Caribou, bot-flies, lemmings and long-term population cycles in the Arctic

Andy Dobson and Peter Molnar,
EEB, Princeton University,
and
Susan Kutz,
Veterinary School,
University of Calgary,

Still very preliminary

- Three parts to the talk:

- Climate change versus land use change

- Metabolic theory of climate change - predicting impacts on free-living infective stages.

- Caribou and parasitoids ~ population cycles and host migration?

3 key questions (Rohr *et al.* 2011)

i. Can a theoretical framework be developed that allows predicting the response of any host-parasite system to climate change?

How?

ii. At which geographical locations will climate change have the greatest impacts?

Where?

iii. Which host-parasite systems are most sensitive to climate change?

Who?

Future land-use and climate change and extinction risk in birds

Walter Jetz

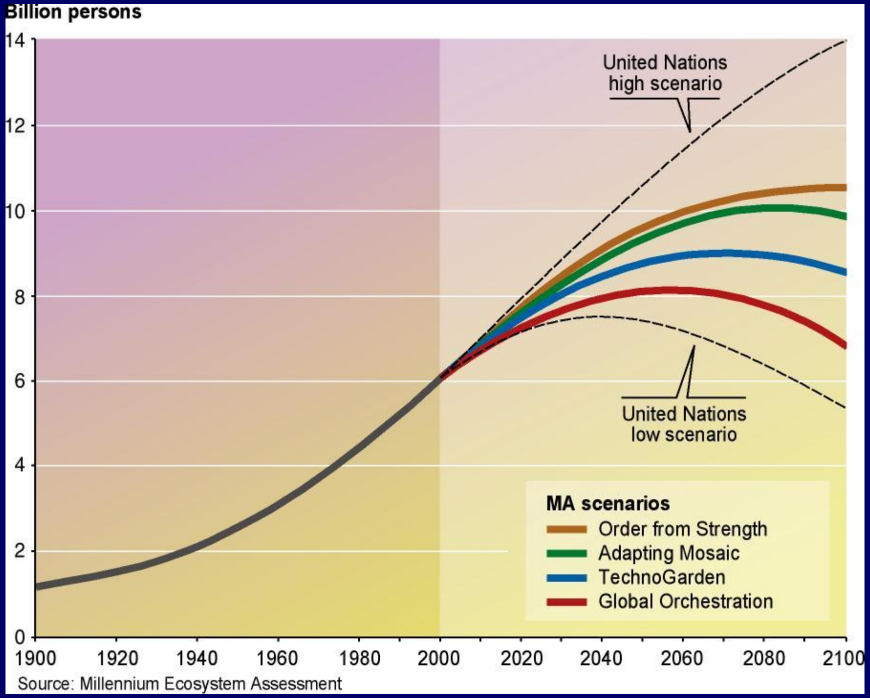
Biological Sciences
University of California San Diego

David S. Wilcove
Andy P. Dobson

Ecology, Evolutionary Biology
Princeton Univeristy

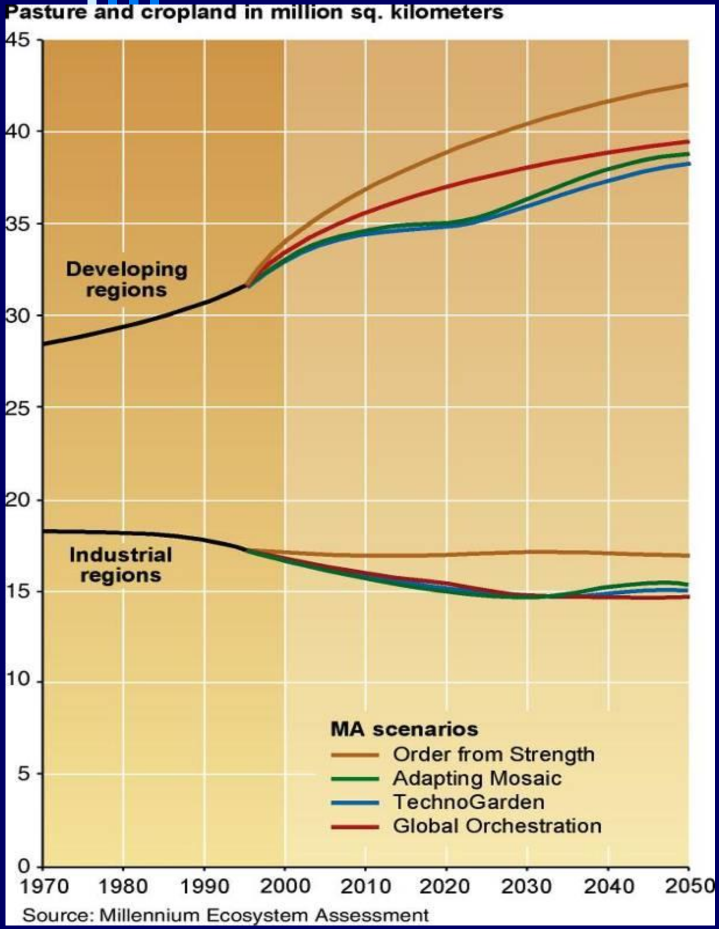
Changes in indirect drivers

- In MA Scenarios:
  - Population projected to grow to 8–10 billion in 2050
  - Per capita income projected to increase two- to fourfold

