related to intense predation

Low and increase phase --- 23% population disappeared overwinter (50% due to predation)

Decline phase ---50-77% disappeared overwinter (70% due to predation).

Decline phase in Yukon --<1% survived entire year (83% predation)

Thus predation is a major factor in the decline phase but seems not to have an effect during the low phase.
Same for microtines

Indirect effects Hypothesis

Response of prey to risk of predation may affect reproductive fitness and ultimately cause the low phase.

Decline - Snowshoe hares minimize risk to predation by altering foraging to areas of dense cover.

The correlate of good cover is poor food quality

Trade-off reproduction for survival

Shift to dense spruce stands which results in poorer nutrition, lower mass of female, reduced fecundity.

This causes chronic stress with long term consequences.

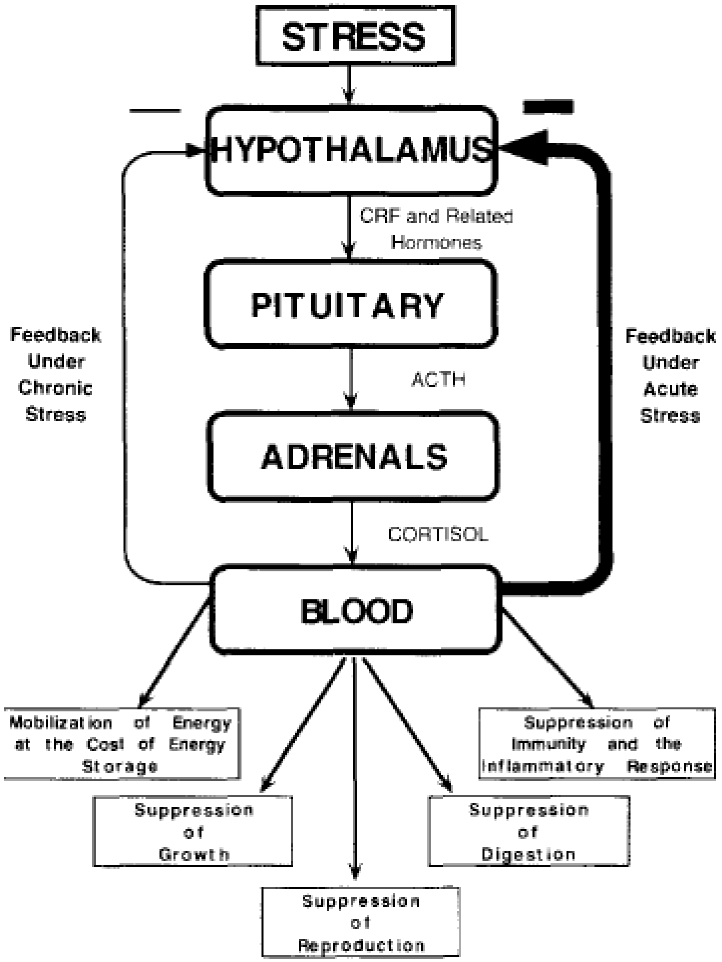


FIG. 1. Schematic representation of the hypothalamic–pituitary–adrenal feedback system response to a stressor, and the main effects on body processes (five boxes at bottom). A stressor causes the hypothalamus to release corticotropin-releasing factor (CRF) and other hormones, which causes the pituitary to release corticotropin (ACTH), and which in turn causes the adrenal cortex to release cortisol. Cortisol feeds back on the hypothalamus and pituitary to cause an inhibition of CRF release. Under conditions where the stressor is acute, the feedback mechanism operates efficiently, and the system rapidly returns to normal, resulting in effects on body pro-

All physiol measurements associated with stress response (immune system, mass loss, reprod hormone response, hypothalamic-pituitary-adrenal response) all were severely affected during the hare decline phase. They did improve remarkably after predators had declined.

Low phase is thus a lag caused by indirect effects of predation

2. Self-regulating model

Something is wrong with the individual

Environment is ok but something is working on individuals to prevent their increase.

Physiol & Behavioral characteristics potential source of limitation

Population Cycles – Continued

2. Self-regulating model

Anecdotal evidence supports hypothesis

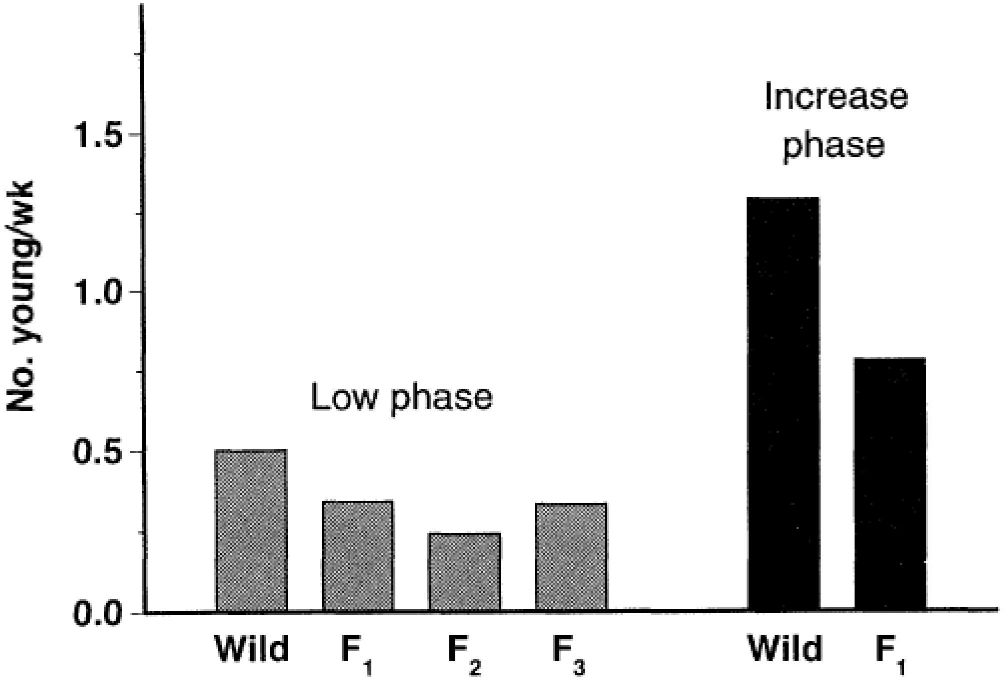


FIG. 5. Number of young produced per week by female meadow voles (*M. pennsylvanicus*) held in the laboratory under ideal conditions. Voles from the low phase of the cycle cannot reproduce as effectively as those brought in from an increasing field population, and this poor performance is transmitted to their offspring. (Data are from Mihok and Boonstra 1992.)

