Lotka-Volterra Model

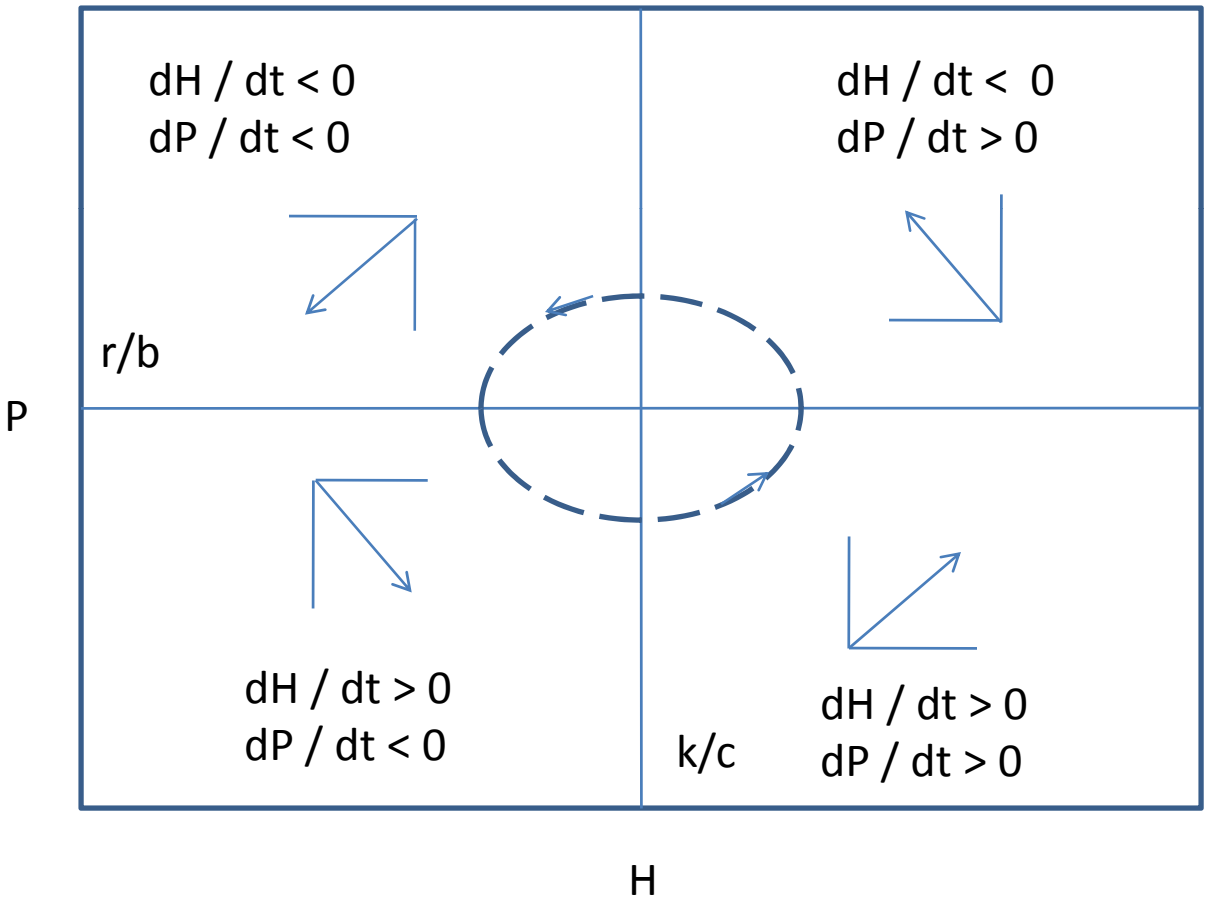
$$dH/dt = rH - bHP$$

H = number of prey
r = prey population growth rate
b = attack rate

$$dP/dt = cHP - kP$$

P = number of predators
c = predator population growth rate due to predation
k = rate of predator decline in absence of prey

Lotka-Volterra Model



Modified Lotka-Volterra Model

$$\frac{dH}{dt} = rH\left(1 - \frac{H}{K}\right) - \frac{aHP}{1 + aHh}$$

$$\frac{dP}{dt} = cP\left(1 - \frac{PJ}{H}\right) - kP$$

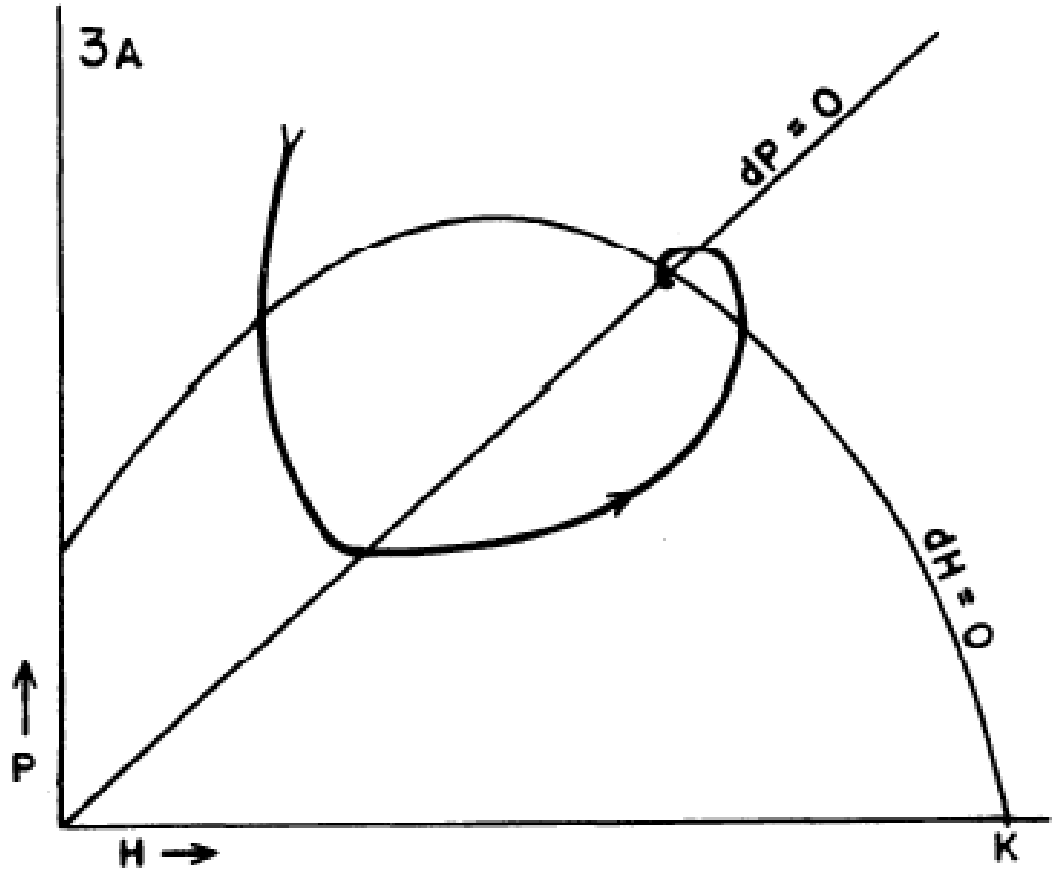
H = number of prey
r = prey population growth rate
b = attack rate
P = number of predators
c = predator population growth rate due to predation
k = rate of predator decline in absence of prey
J = prey density required to support 1 predator per area

Stability

- Tanner (1975 Ecology 56:855)
- Explored features of this model to find general properties, particularly model stability
- Does the “critical point” where predator and prey isoclines cross produce a:
  - stable equilibrium (“focus point”)
  - limit cycle
  - unstable
- predator growth / prey growth rates (s/r) (note $c = s$)

Tanner (1975)

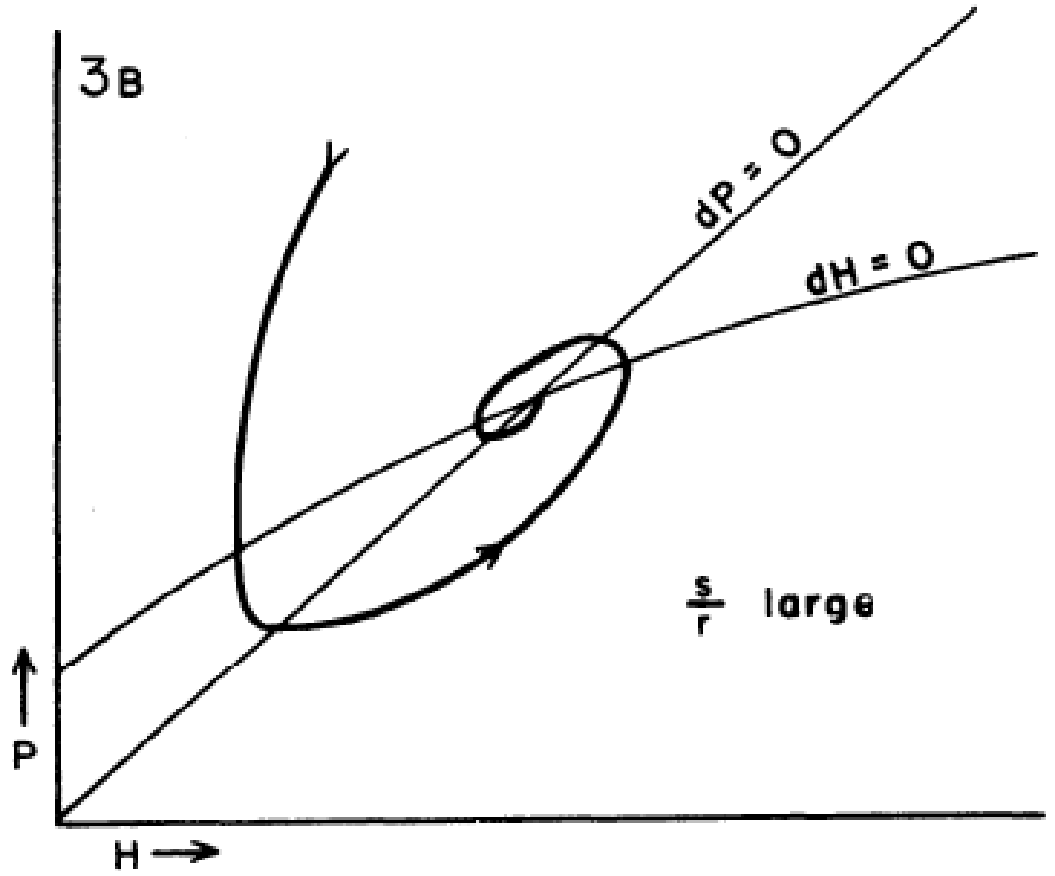
Stable focus when the critical point falls to the right of the prey zero isocline peak for all values of s/r