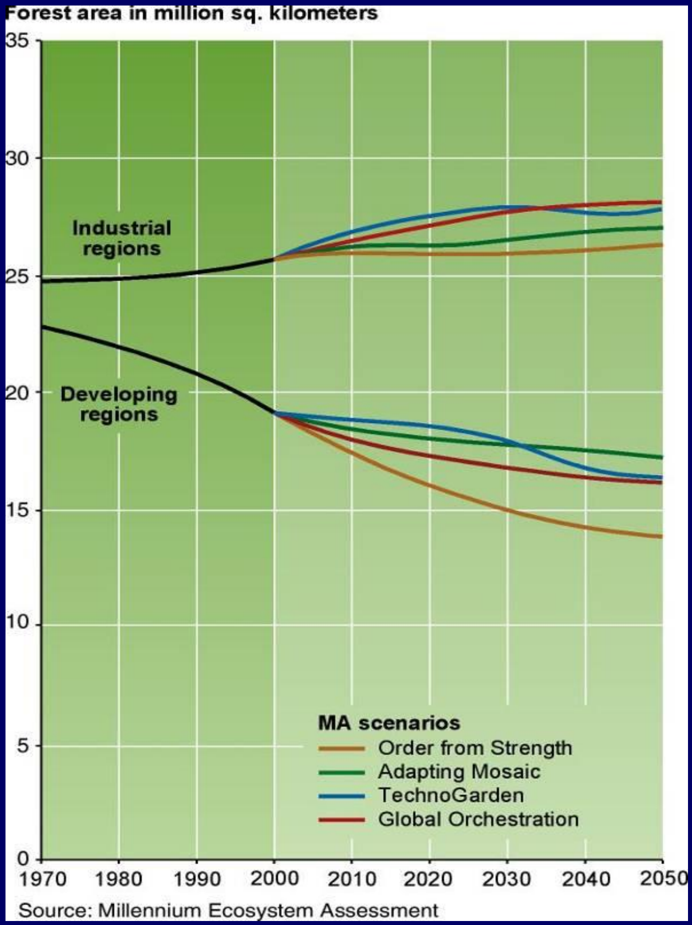


Source: Millennium Ecosystem Assessment

Changes in direct drivers

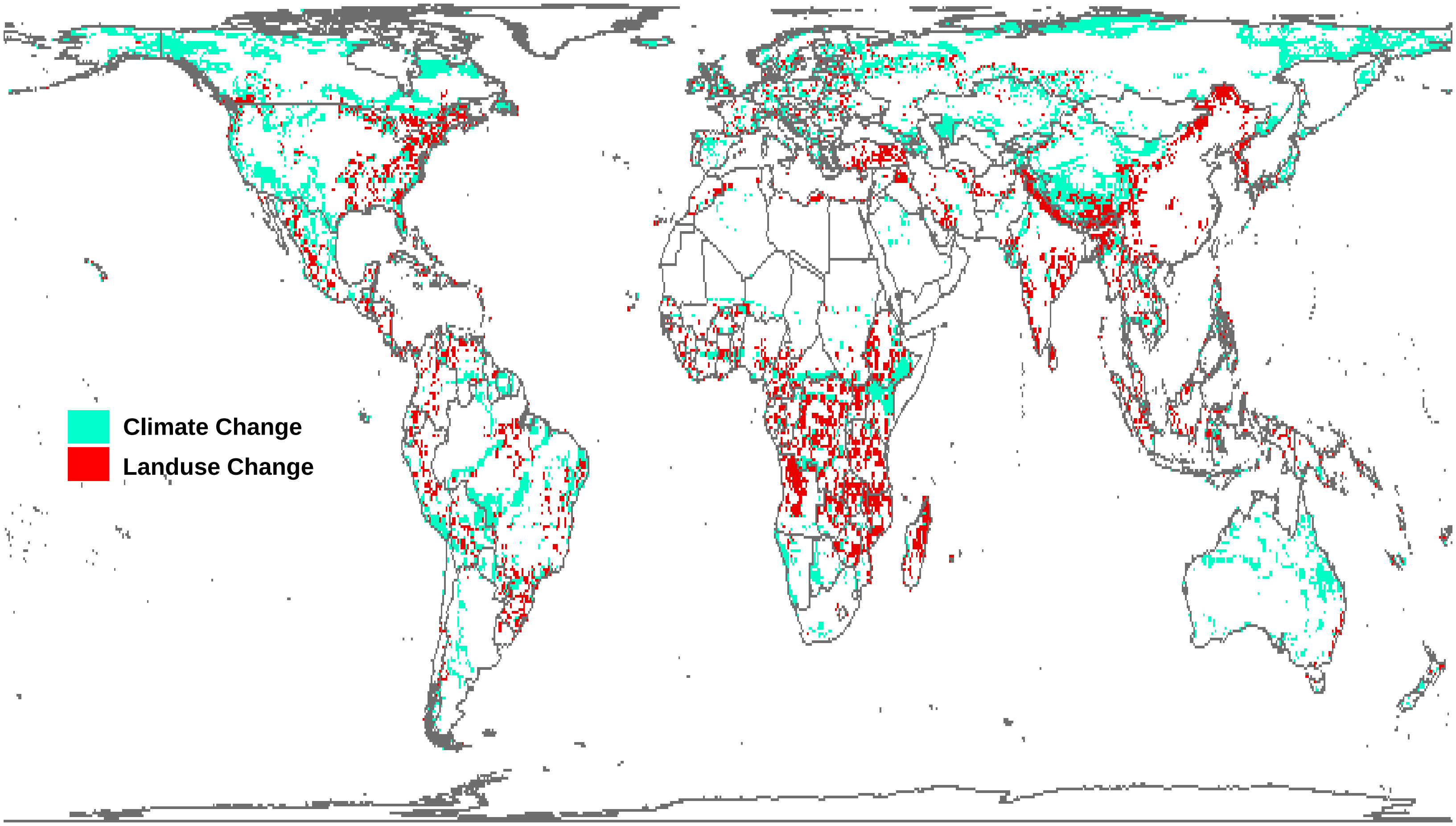


Crop Land



Forest Area

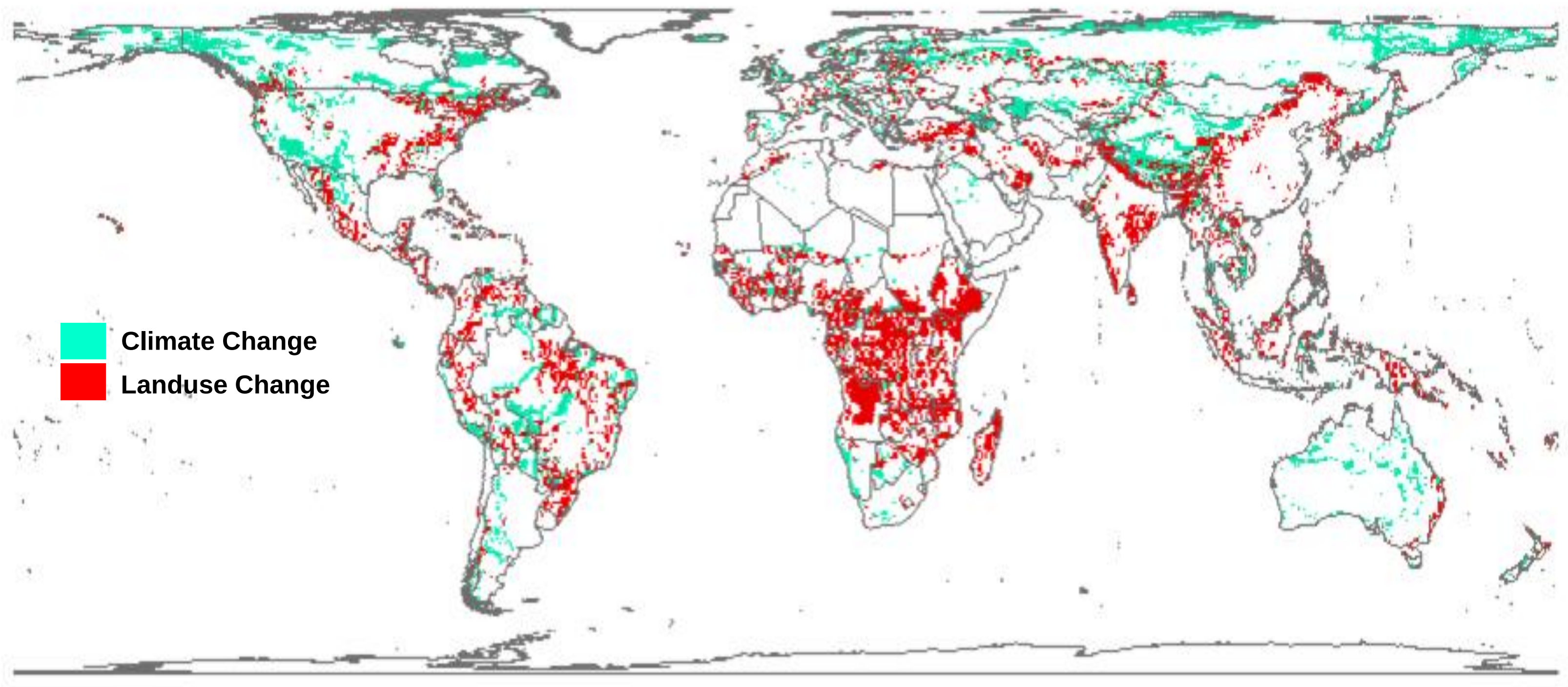
Climate and Land-use Change