Population Cycles – Continued

2. Self-regulating model

Maternal Effects Hypothesis

Change in maternal quality occurs during peak phase and carries over to decline and low phase

Maternal Effects Hypothesis

Produced through d-d social inhibition of maturation in peak years

Yg born in spring forced to delay reproduction till next breeding season

- **shift in population age structure**
- **older age mothers more prone to decline in reproduction and offspring quality**


PGC Photo/Hal Korber

INTRASPECIFIC COMPETITION

The use of a resource by two or more different individuals, or the interference by one individual with the resource use by others

COMPETITION:

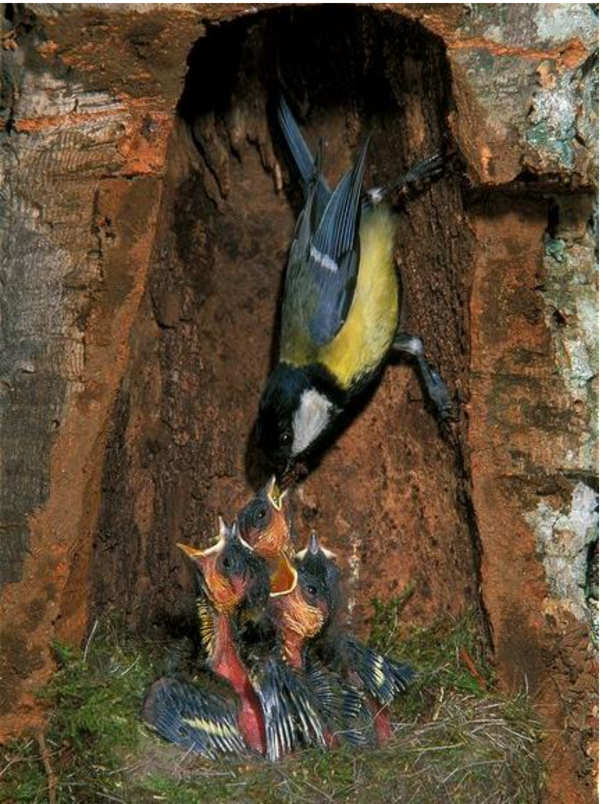
- Exploitation – competition in which 2 or more individuals consume the same limited resource
- Interference – competition in which one organism prevents the other from having access to a limiting resource. Active inhibition is used to deny others the resource

CHARACTERISTICS OF INTRASPECIFIC COMPETITION

- Ultimate effect is decreased contribution of organism to next generation. To be apparent competition must lead to a reduction in survivorship or fecundity.
- Resource must be limited.
- The effect of competition on any individual is greater, the greater the number of competitors there are (density dependent)

- 11 young/year
- 27% adults survive
- 6% of young

Does intraspecific competition limit population size of Great Tits?



Over 4 years

- removed 60% of young (4 young/year)

Do results suggest survival rates are density-dependent?

Treatment	Adult Survival	Young Return
Control	27%	6%
Removal	56%	22%

Increases were sufficient to compensate for the loss of young and breeding numbers continued to fluctuate around same numbers as before.

Competition in plant hoppers

Denno and Roderick 1992. Ecology 73:1323

Lives on
salt marsh
grass -
Spartina

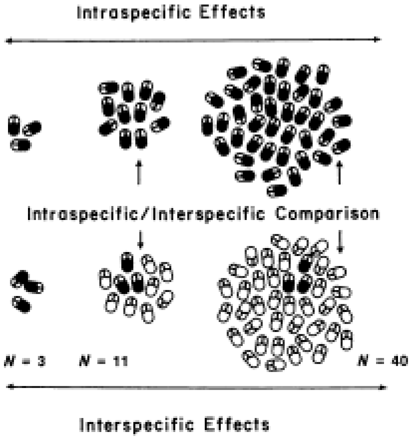


FIG. 1. Experimental design used to evaluate the inter- and intraspecific effects of crowding on the wing form and fitness (survivorship, development time, and body size) of two species of *Prokelisia* planthoppers. Intraspecific effects were evaluated by raising each species in pure culture at densities of 3, 11, and 40 individuals per cage (dark planthoppers in top row). Interspecific effects were assessed by comparing the response of three individuals of one species (dark planthoppers) raised in pure culture to the response of three individuals (dark planthoppers) raised in mixed cultures with the other species (light planthoppers) at combined densities of 11 and 40 inds./cage (bottom row). The relative effect of interspecific crowding was evaluated at densities of 11 and 40 inds./cage (columns) by comparing the response of individuals of one species reared in pure culture (dark planthoppers in top row, the intraspecific effect) to when they were rare, but reared at the same combined density in the presence of the other species (three dark planthoppers in bottom row, the interspecific effect).

Density controlled by enclosing insects with Spartina seedlings
3, 11, 40

Results

-survivorship
-development
-Body length
- % Macropterous females

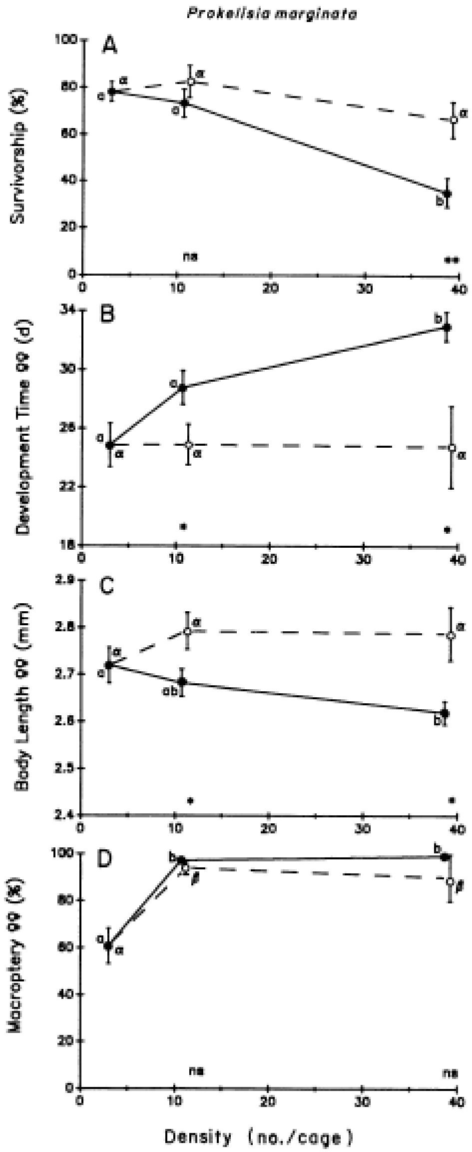


FIG. 2. The survivorship (A), development time from nymph to adult (B), body length (C), and the percentage of macropterous females (D) of *Prokelisia marginata* subjected to intraspecific crowding (——) and interspecific crowding with *Prokelisia dolus* (— — —). Intraspecific effects were assessed in pure culture at densities of 3, 11, and 40 individuals per cage (least squares means ± 1 SE with different lowercase Roman letters are significantly different, $P < .05$, ANOVA followed by Sidak's adjustment for multiple comparisons). Interspecific effects were assessed by comparing the response of three individuals of *P. marginata* reared in pure culture to the response of three individuals of *P. marginata* reared in the presence of 8 and 37 individuals of *P. dolus* at combined densities of 11 and 40 individuals per cage, respectively (least squares means ± 1 SE with different lowercase Greek letters are significantly different, $P < .05$, ANOVA followed by Sidak's adjustment for multiple comparisons). The effect of inter- relative to intraspecific crowding was evaluated by comparing the response of individuals of *P. marginata* reared in pure culture at densities of 11 and 40 individuals per cage to when they were rare (three individuals per cage), but reared at the same combined density (11 and 40 individuals per cage) in the presence of *P. dolus*. Differences between intra- and interspecific means at densities of 11 and 40 are indicated just above the abscissa of each graph (**$P < .01$, * $P < .05$, NS = not significant; *t* test).