Tanner (1975)

When the critical point falls to the left of the prey zero isocline peak,

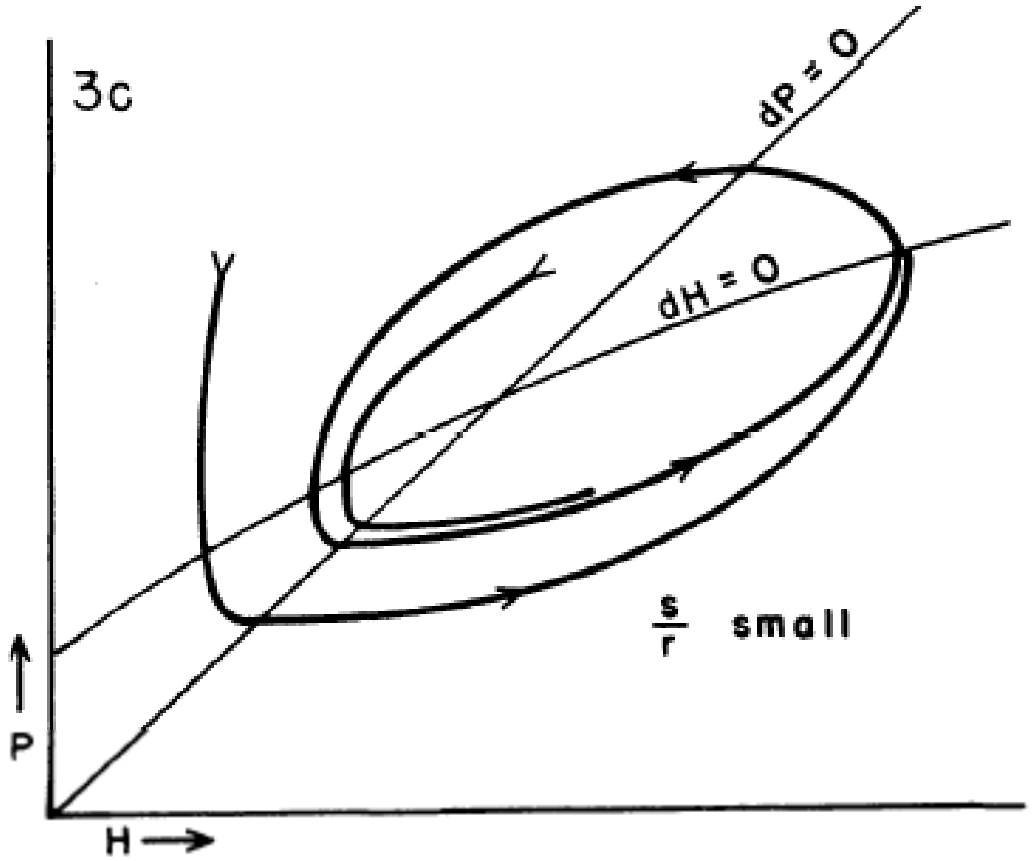
1) stable focus if s/r is large



Tanner (1975)

When the critical point falls to the left of the prey zero isocline peak,

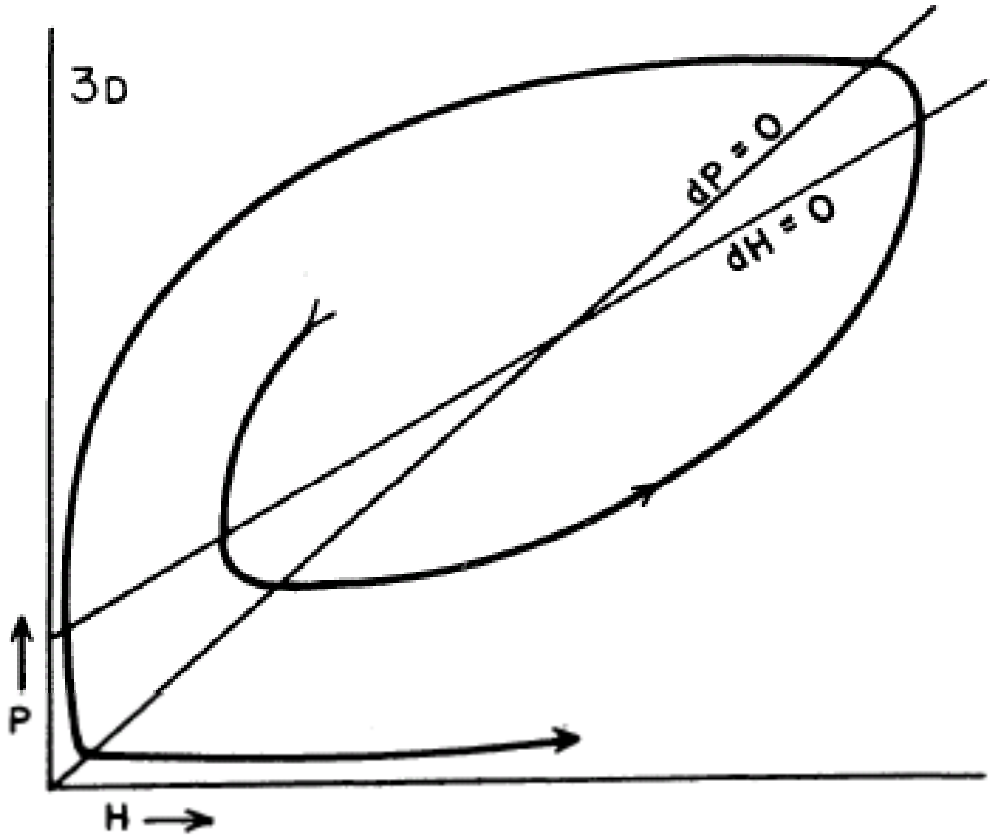
2) **limit cycle** if s/r small



Tanner (1975)

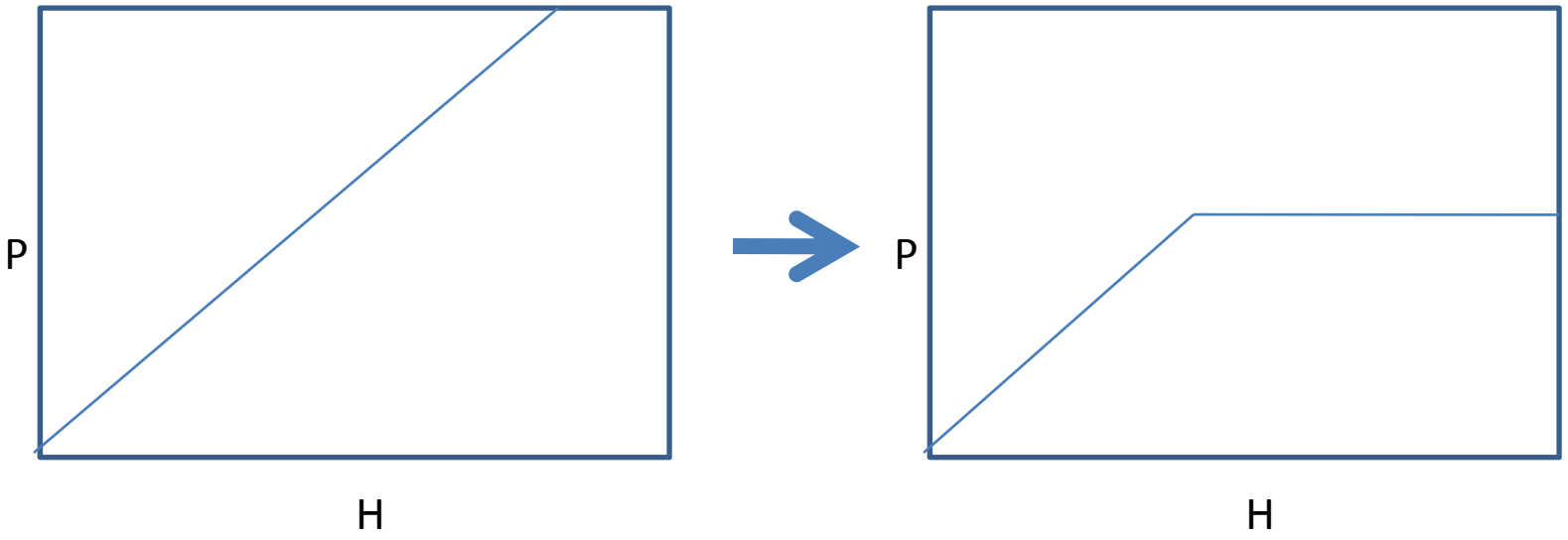
When the critical point falls to the left of the prey zero isocline peak,