Adapting Mosaic 2100

Model: Image 2.2
(Strengers et al 2005)

Climate and Land-use Change

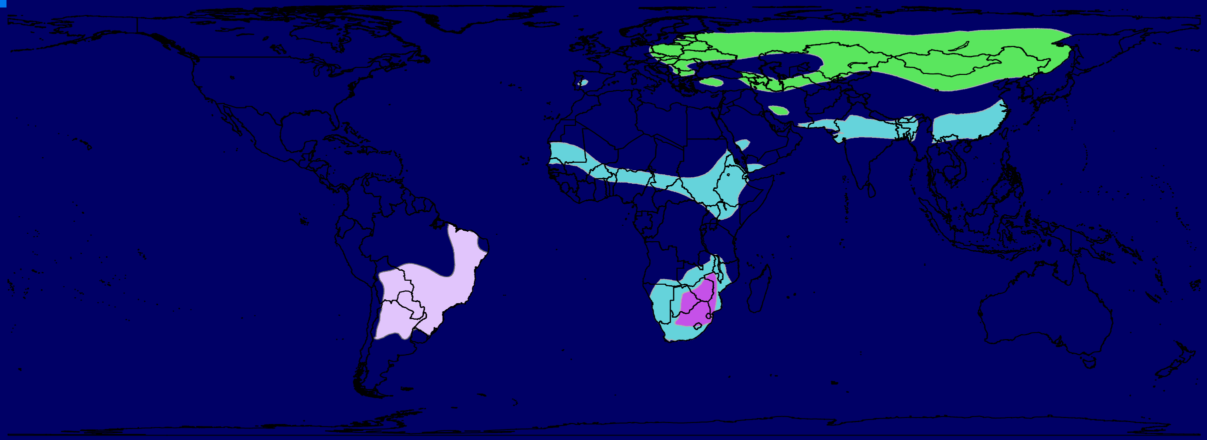


Order from Strength, 2100

Model: Image 2.2
(Strengers et al 2005)

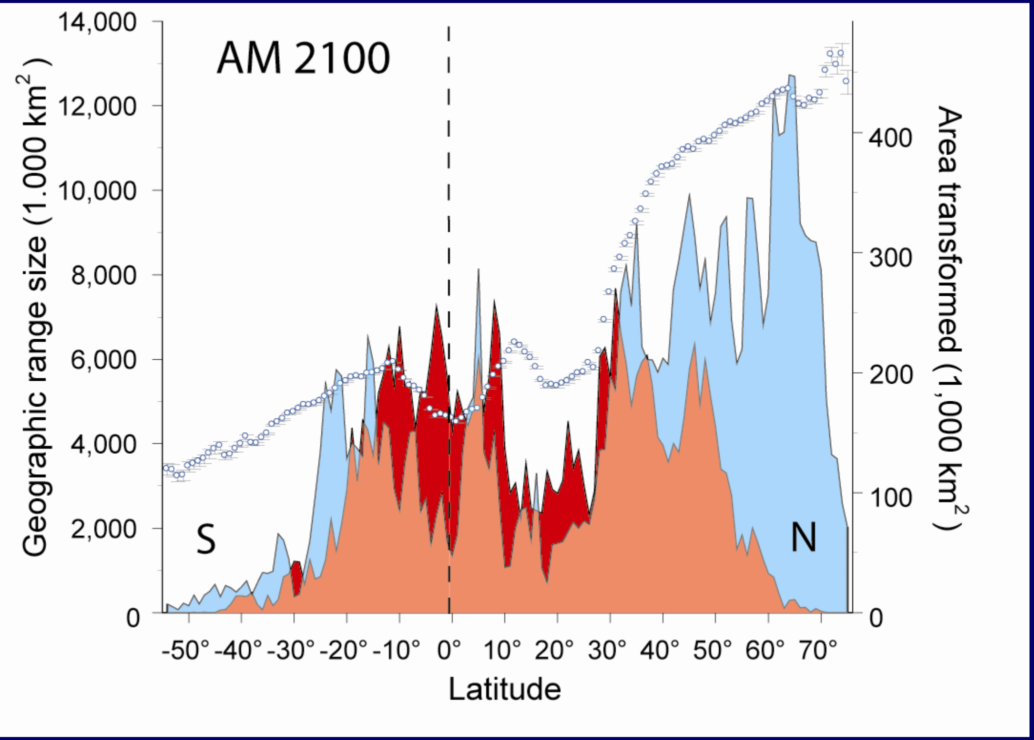
?