Colonial Species

Suggested that density may have a positive effect

- Fecundity increases with increased density

Common Guillemot

- Breed in subcolonies of different densities

- Females lay 1 egg

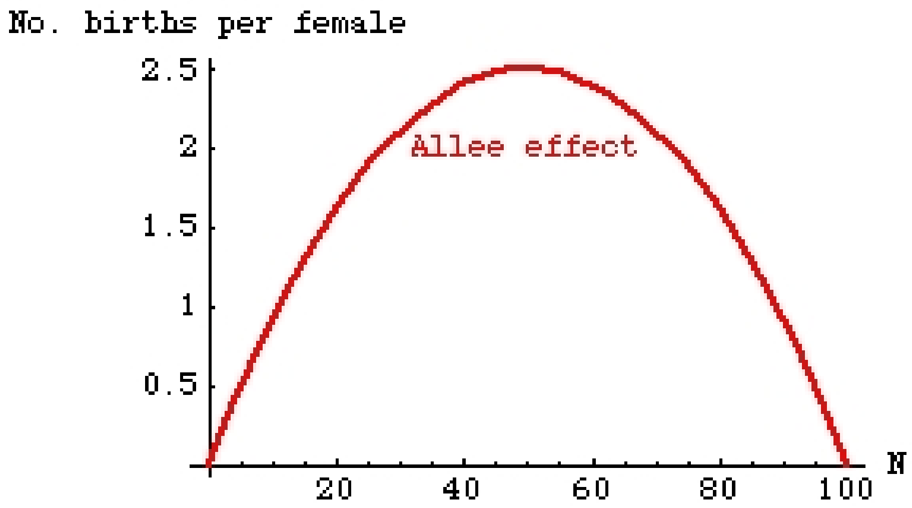
- Subcolonies with higher densities had higher reproductive success

Common Guillemot

- Inverse density-dependence

Common Guillemot

- Driving factor – deterrence of predators (Great Black-backed Gulls and Herring Gulls)



Tendency for destabilizing effect – as birth rates rise with increased density, death rates remain the same

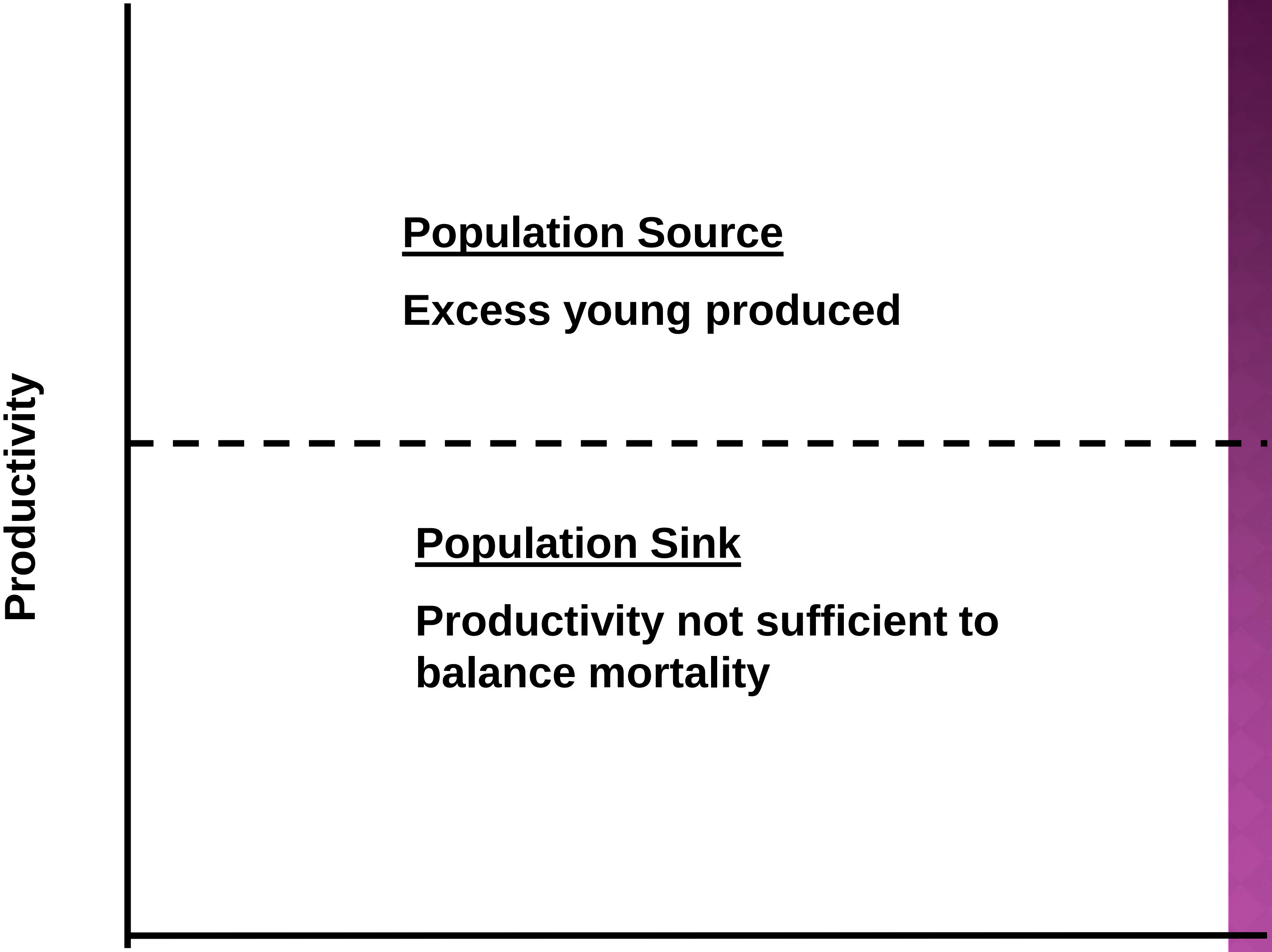
Large populations get larger
Small populations get smaller

Other Mechanisms of Allee Effects

- predator dilution/swamping
- antipredator vigilance
- social thermoregulation
- reduction of inbreeding
- genetic drift
- antipredator aggression
- social facilitation of reproduction

SOURCE AND SINK POPULATIONS

Too simplistic to think environmental conditions are equally favorable everywhere an organism exists



Productivity

Population Source

Excess young produced

Population Sink

Productivity not sufficient to balance mortality

What level of nesting success is needed to sustain a “healthy population”?