3) unstable focus if s/r small and K is very large – extinction; no coexistence



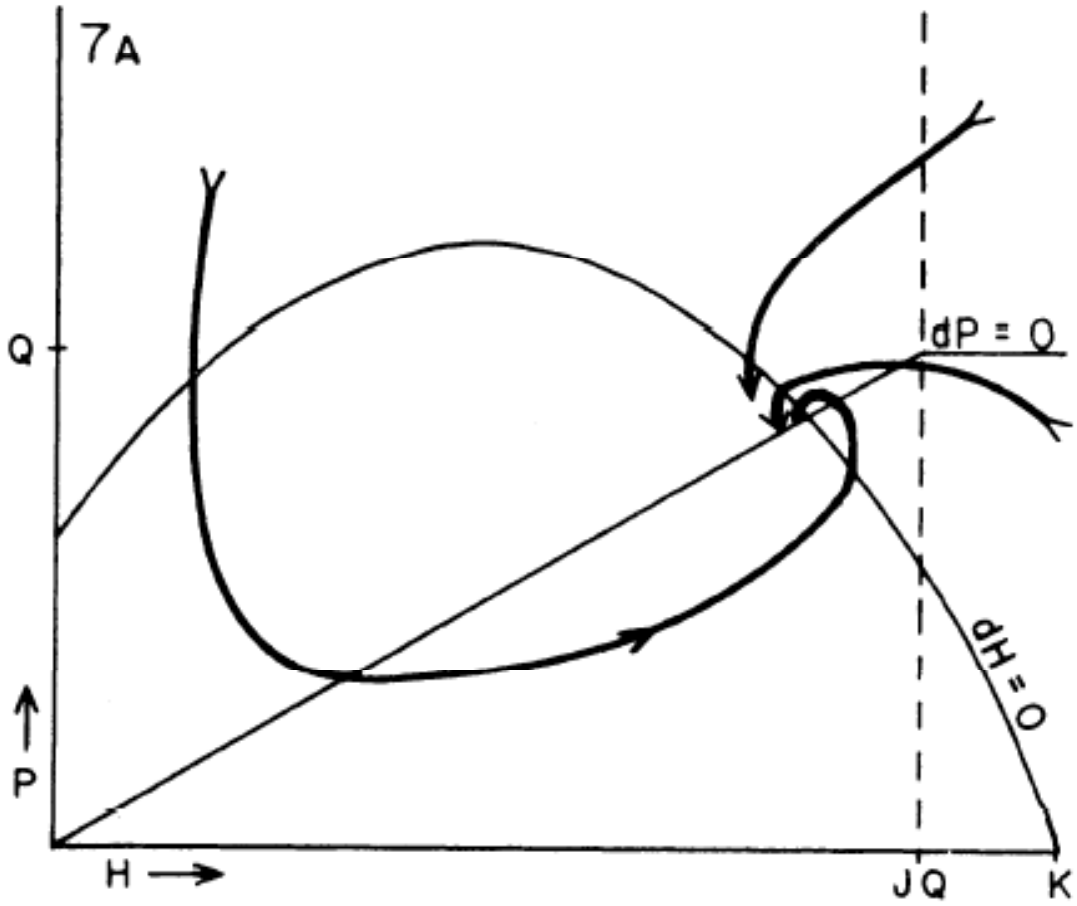
Tanner 1975

- What if predator is limited a resource that is independent of both predators and prey such as nest sites or space rather than prey or predator numbers?



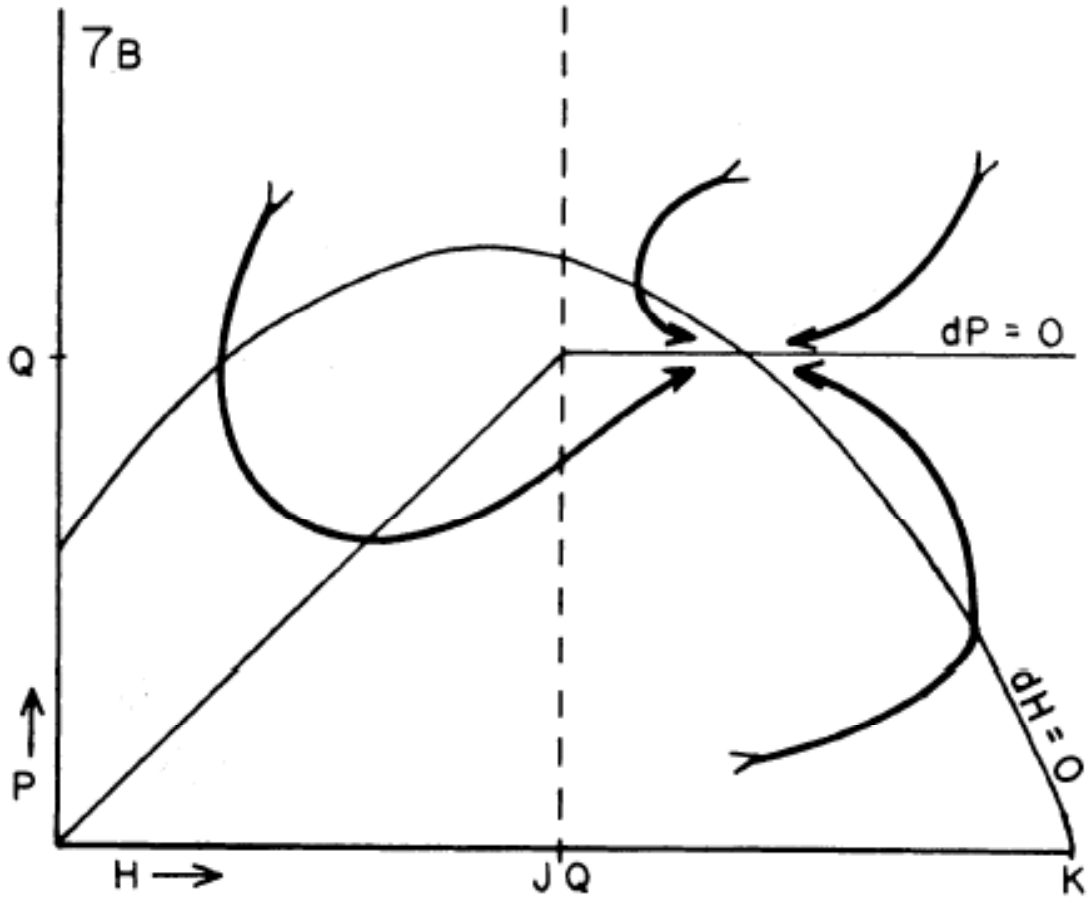
Tanner (1975)

Once again, since the critical point falls to the right of the prey zero isocline peak, a stable focus results for all values of s/r



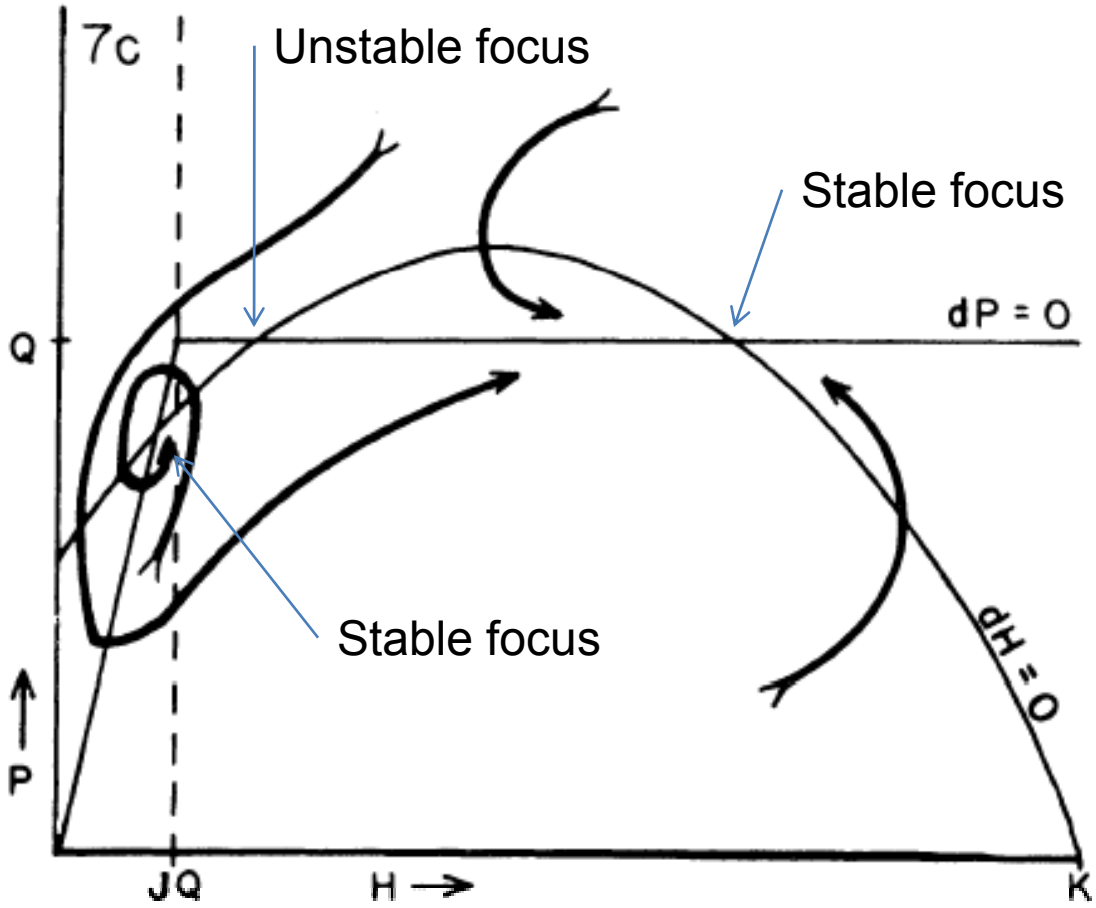
Tanner (1975)

Again, since the critical point falls to the right of the prey zero isocline peak, a stable results for all values of s/r