A global distribution database



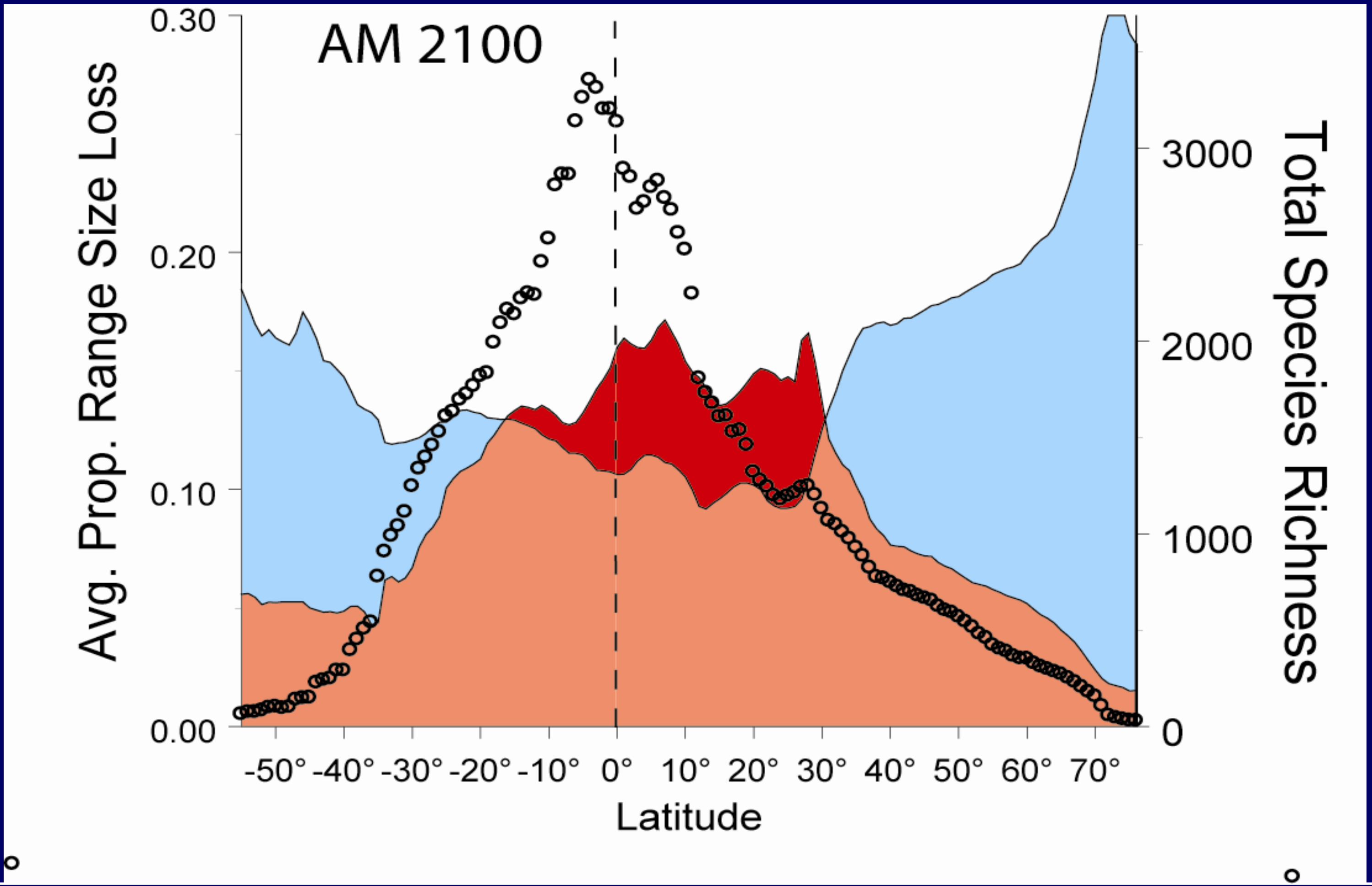
- Distribution ranges of all 9,754 species, geo-registered to known projection
- Following analysis:
  - polygon ranges resampled to 0.5° grid (259,200 quadrats)
  - 11,418,435 quadrat records
  - Excluded 838 freshwater, marine and pelagic species
  - Breeding ranges only