SNPL

	Mayfield Nesting Success (%)						
Study Site	2005	2004	2003	1993	1992	1991	1990
BEAR	24.5	50.4	53.8	-	-	-	-
FARM	42.1	61.8	54.3	-	-	-	-
SHORE	-	13.9	24.7	34.5	12.9	11.3	38.1

(Paton 1995)

CALCULATION OF LAMBDA

(finite population growth rate)

SNPL

$$\lambda = P_A + P_J\,\beta$$

where,

P_A = annual adult survival (set to 74% or 50% based on Paton 1994 and Nur et al. 1999);

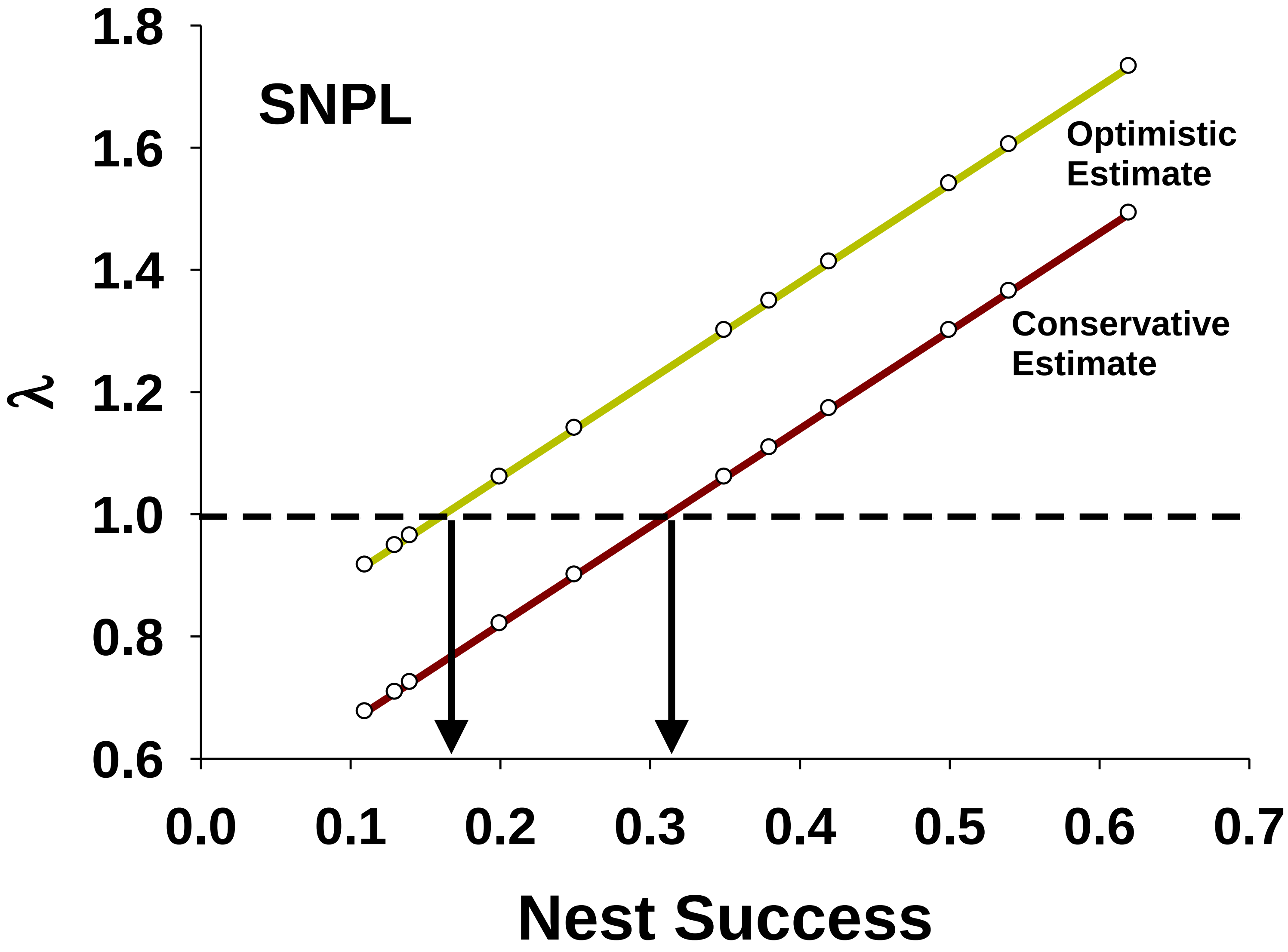
P_J = juvenile survival from fledging to the following breeding season (set to 50% based on Nur et al. 1999)

β = mean annual production (calculated from this study, Paton 1995, Nur et al. 1999)

$\lambda = P_A + P_J \beta$

$\lambda > 1$ Population Source

$\lambda < 1$ Population Sink


SNPL
λ
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Nest Success
Optimistic Estimate
Conservative Estimate

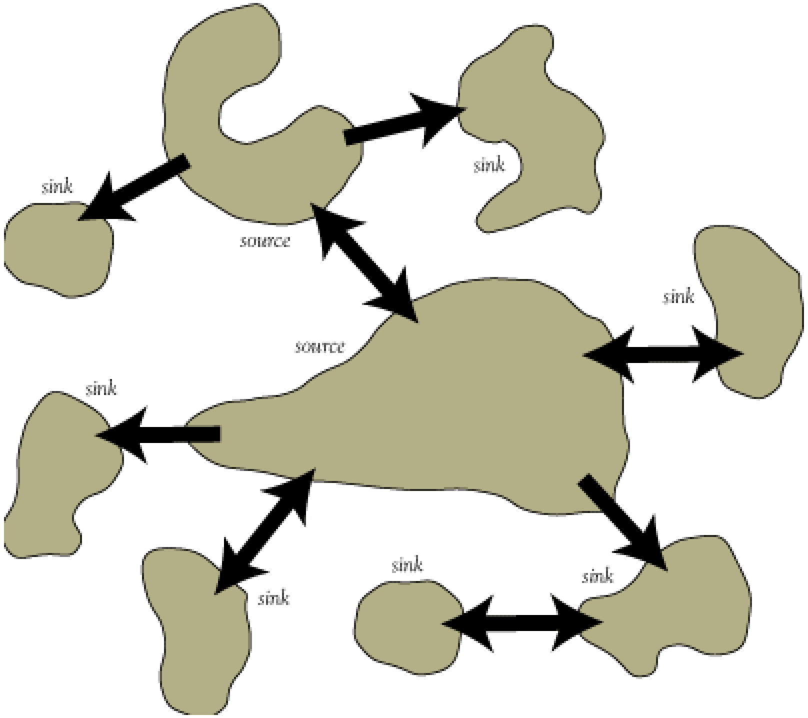
SNPL

	Mayfield Nesting Success (%)						
Study Site	2005	2004	2003	1993	1992	1991	1990
BEAR	24.5	50.4	53.8	-	-	-	-
FARM	42.1	61.8	54.3	-	-	-	-
SHORE	-	13.9	24.7	34.5	12.9	11.3	38.1

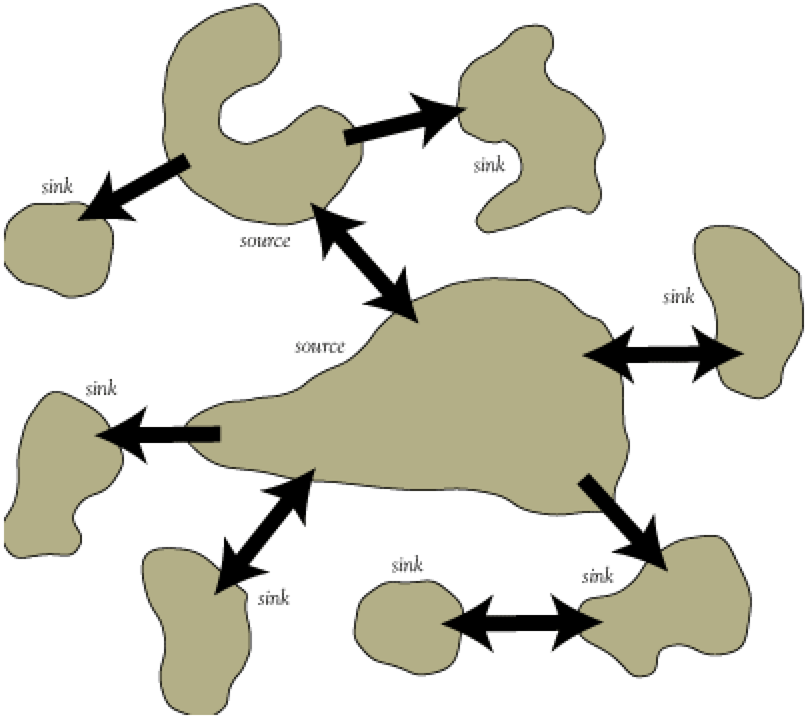
(Paton 1995)

METAPOPULATIONS

A ‘metapopulation’ is a “population of populations” (Levins 1969,1970); in which distinct subpopulations (local populations) occupy spatially separated patches of habitat.