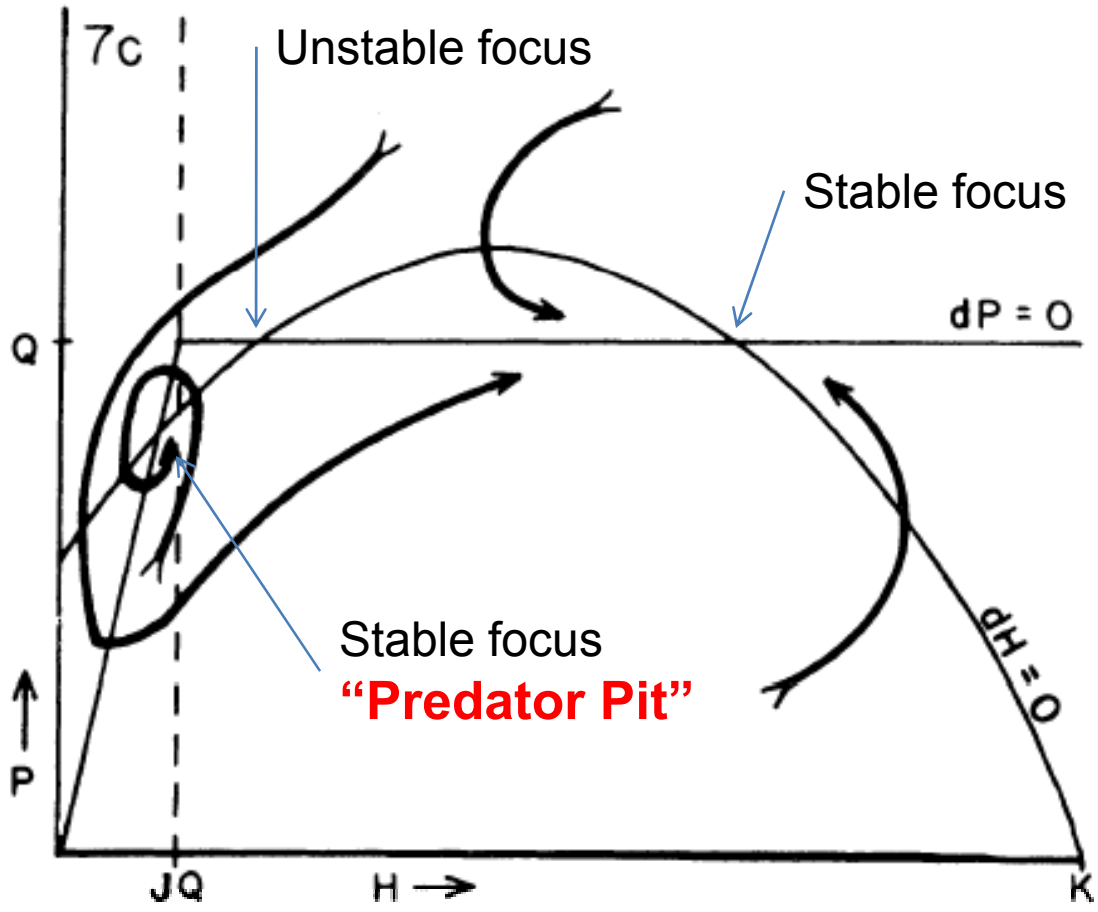
Tanner (1975)

When the predator and prey zero isoclines cross three time, two stable and one unstable ("saddle") points are created. Population can "jump" from one to the other depending on starting point and other model constants or



Tanner (1975)

The prey population can get "stuck" at very low density unless predation rates drop substantially , called a predator pit



Tanner 1975

- Complex model behavior, nearly any outcome!
- So what? Is this useful?

Tanner 1975

- Complex model behavior, nearly any outcome!
- So what? Is this useful?
- Tanner reflected on the general patterns from models
- Hypothesized that **stable** prey species were either strongly self-limited (e.g., by territoriality) or the prey population growth rate was less than that of the predator
- How would you test?

Tanner 1975

- Hypothesized that stable prey species were either strongly self-limited (e.g., by territoriality), or the prey population growth rate was less than that of the predator
  - Prey growth rate appeared higher ($s/r < 1$) for:
    - sparrow hawk / house sparrow and
    - Mink / muskrat
  - *And* both prey species thought to be self-limited (sparrows: food or breeding sites; muskrats: territories)

Tanner 1975

- Hypothesized that stable prey species were either strongly self-limited (e.g., by territoriality), or the prey population growth rate was less than that of the predator
  - Prey growth rate appeared similar(s/r = 1) for
    - Lynx / snowshoe hare
  - Hare and lynx show cycles

Tanner 1975

- Hypothesized that stable prey species were either strongly self-limited (e.g., by territoriality), or the prey population growth rate was less than that of the predator
  - Prey growth rate appeared lower($s/r > 1$) for several prey species with weak self-regulation:
    - Mt. lion / mule deer
    - Wolf / (moose, caribou, WT deer, white sheep)

Model assumptions

- No time lags
- No prey refuges
- Predator searching constant, not affected by external factors
- No differences in prey susceptibility

Optimal Foraging Theory

- How does a predator choose which prey to hunt for and for how long?
- Theory developed to identify the optimal choices based on profitability of prey items or foraging patches where

  profitability = energy / handling time

- The optimal diet or foraging patches are those maximizing profitability
- Perfect match unlikely because animals must explore choices to learn profitabilities and profitabilities change through time

Model assumptions

- No time lags
- No prey refuges
- Predator searching constant, not affected by external factors
- No differences in prey susceptibility
- Prey switching and switching of habitats
  - Predators switching to another prey at low prey density essentially creates a refuge, theoretically increasing stability.
  - Evidence?

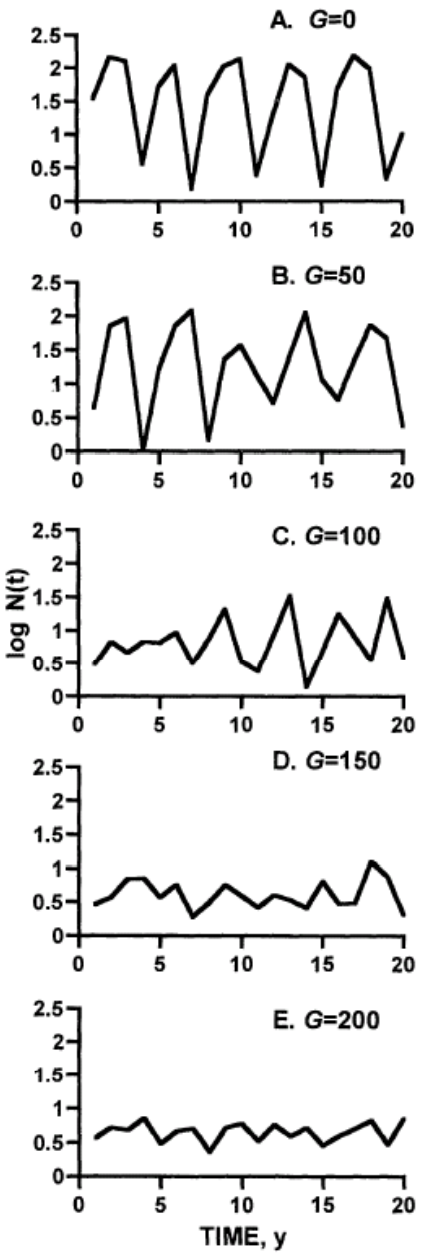
Hanski et al. 1993 and Turchin and Hanski

- Vole population dynamics in northern Europe
- Few, relatively specialized predators in northern populations
  - Numerical response to increased voles
  - With a time lag
- More and more generalist predators in southern populations
  - Relatively constant population size
  - Rapid behavioral response (functional response) to increasing vole densities

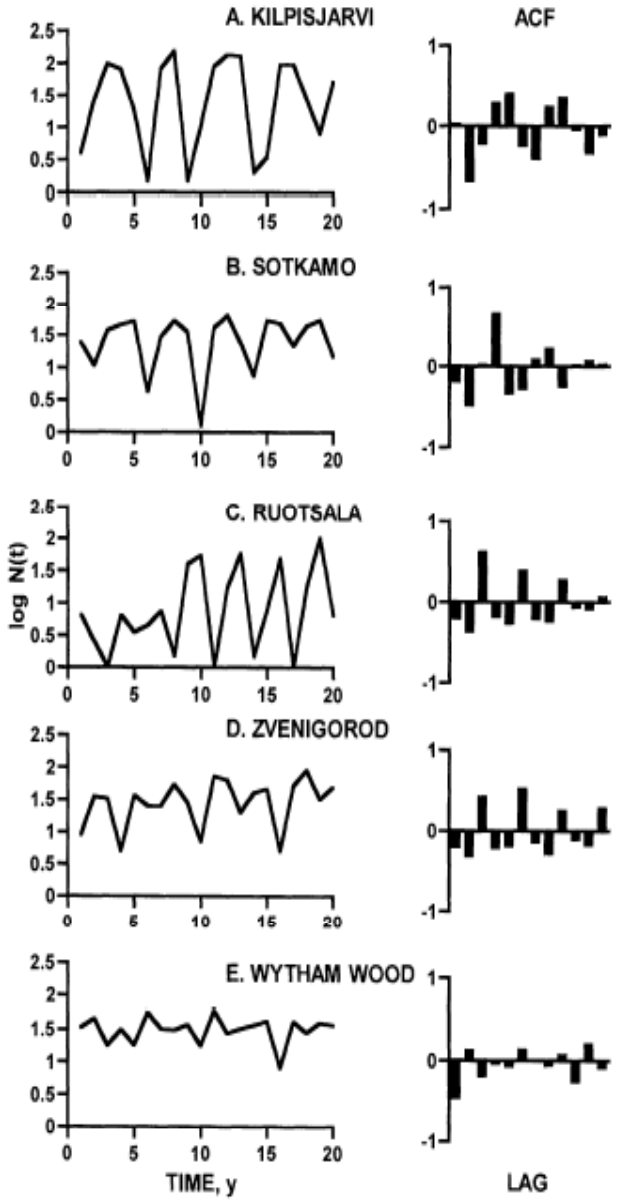
Turchin et al. 1997

- Modified Tanner model
  - Seasonality
  - Stochasticity
  - Parameterized with independent data
  - Tested the hypothesis that population stability depends on type of predators

Model Predictions



Observed dynamics



Northern Populations
Relatively specialized predators
Few alternative prey

Southern Populations
Relatively generalized predators
More diverse prey

FIG. 6.—The dynamical shift in vole population dynamics in the data. *Left graphs,* time-series data from five locations. All data are plotted using identical *X* and *Y* scales (only the first 20 points are shown). *Right graphs,* autocorrelation functions for each trajectory.

Can predators limit populations?