Latitude, Range Size and Type of Change



Red: Land-use change
Blue: Climate Change

Latitude and Proportional Range Loss



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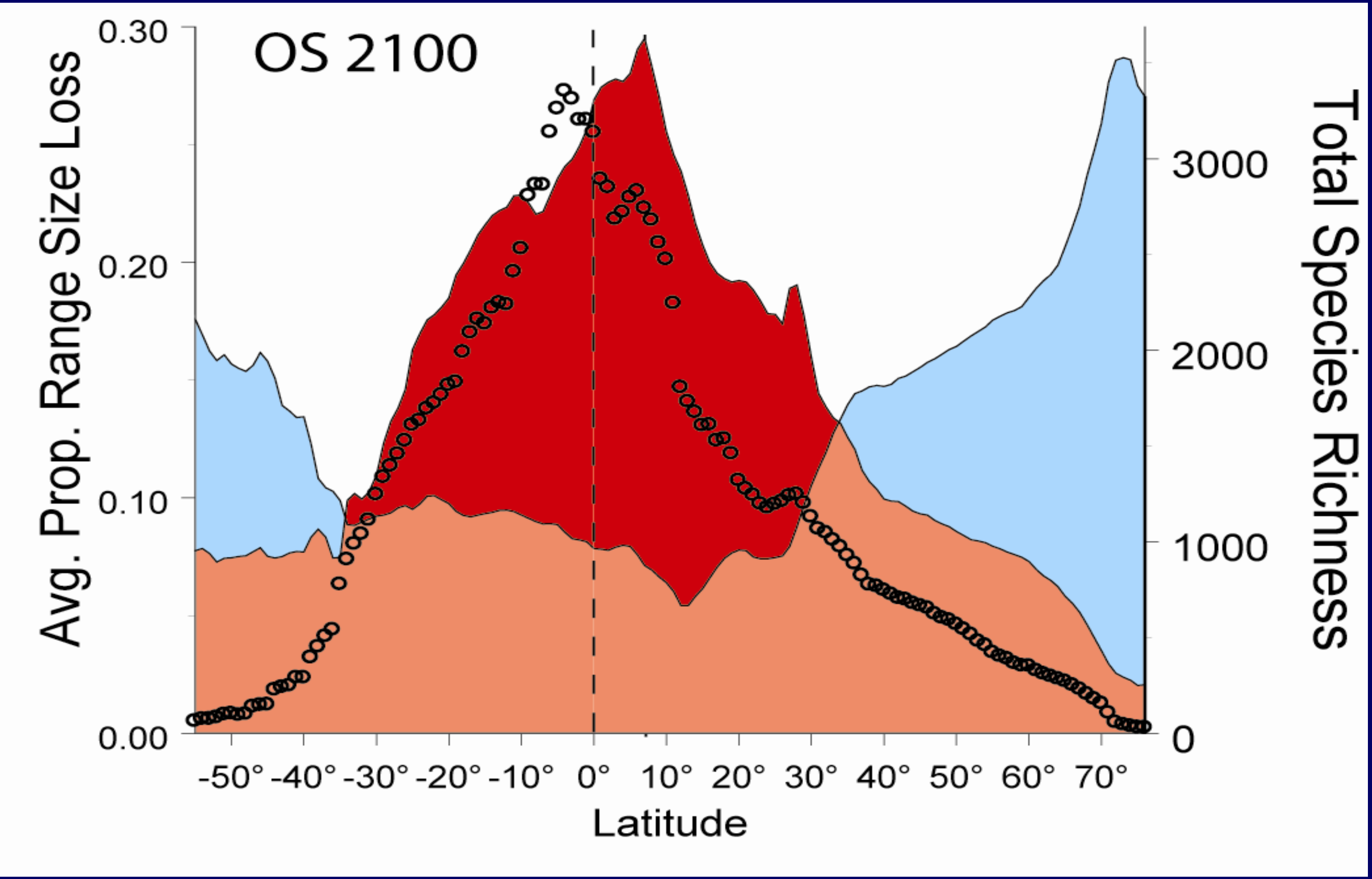
Latitude and Proportional Range Loss