A metapopulation exists when dispersal rates are “low-moderate”, meaning that an individual will move from one patch to another at a rate high enough to maintain some interaction among subpopulations but low enough that those subpopulations remain distinct.



High rates of dispersal lead to the unification of patches into a single large, patchy population.   All “patchy” populations are not necessarily metapopulations.

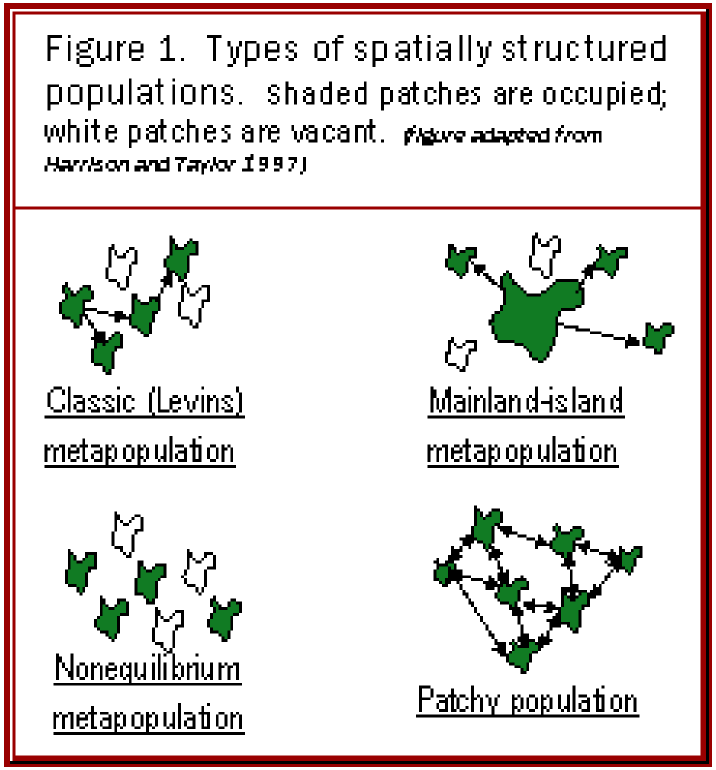


Figure 1. Types of spatially structured populations. shaded patches are occupied; white patches are vacant. (figure adapted from Harrison and Taylor 1997)

Metapopulation theory is particularly useful to wildlife biologists because most wildlife habitats are fragmented or maintain some degree of patchiness.

Animal dispersal among patches is an obvious concern for populations existing in heterogeneous landscapes. Rate of animal dispersal is affected by aspects of life history traits and population dynamics, but animal movement is also affected by aspects of landscape heterogeneity, including patch size, patch isolation, edge characteristics, and matrix characteristics.

LIFE HISTORY THEORY REVISITED

Life History Theory
A. Defined

Definition – Set of evolved strategies including behavioral, physiological, and anatomical adaptations that influence survival and reproductive success directly

Everything we know about NS indicates that those individuals with fecundity and survivorship schedules most suited to maximize fitness will be favored.

TELEOLOGY AND EVOLUTION OF LIFE HISTORY STRATEGIES

- Teleology is the idea that purpose exists in evolution in the same sense that it does for human intention.
  - Evolution has no predesigned or intentional goal

TELEOLOGY AND EVOLUTION OF LIFE HISTORY STRATEGIES

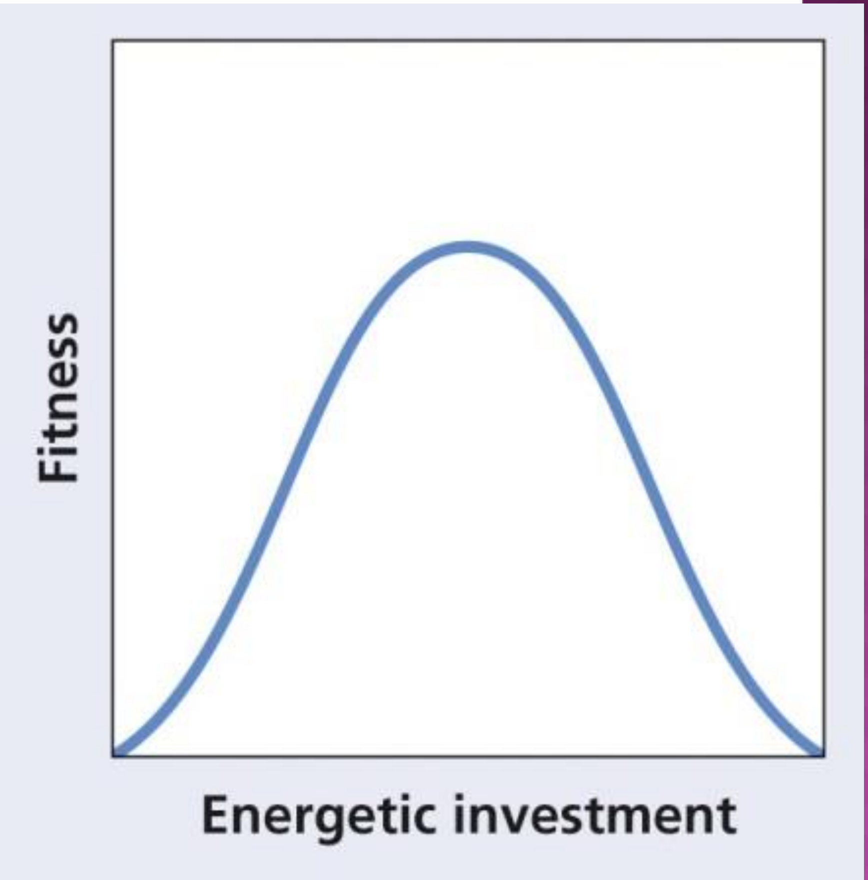
- “Strategy” does not imply a conscious choice by the organism.
- Adaptive strategy does not mean the best possible.
  - Like all adaptations, life history strategy is subject to constraints and needs only to be good enough.
  - Optimal life history strategy means the best of those existing in a certain population under certain environmental conditions.

Crucial aspects of these schedules represent

LH Strategies

1. Age and size reproduction begins
2. Relative effort devoted to growth, reproduction, and survival
3. The apportionment of reproductive effort between many small or few large offspring
4. Distribution of reproductive effort over lifetime

- Investment in each life history trait has a benefit and a cost to the organism.
- Investment beyond that optimum reduces fitness by limiting energy available for other important functions.



B. Trade-offs

Hypothetical Organism

-Reproduces immediately after birth

- Large number of Large offspring
- Lavishes parental Care
- Reproduces repeatedly throughout a long life

$TE = G+M+R_{(c+f)}$

For real organisms, its LH Strategy must be a compromise or a trade-off

C. Cost of Reproduction

Individuals devoting considerable energy to one aspect of its strategy must pay for it by reducing investments in another.