- Connolly (1978) review of ungulate studies
  - 31 studies provided evidence of predator regulation
  - 27 did not
- Cote and Sutherland (1997) Meta analysis of bird predator removals showed increased hatching success, and larger post-breeding population size, and breeding population size in next season.

Introduced predators

- Freshwater systems appear to be much more sensitive to introduced predators than prey in terrestrial systems on continents (but not islands)
- Cox and Lima (2006) argued terrestrial prey are seldom naïve to predators because of historical biotic exchanges among continents. Marine prey have also experienced biotic exchanges
- In contrast, FW habitats have high heterogeneity in predator regime and lower dispersal rates, promoting naiveté in prey

Indirect effects and the “ecology of fear” (Lima 1998)

- Predators eat prey
- Also strongly affect prey behavior
- When obtaining food is dangerous, altered behavior may affect prey foraging rates, growth rates, survival and population growth rates…in other words, fear may reduce indirectly fitness: “indirect” or “sublethal” effects
- behavioral trophic cascade

Yellowstone northern winter elk range

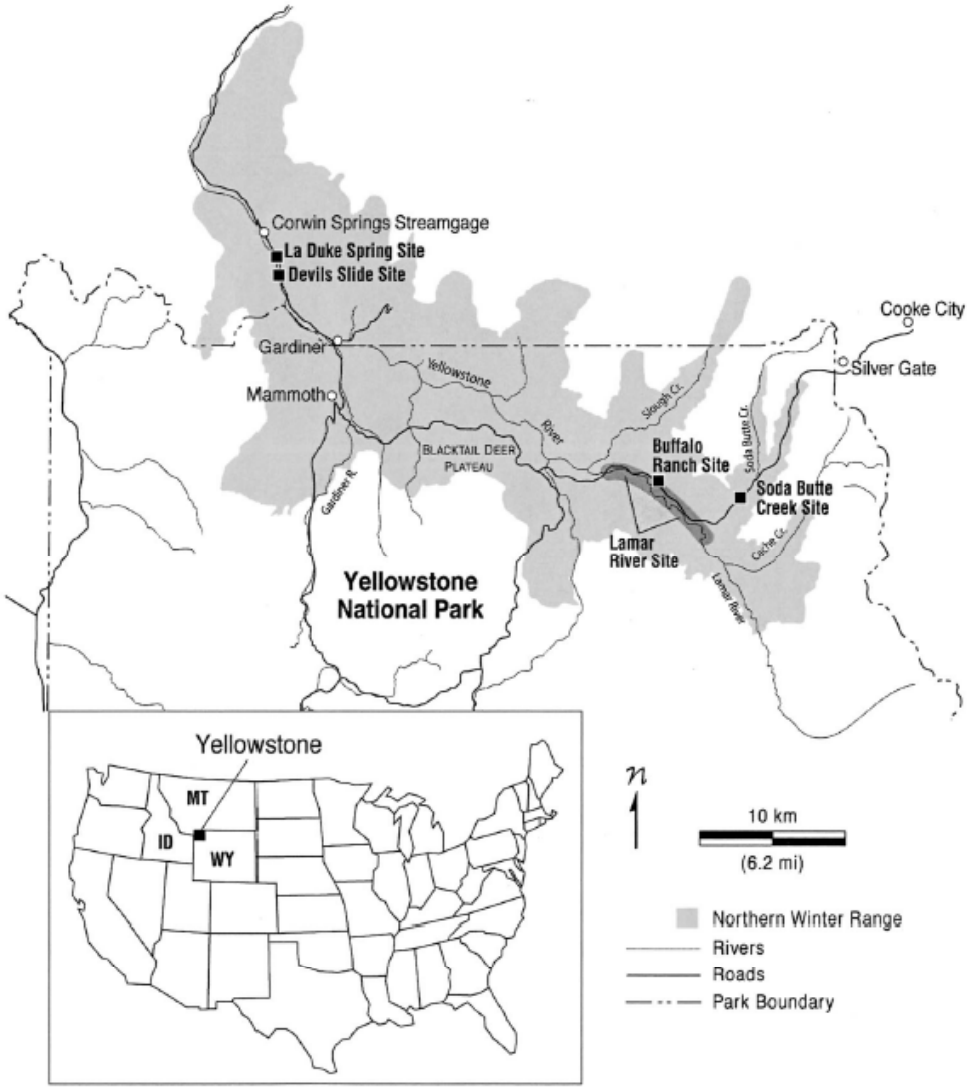


FIG. 2. Location of study sites within the northern Yellowstone elk winter range.

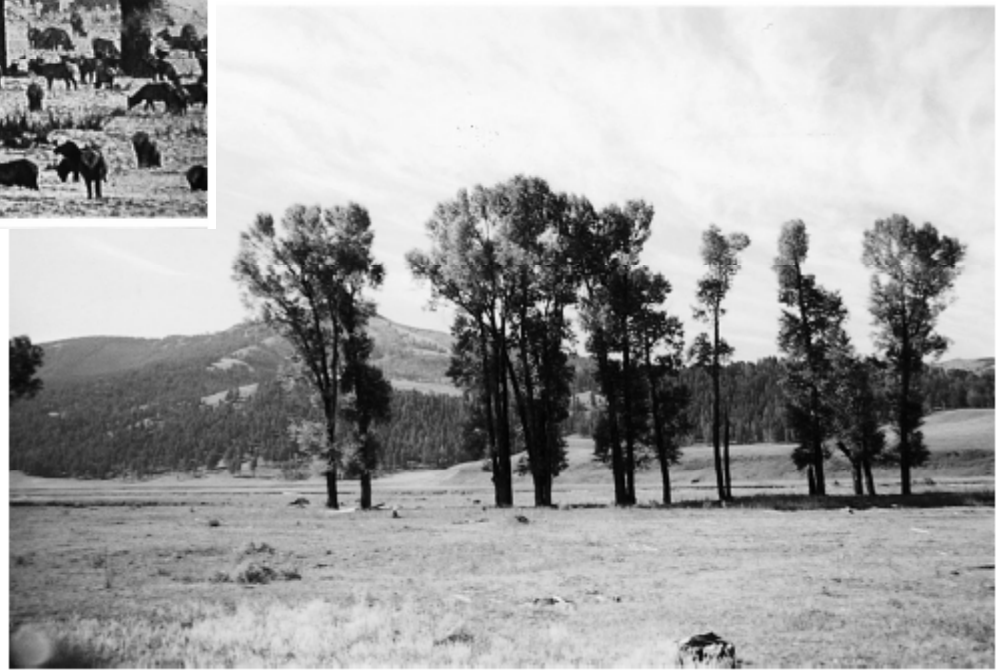
Yellowstone

- Park established in 1872. Policy of ungulate protection begun in 1886 when US Cavalry began managing park. NPS continued policy when it assumed control in 1918
- Wolves hunted and poisoned in and out of park during this period, last recorded in 1920s. Simultaneously, administrators became concerned about overgrazing.
- Removal program: ~10,000 elk in 1930s to 3000-4000 in mid-1960s.

Yellowstone

- Control efforts ended in 1968, period of "natural regulation" followed
- Herd increased to average 10,350 in 1970s, 15,550 in 1980s and 16,570 in 1990s.
- Wolf reintroduction winter 1995-6. 2002 northern range population ~78.
- Elk constitute 83% of annual wolf diet
- Elk grazing controls height of woody browse (aspen, willow, cottonwood)
- Wolves alter elk foraging location and rates

Cottonwoods 1970s (a), 2000



Beschta 2005 Ecology 86:391

Cottonwoods 1970s (a), 2000

Beschta 2005 Ecology 86:391

Beschta 2005 Ecology 86:391

Elk refuge

Elk refuge

Climatic factors?

Elk range

Elk Range

Bison Ranch

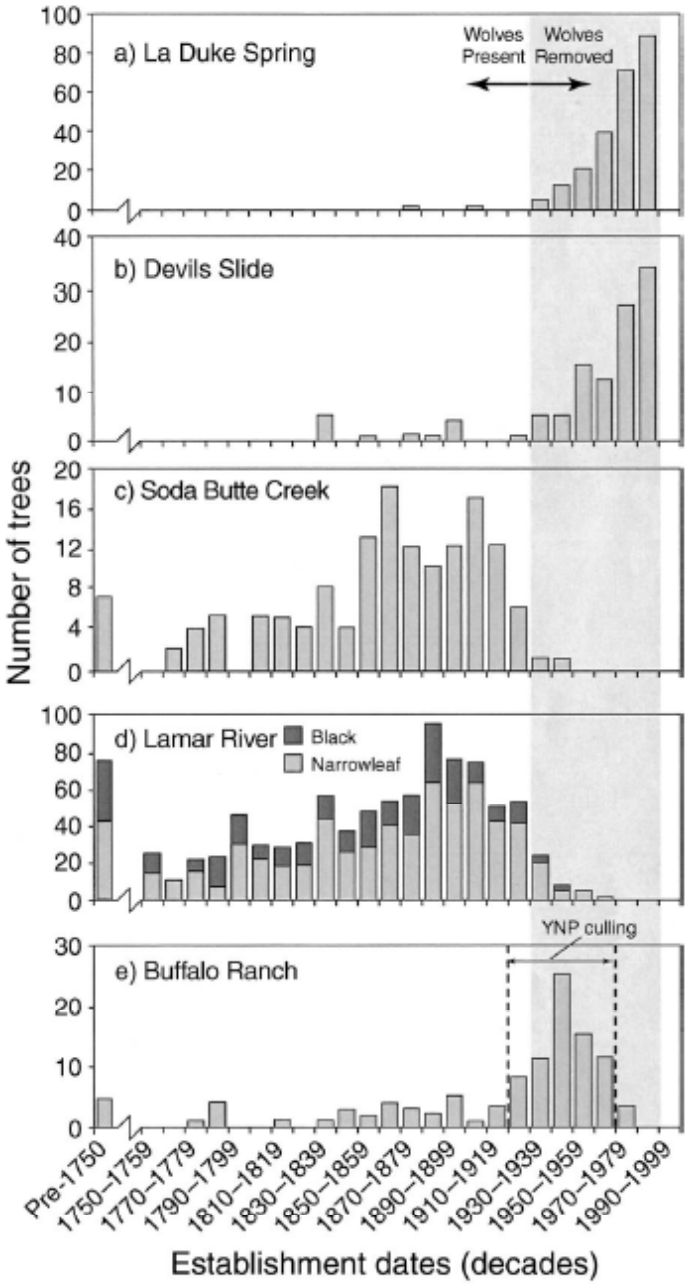


FIG. 7. Frequency distributions of cottonwood establishment dates for trees ≥5 cm in diameter at breast height (dbh) at five study sites in the northern Yellowstone elk winter range.