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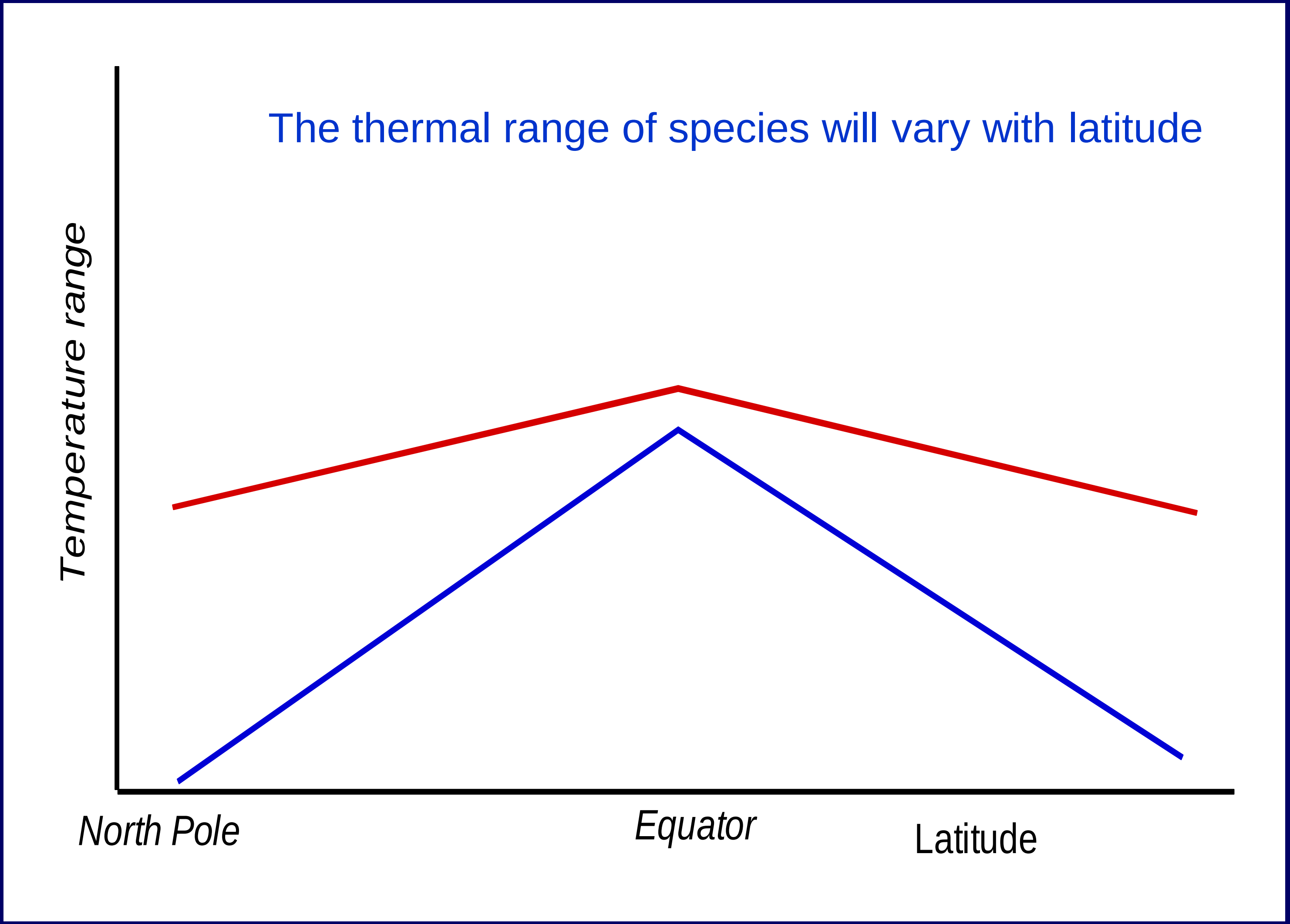
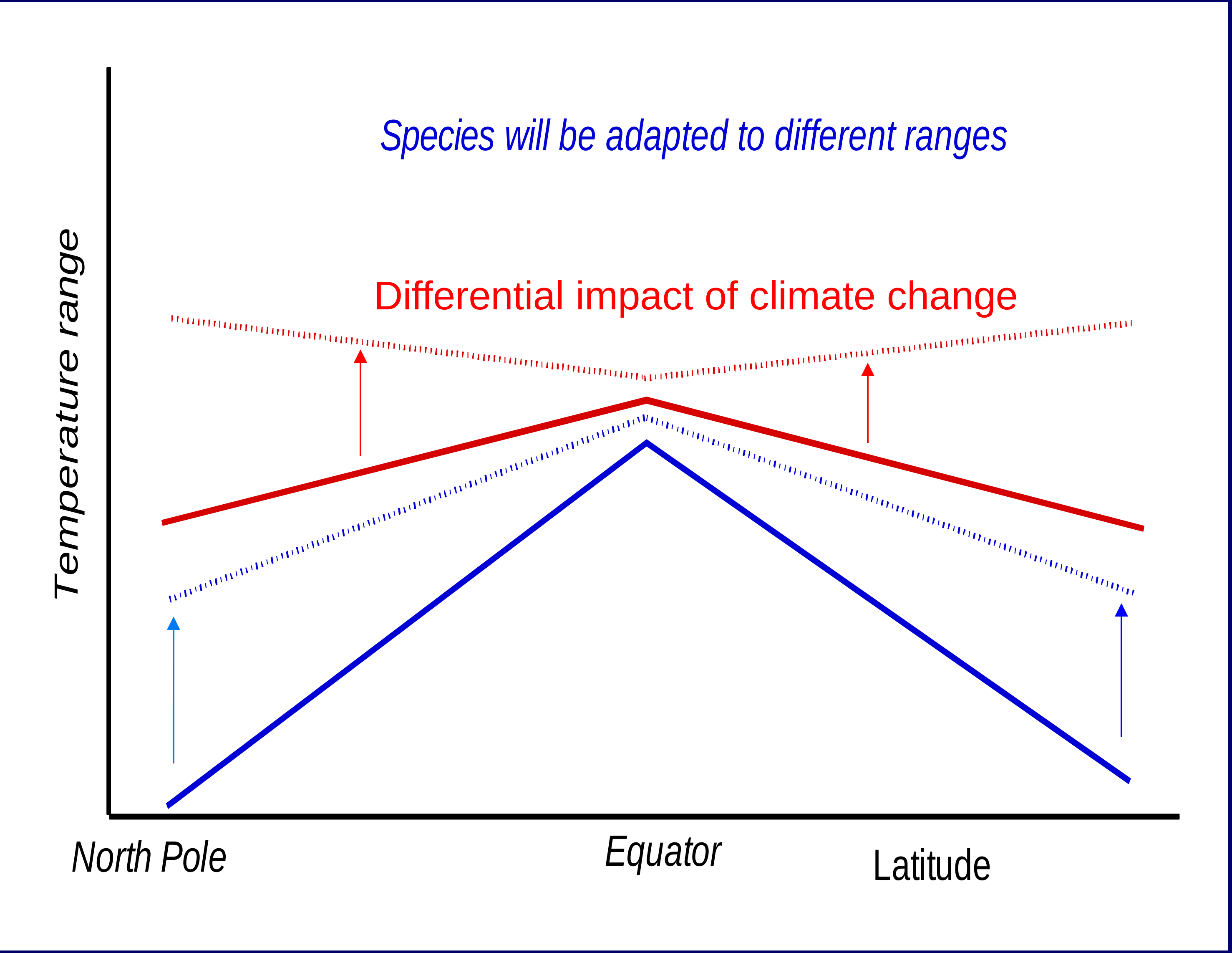
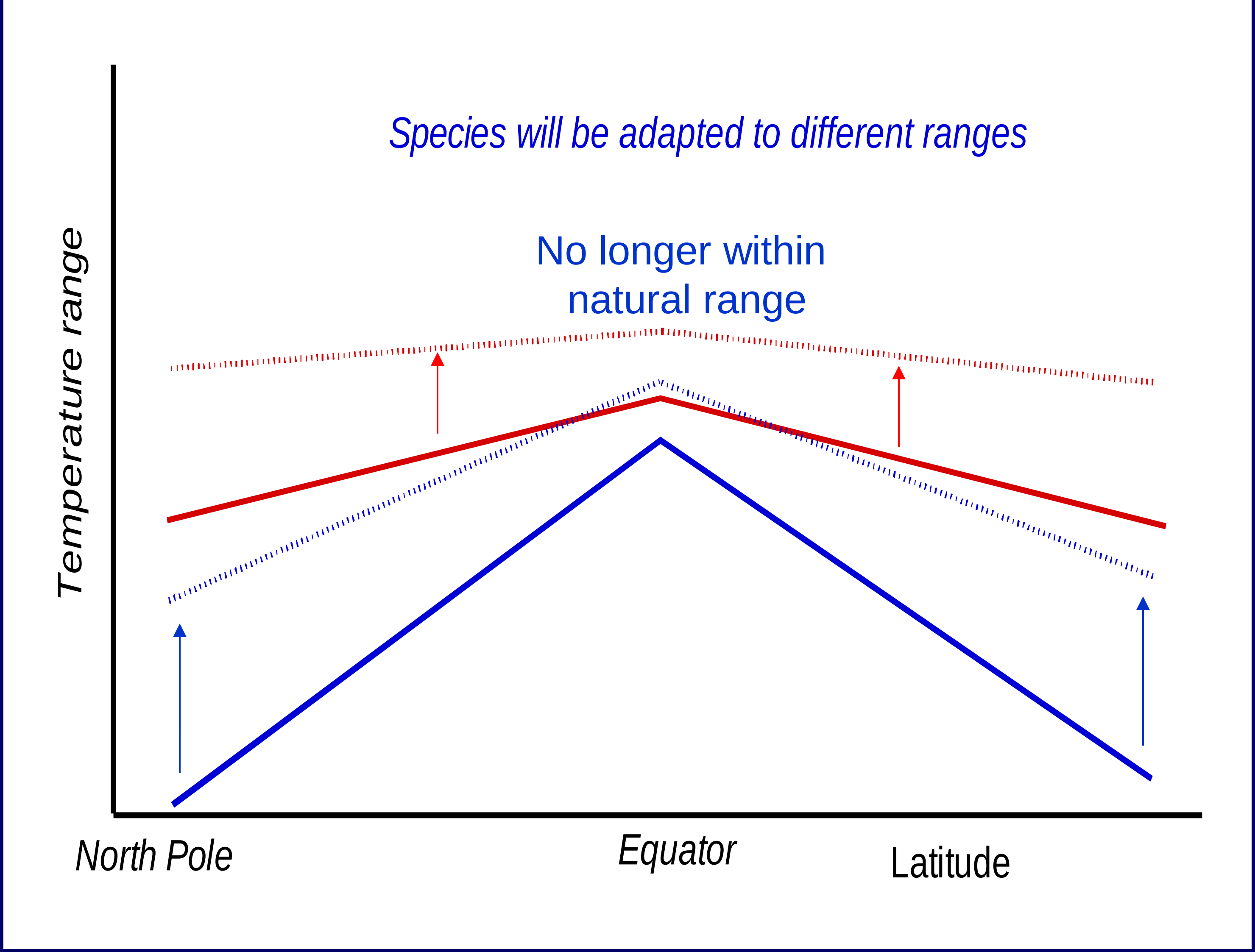