Is there a cost to reproduction?

Nur Journal of Animal Ecology 53:479:496

HIGH REPRODUCTION DOES NOT ALWAYS INCREASE FITNESS

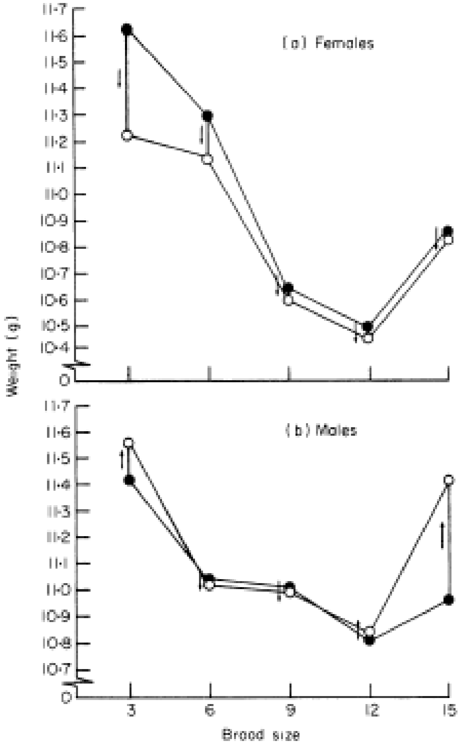


FIG. 5. Adult weight during the nestling period in relation to brood size (1980): comparison of first and last weighings. (a) Females, (b) Males. Mean weight at first weighing, (●); mean weight at last weighing, (○). The arrows indicate direction of weight change. 76% of the adult weights at 'first-capture' were obtained on days 8–10, 16% on day 11, and 8% on days 12–14. 76% of the weights at 'last-capture' were obtained on days 13–16, 8% on day 12, and 16% on days 9–11. In this figure, the mean weight of females rearing broods of fifteen is greater than that of females rearing broods of nine and twelve. This anomaly is explained by the fact that females rearing broods of fifteen were heavier than other females before the manipulation of brood size. When the weight of all females was adjusted for their weight at incubation (by regressing female weight at day 10 on female weight at incubation and comparing the residuals), the mean weight for this group was shown to be 0.20 g lighter than any other brood-size group.

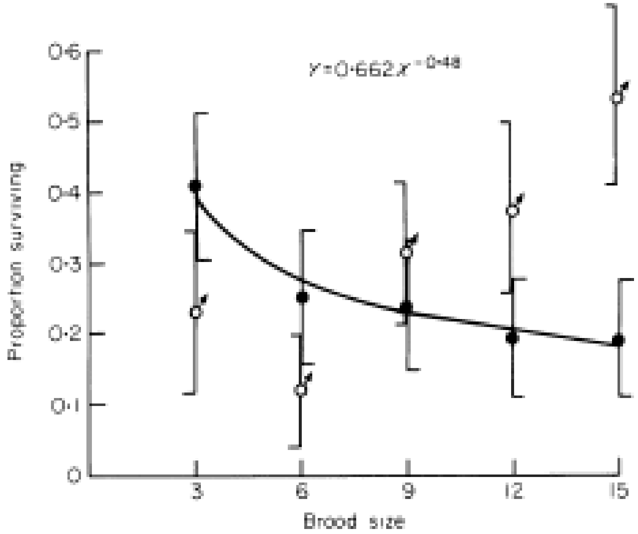
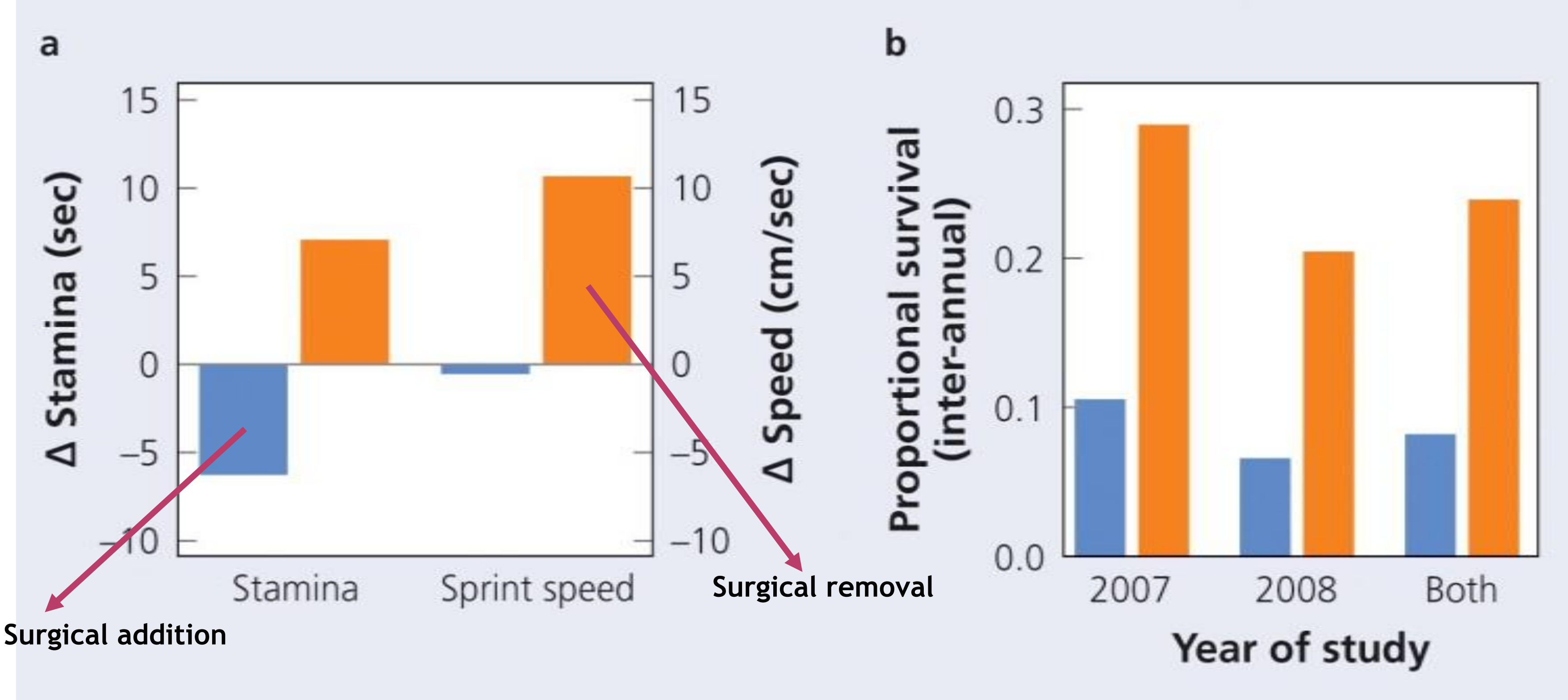


FIG. 6. Adult survival in relation to brood size in 1978. Female survival rate (as indicated by subsequent recapture) is represented by filled circles, male survival by the symbol ♂. For both males and females, bars indicate ± standard error of the mean survival rate for each brood size (assuming survival is binomially distributed). For females, n = 22, 20, 21, 21, and 21, respectively; for males, n = 13, 17, 19, 16, and 15, respectively. The plotted curve and its equation, a power function of form $Y = \alpha X^{\beta}$, indicate the best-fitting line as determined by the regression of ln(female survival) on ln(brood size). The 95% confidence interval for α is 0·419–1·028 and for β is −0·691– −0·268. Similar results were obtained when the arcsine-square root transformation was applied to the survival rate.