Trophic cascade

- Does this represent a classical cascade? Or a behavioral trophic cascade?
- Removal program: ~10,000 elk in 1930s to 3000-4000 in mid-1960s.
- Herd increased to average 10,350 in 1970s, 15,550 in 1980s and 16,570 in 1990s.

Beyer et al. 2007

Compared willow growth rates from before and after the reintroduction

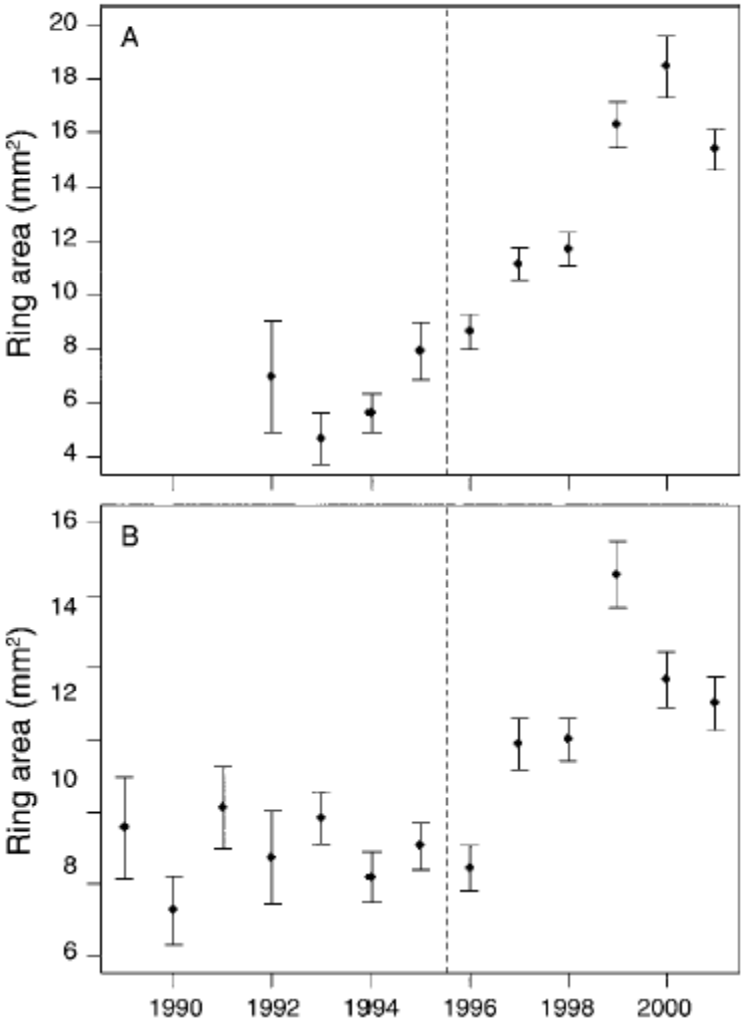


FIG. 4. Annual ring areas (mean ± SE) for (A) *Salix boothii* stems and (B) *S. geyeriana* stems, by year, collected in 2001 at 17 and eight sampling sites, respectively, on Yellowstone's northern range. The dashed line represents the first winter in which released wolves were present on the northern range following reintroduction.

Beyer et al. 2007

TABLE 2. Log likelihood values (LL), Aikaike's information criteria scores (AIC), change in AIC score (ΔAIC), and AIC weights (w_i) for the top candidate models and two reference models relating variables to annual stem ring area of *Salix boothii* and *S. geyeriana* on Yellowstone's northern range.

Model description	LL	AIC	ΔAIC	w_i
Salix boothii				
ELEV, NPIW, PRECIPA, WOLF	−1055.2	2128.4	0.0	0.53
ELEV, NPIW, PRECIPA, WSHED, WOLF	−1054.6	2129.3	0.8	0.35
ELEV, NPIW, PDSI, WOLF	−1057.3	2132.7	4.3	0.06
ELEV, NPIW, PDSI, WSHED, WOLF	−1056.8	2133.6	5.2	0.04
ELEV, NPIW, PRECIPA	−1061.3	2138.6	10.2	0.00
ELEV, PDSI, ELK	−1078.1	2172.2	43.8	0.00
Salix geyeriana				
ELEV, NPIW, WOLF	−706.0	1428.0	0.0	0.81
ELEV, NPIW, STRFLWS, WOLF	−707.2	1432.5	4.5	0.09
ELEV, NPIW, PRECIPS, WOLF	−707.4	1432.7	4.8	0.08
ELEV, NPIW, PRECIPA, WOLF	−708.7	1435.3	7.3	0.02
ELEV, NPIW	−714.3	1442.5	14.5	0.00
ELEV, NPIW, ELK	−724.6	1465.2	37.2	0.00

Notes: Variables include elevation (ELEV), watershed area (WSHED), mean winter North Pacific index (NPIW), mean annual precipitation (PRECIPA), total growing season precipitation (May–August; PRECIPS), the annual Palmer drought severity index (PDSI), a binary variable representing the presence of wolves on the landscape (WOLF), and the northern range elk population size (ELK). ELEV and WSHED are site-level variables; all the other variables are study area variables that vary between years but not between sites within a year. Only models with a weight ≥ 0.01 are reported for the top models. The reference models include the highest ranked model with the WOLF variable removed, and the highest ranked model that uses the ELK variable, but not the WOLF variable. Variable abbreviations are described in *Methods*.

Elk population size

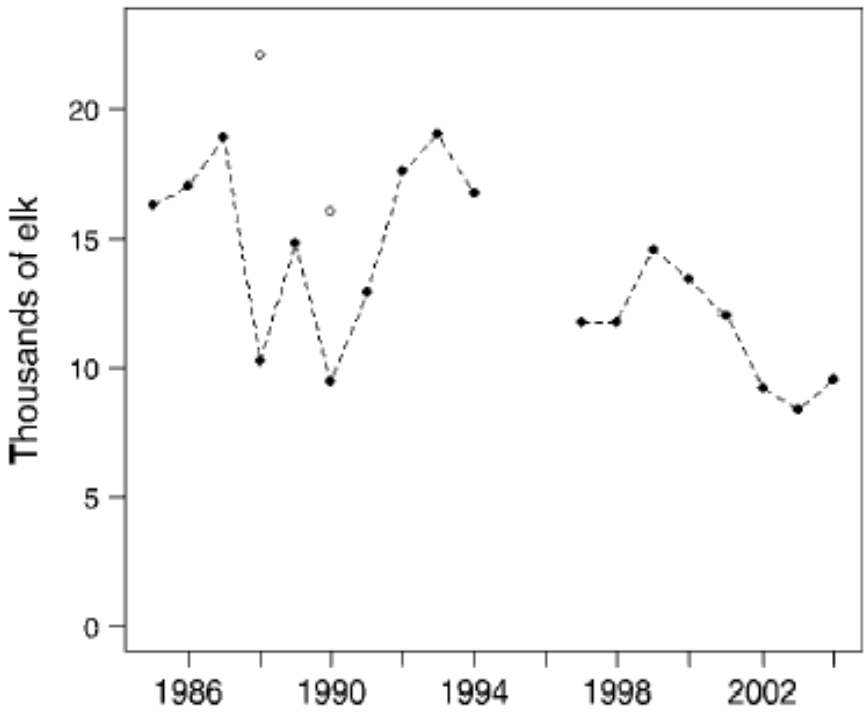


FIG. 2. Elk population counts (solid circles) on the northern winter range of Yellowstone National Park, USA (White and Garrott 2005*a*). The year corresponds to the December of the winter in which the count took place. No counts took place in the winters of 1995 and 1996. Due to poor survey conditions the counts for 1988 and 1990 are likely underestimates (White and Garrott 2005*b*); counts adjusted for sightability (open circles) in these winters were estimated by Coughenour and Singer (1996).

Herd size declining at ~4.5% /year since reintroduction, but not a good predictor

Behavioral Trophic Cascade

Changes in elk distribution or feeding habits?

Byer et al. 2007 Ecol Appln 17: 1563

Beschta and Ripple 2006

- Willows, cottonwood, aspen are all riparian species
- Can wolves affect stream riparian vegetation and stream channel morphology?