The thermal range of species will vary with latitude
Temperature range
North Pole
Equator
Latitude


Species will be adapted to different ranges
Differential impact of climate change
Temperature range
North Pole
Equator
Latitude



Species will be adapted to different ranges
No longer within natural range
Temperature range
North Pole
Equator
Latitude

INTEGR. COMP. BIOL., 44:140–151 (2004)

Keeping Pace with Fast Climate Change: Can Arctic Life Count on Evolution?[1]

DOMINIQUE BERTEAUX,[2,*] DENIS RÉALE,† ANDREW G. MCADAM,‡ AND STAN BOUTIN‡

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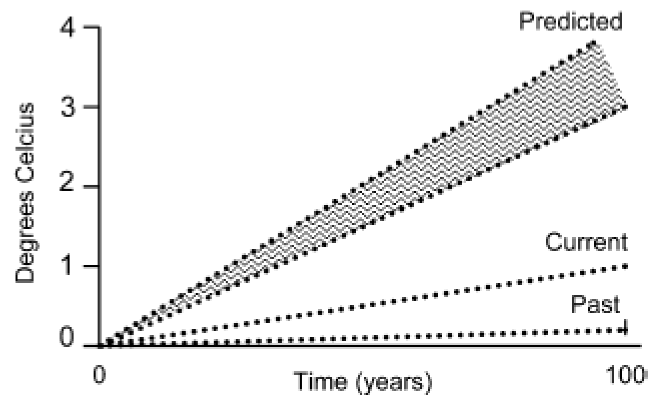

FIG. 1. Past, current, and predicted surface air temperature increases in the Canadian Arctic and Northern Hemisphere, expressed over a period of 100 years. Past increase calculated over the period 800 to 2000 from Mann-Bradley-Hughes multiproxy reconstruction of Northern Hemisphere annual temperatures (data from Fig. 3 in Esper *et al.*, 2002). Current increase calculated over the period 1900 to 2000 from surface air temperatures in the Arctic (data from Fig. 1a in Moritz *et al.*, 2002). Predicted increase calculated over the period 2000–2100 for the Arctic from the general circulation models combining the effects of projected greenhouse gas and sulphate aerosol increases—Canadian model (data from Fig. 6 in Hengeveld, 2000). Shaded area represents incertitude of model predictions.

Ecological Dynamics Across the Arctic Associated with Recent Climate Change

Eric Post,[1,2]* Mads C. Forchhammer,[2] M. Syndonia Bret-Harte,[3] Terry V. Callaghan,[4,5] Torben R. Christensen,[6] Bo Elberling,[7,8] Anthony D. Fox,[9] Olivier Gilg,[10,11] David S. Hik,[12] Toke T. Høye,[9] Rolf A. Ims,[13] Erik Jeppesen,[14] David R. Klein,[3] Jesper Madsen,[2] A. David McGuire,[15] Søren Rysgaard,[16] Daniel E. Schindler,[17] Ian Stirling,[18] Mikkel P. Tamstorf,[2] Nicholas J.C. Tyler,[19] Rene van der Wal,[20] Jeffrey Welker,[21] Philip A. Wookey,[22] Niels Martin Schmidt,[2] Peter Aastrup[2]

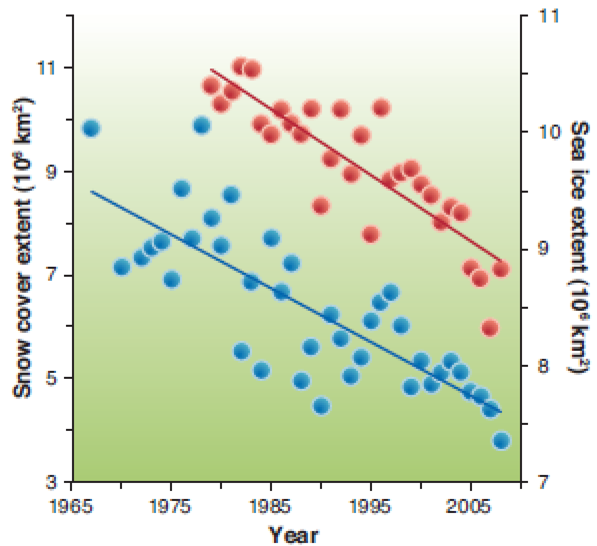

Fig. 1. Reductions in terrestrial snow cover (blue) and sea ice (red) extent during June to August over the Northern Hemisphere since the late 1960s and 1970s, respectively. Data are from the Global Snow Lab, Rutgers University, New Jersey, and the U.S. National Snow and Ice Data Center, University of Colorado, Boulder.