HIGH REPRODUCTION DOES NOT ALWAYS INCREASE FITNESS



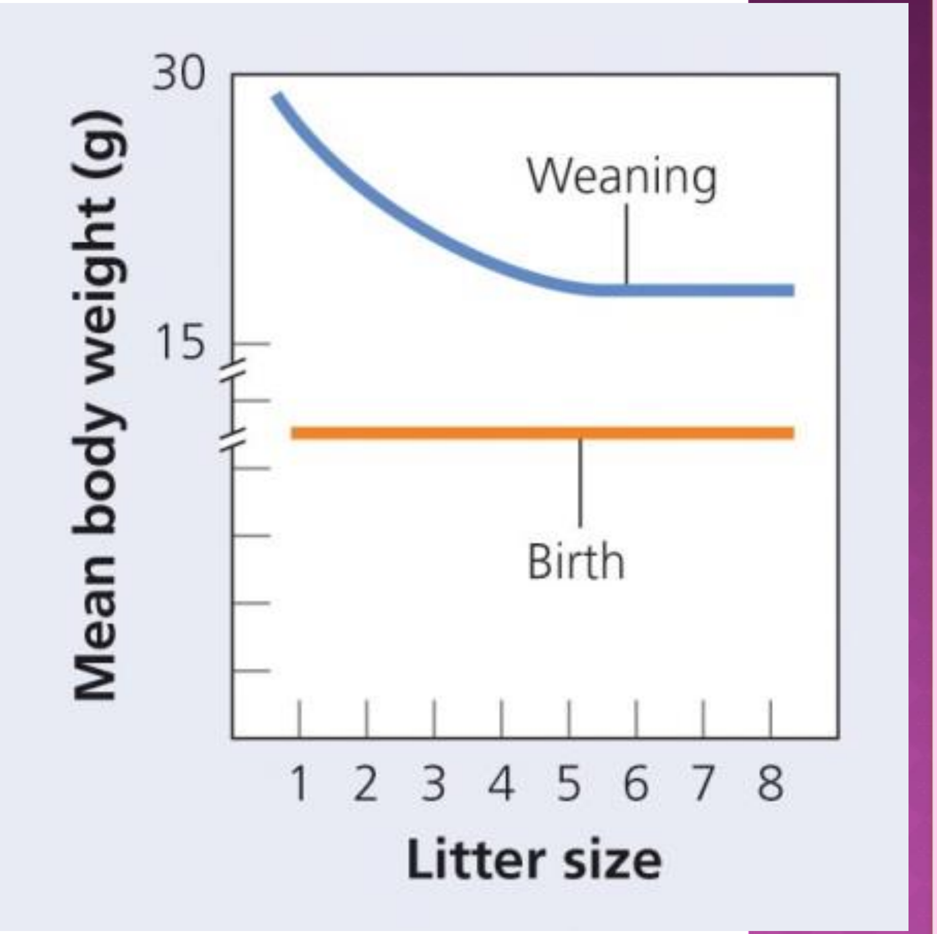
Surgical addition

Surgical removal

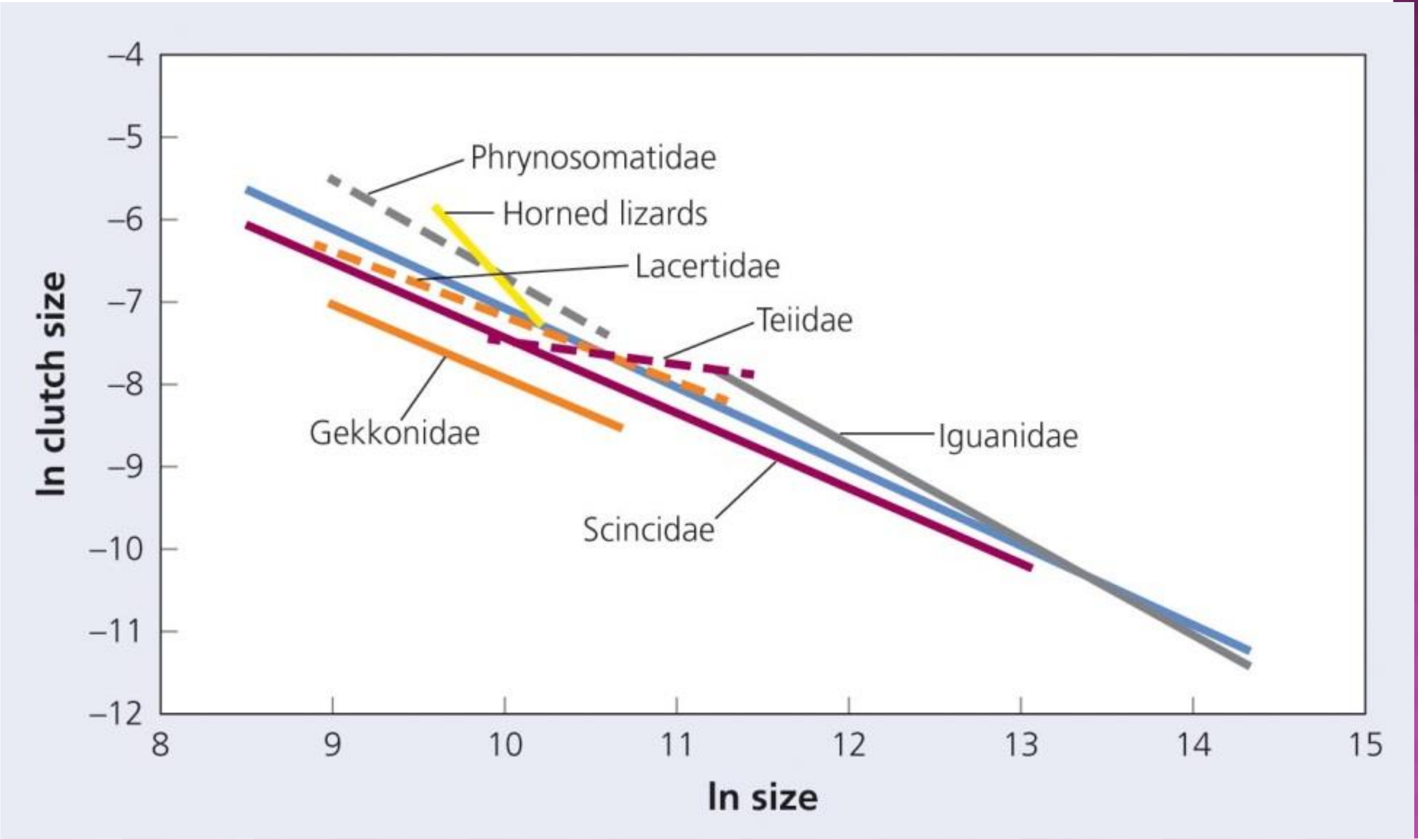
- Removal of an egg from the female Anole lizards (*Anolis sagrei*) leads to higher survival to the next reproductive event due to the increase in female's stamina, sprint speed, and growth.