1924

1949

1961

1924

Figure 1. Photo chronosequence of the Gallatin River and floodplain showing the status of riparian willow communities along reach B in (A) summer of 1924, (B) summer of 1949, (C) late spring of 1961, and (D) summer of 2003. 'Highlining' (i.e. loss of lower branches from browsing) of relatively unpalatable conifers in the foreground is common in the 1949 photo, indicating heavy browsing pressure from elk. Extensive riparian willow communities associated with the floodplain in 1924 show progressive decline in the 1949 photo and are largely absent by 1961. Major channel changes occur between the 1949, 1961 and 2003 photos. Reach B cross-section measurements (see methods) were obtained along the floodplain shown in the right-center portion of the photos (but are largely obscured by conifer vegetation in the 2003 photo). Since wolves returned to this basin in the mid-1990s, clumps of willows have begun to grow taller and become more common as shown on the lower left portion of (D) (see also Ripple and Beschta, 2004b). Black Butte is the prominent peak in the center of each photo. [Photos: (A), (B), (C), Montana Fish, Wildlife and

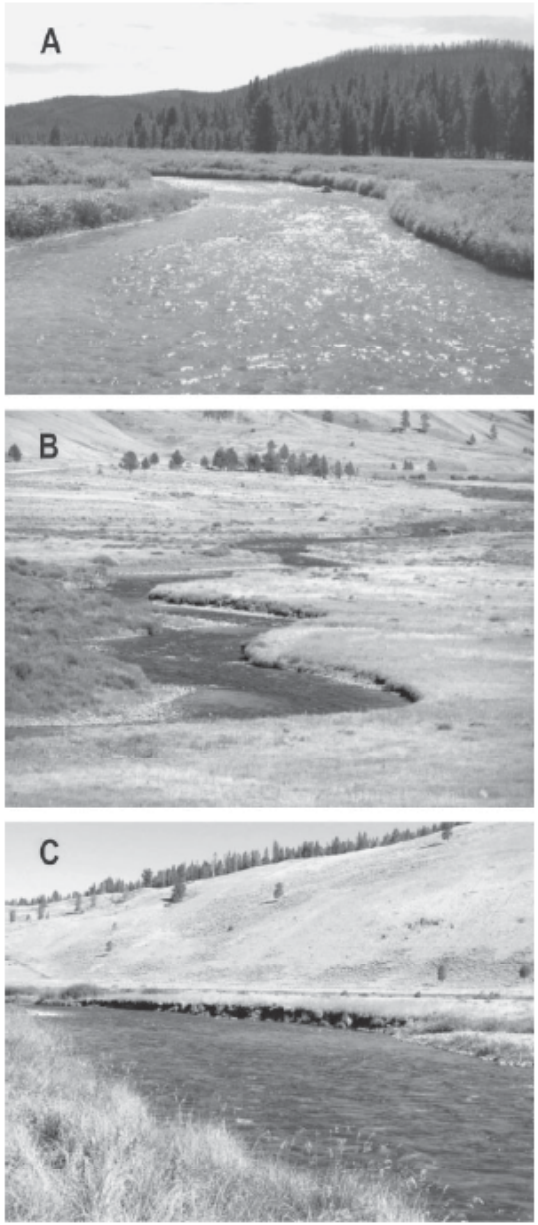


Figure 4. Photographs of (A) reach A, (B) reach B and (C) reach C along the Gallatin River in August of 2004. Note extensive cover of sedges and willows along streambanks and across the floodplain at reach A. While the willows shown along the left side of the reach B photograph represent some that have begun to recover since wolves returned to this basin in the mid-1990s, willows remain largely absent and eroding banks are common for most of reaches B and C. (Photos: R. L. Beschta.)

Flood frequency

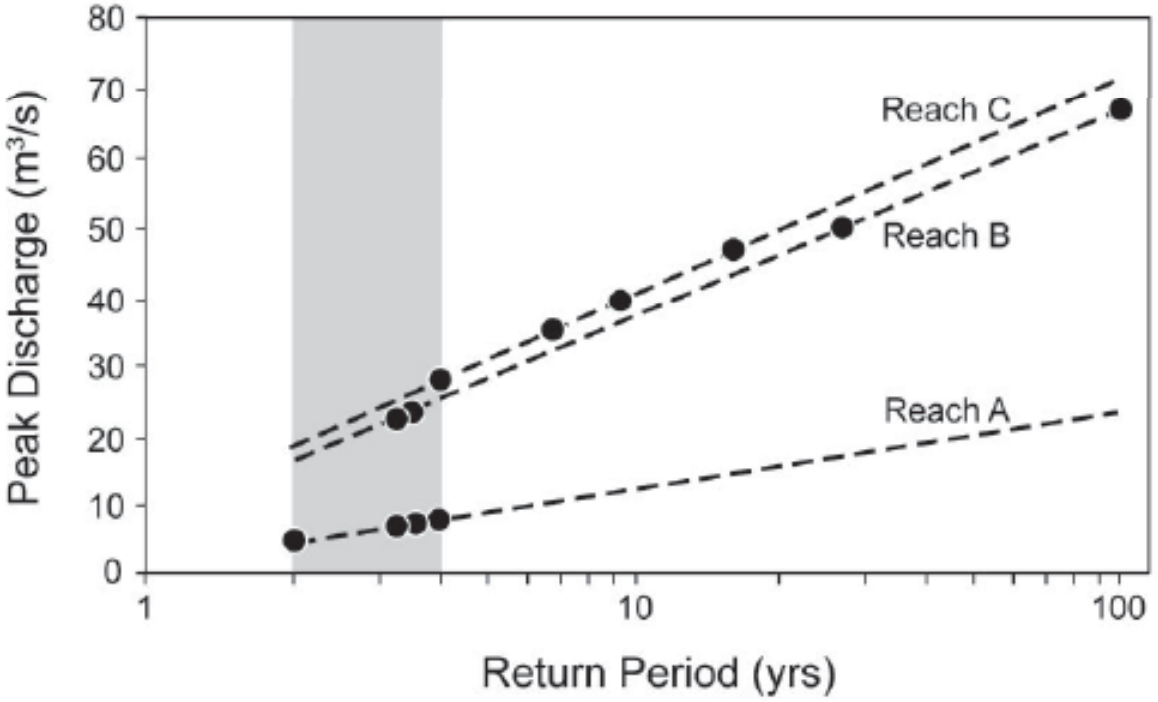


Figure 6. Discharge–frequency relationships (dashed lines) for reaches A, B and C (from regional equations in Parrett and Johnson, 2004). Plotted points represent calculated bankfull flows and associated recurrence intervals for individual cross-sections at each study reach; the shaded area encompasses the range of return periods for reach A (control).

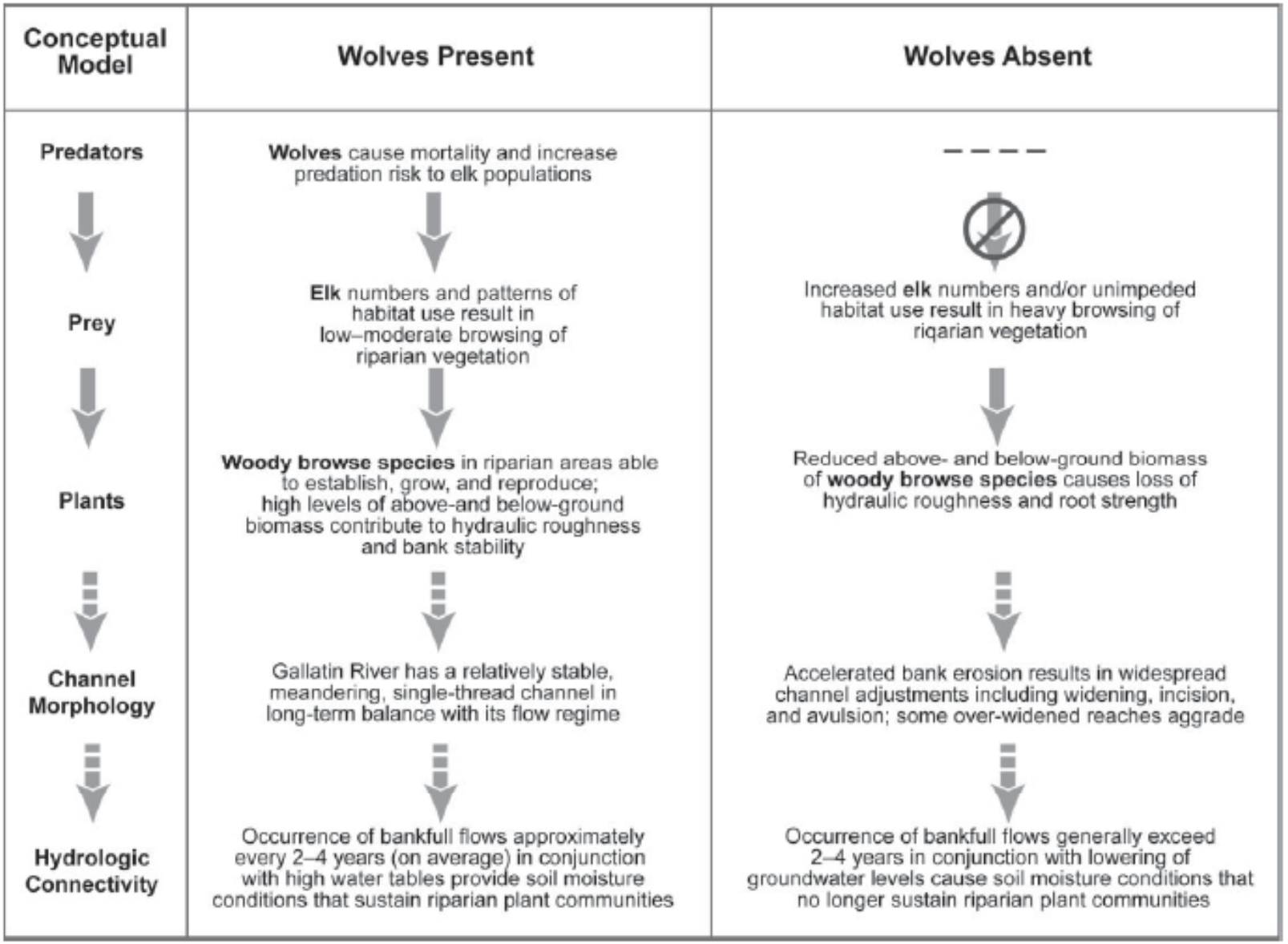
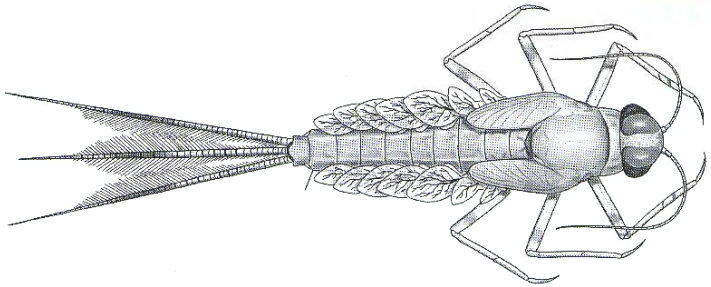
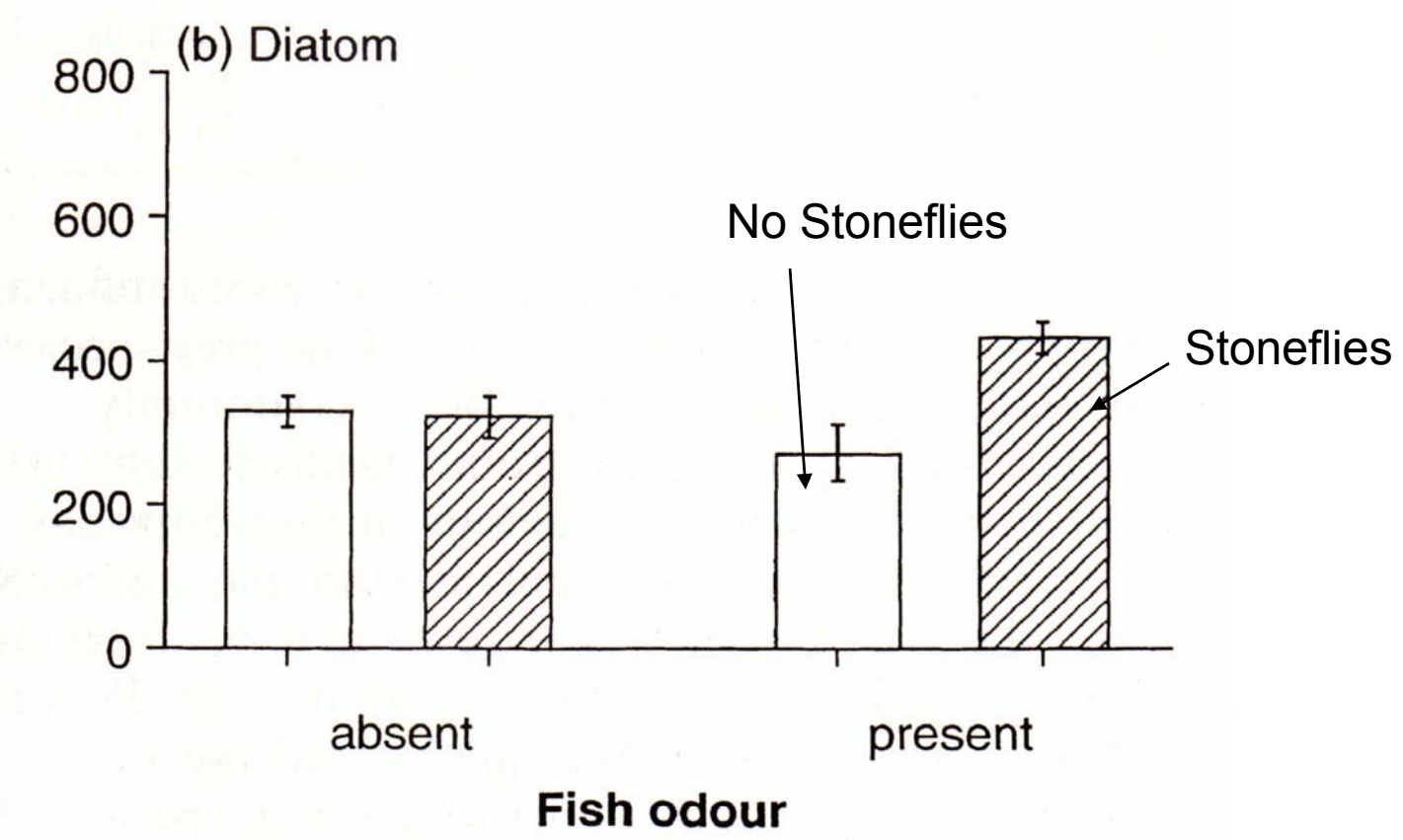


Figure 7. Summary of 'top-down' trophic cascades (solid arrows) and hydrogeomorphic processes (dashed arrows) conceptual model with and without wolves for floodplain riparian systems in the upper Gallatin elk winter range. Potential effects of bottom-up influences and interactions (see, e.g., Bower *et al.*, 2005) involving such factors as environmental carrying capacity (*k*), climate, plant succession and others are not included.

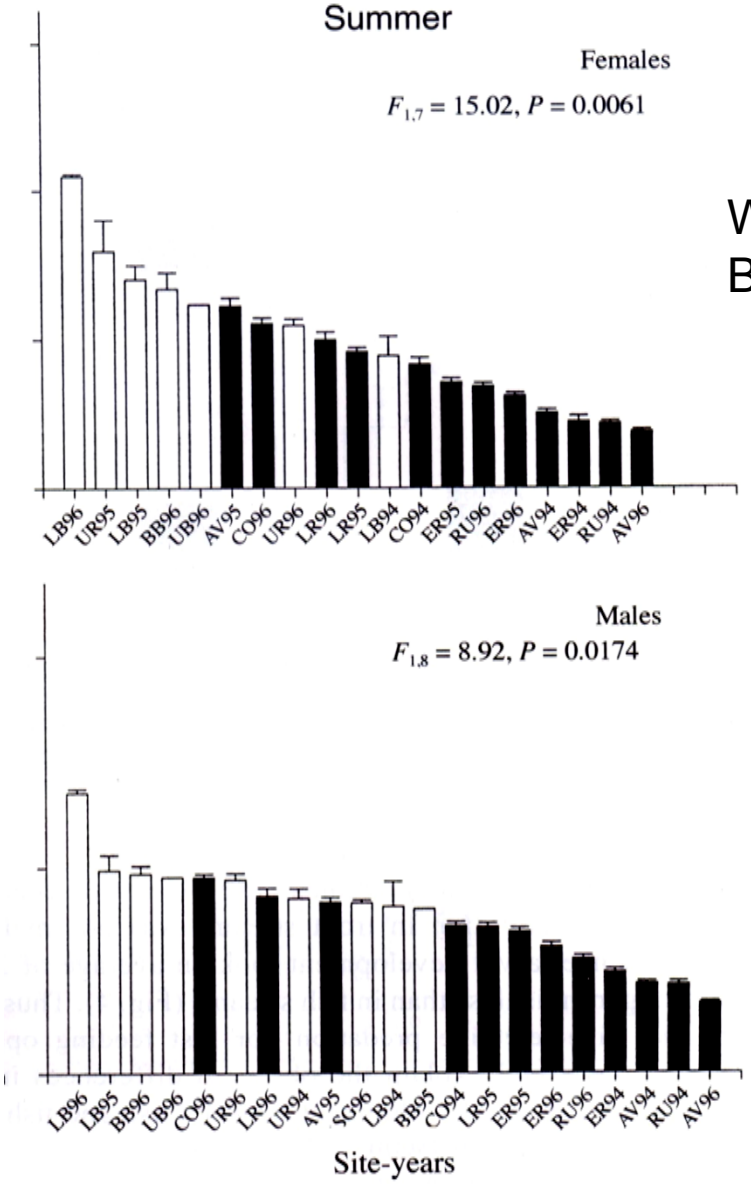
Life Cycle of *Callibaetis ferrugineus hageni:*



Stoneflies & trout cues decrease grazing on algae (behavioral trophic cascade):



Baetis size at emergence in natural populations:



White = fishless stream
Black = trout stream

Peckarsky et al. 2001

Whole-stream manipulation

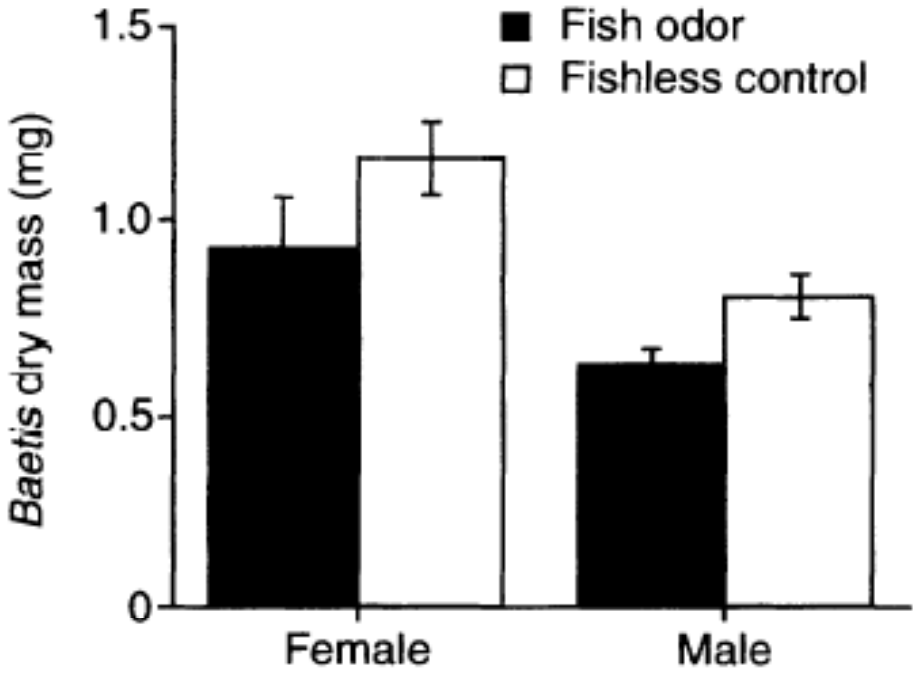


FIG. 1. Dry mass (mean ± 1 SE) of mature (black wing-pad) female and male *Baetis* larvae was lower in streams with brook trout chemicals added (solid bars) compared to control streams with only fishless water added (open bars). Data are for the summer generation, 1999.

Indirect effects of trout cues > direct effects of trout mortality on fitness:

- A demographic model suggest that removing trout mortality would increase fitness by 38.8% (λ natural population: 1.993 vs. 2.765)
- However, removing the indirect negative effects of trout on growth would increase fitness by 114.0% (λ=4.264)

McPeek and Peckarsky 1998

Wolves to mayflies?

- Could wolves affect mayfly fitness indirectly?

Fish Projects

- Flow: USGS
- Stream temperature: Not much available. Could use proxy measures.
- Ranks (high water vs. low water, warm vs. cool)