HIGH REPRODUCTION DOES NOT ALWAYS INCREASE FITNESS

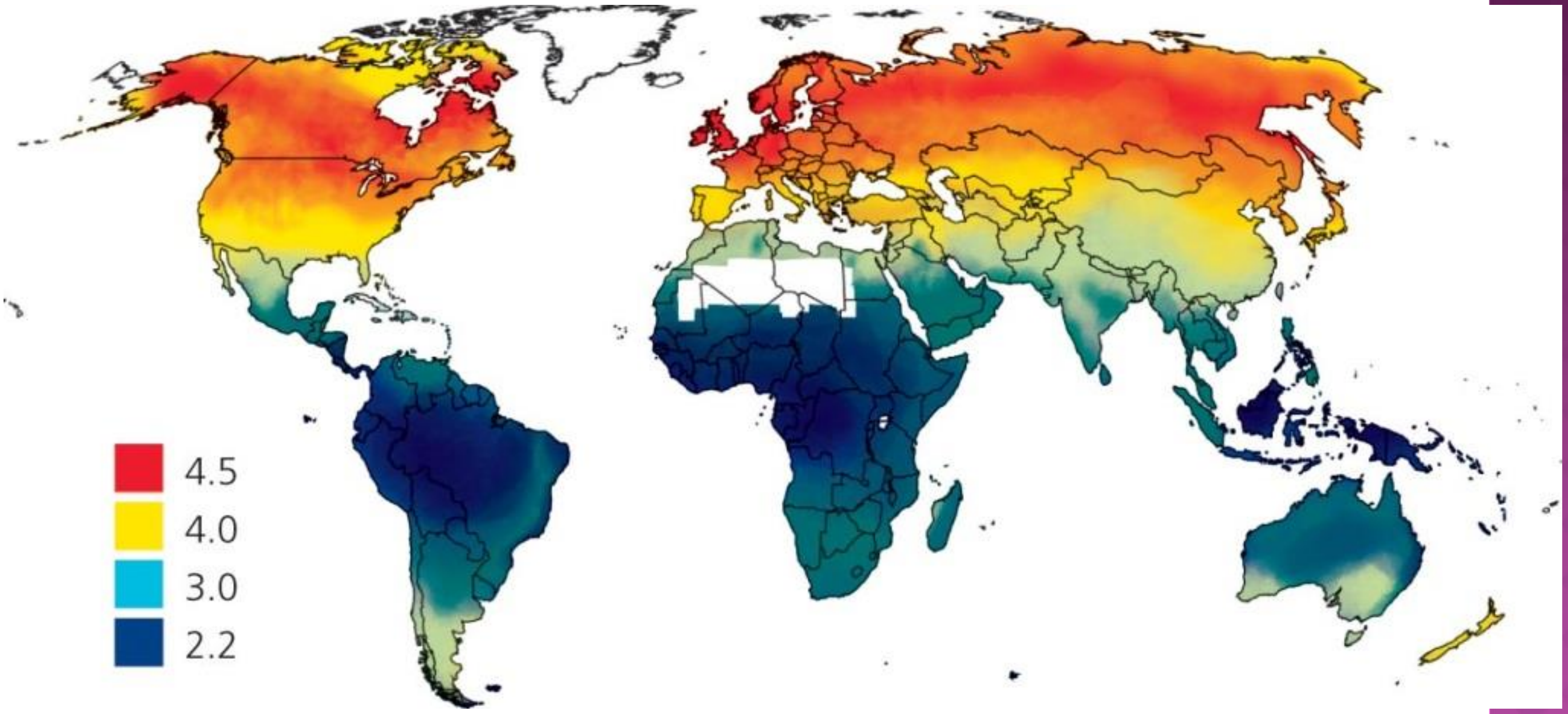
- The collared lemming (*Dicrostonyx groenlandicus*): the weaning weight of individuals in large litters is less than that in small litters.



REPRODUCTIVE TRADE-OFFS BETWEEN THE NUMBER AND THE SIZE OF OFFSPRING



ECOLOGICAL CORRELATES OF REPRODUCTIVE TRADE-OFFS



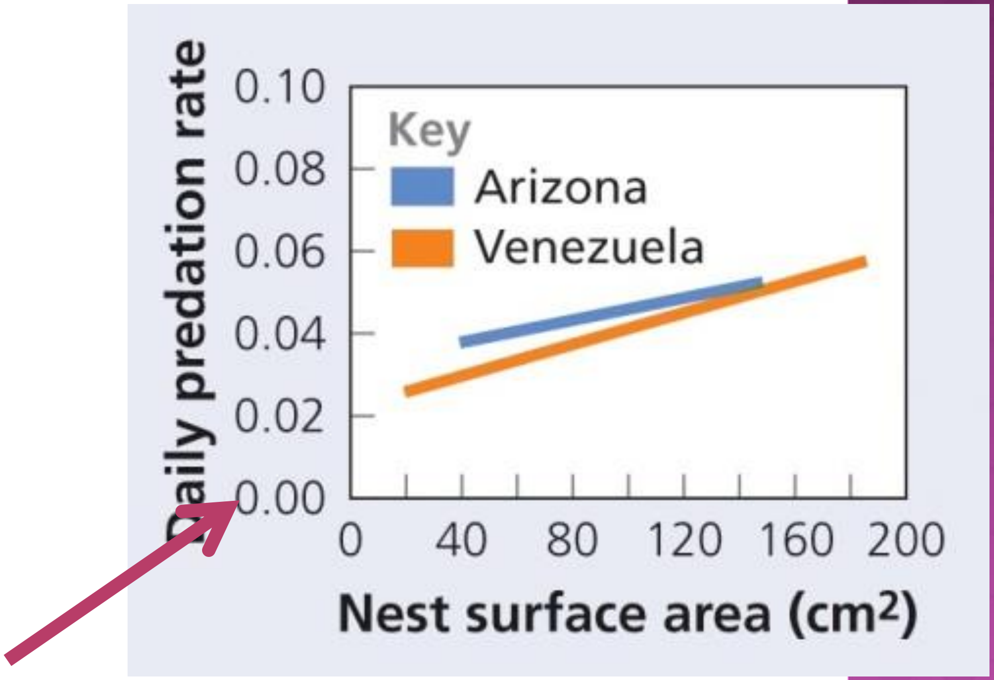
Average clutch size in birds increases with the latitude

PREDATION AS A FACTOR EXPLAINING THE LATITUDINAL TREND IN THE CLUTCH SIZE

- A study of nest predation in Venezuelan cloud forest.
- **Hypothesis:** High predation rates in the tropics select for smaller nests and thus smaller clutch sizes.
- **Prediction 1:** Nest predation rates increase with nest size.
- **Prediction 2:** Clutch size increases with nest size.
- **Prediction 3:** Nests in the tropics are smaller than nests at higher latitudes.

PREDATION AS A FACTOR EXPLAINING THE LATITUDINAL TREND IN THE CLUTCH SIZE

- Test 1: Nest-swap experiments in tropical and temperate sites.
- Two nests of different sizes placed near a natural nest in the environment.
- Nests baited with quail eggs and checked daily for predation.
- **Prediction 1 supported.**



PREDATION AS A FACTOR EXPLAINING THE LATITUDINAL TREND IN THE CLUTCH SIZE

- When the nest size was adjusted for body size, there was no increase in clutch size in large nests.
- **Prediction 2 not supported.**
- Tropical nests were not smaller relative to body size in the tropics than at higher latitude.
- **Prediction 3 not supported.**