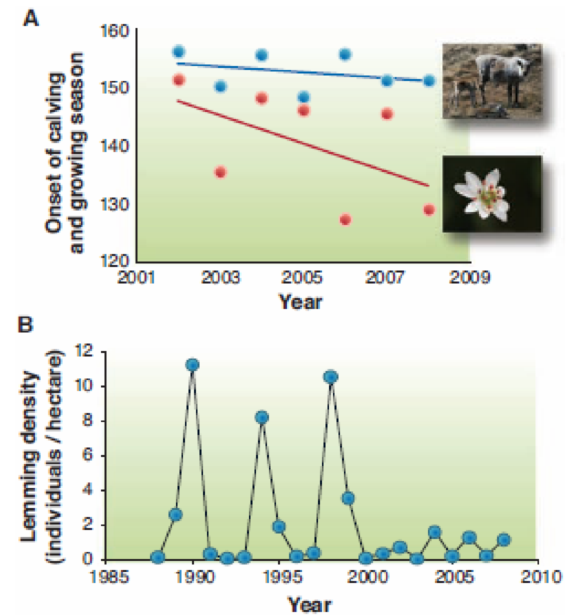

Fig. 3. Complex responses to Arctic climate change that may have broader community and ecosystem consequences. **(A)** A developing trophic mismatch between the timing of caribou calving (blue), which has not changed, and the timing of plant growth (red), which is advancing with warming in Greenland [updated from (*33*)]. **(B)** The recent observed collapse in the population cycles of small rodents, shown here for lemmings in northeast Greenland, as a result of diminished snow cover in the Arctic [from (*36*)].

Science AAAS

Ecological Dynamics Across the Arctic Associated with Recent Climate Change
Eric Post, *et al.*
Science **325**, 1355 (2009);
DOI: 10.1126/science.1173113

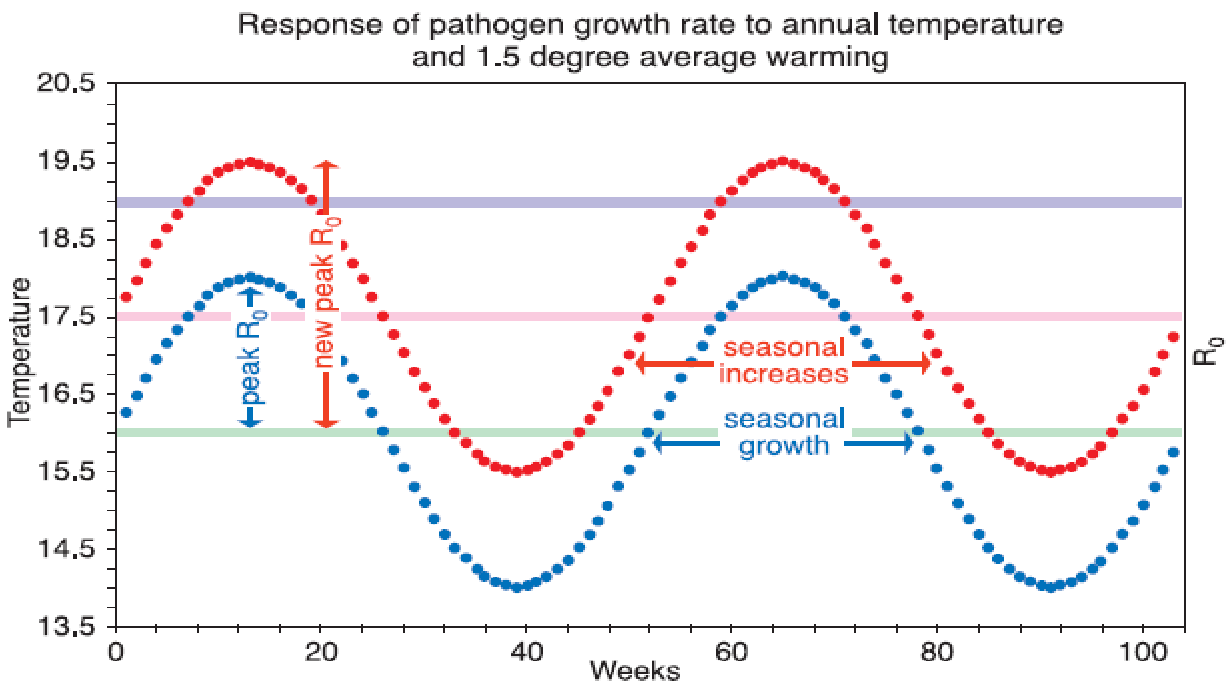

Fig. 2. The influence of an average 1.5° rise in temperature on the basic reproductive number R_0 of a hypothetical pathogen. When R_0 is above 1, a pathogen will increase. The lower blue line illustrates the average weekly temperature before climate change; the upper red line illustrates average weekly temperature after an average 1.5° temperature increase. The lower green line corresponds to $R_0 = 1$; below this temperature the pathogen declines in abundance. The pathogen increases at temperatures above this, and we assume that disease problems become severe when temperature exceeds the pink line and epidemic above the purple line. The figure illustrates that increases in temperature not only allow the peak value of R_0 to increase, but also lead to an increased annual duration of the period during which the pathogen is a problem.

Climate Warming and Disease Risks for Terrestrial and Marine Biota
C. Drew Harvell *et al.*
Science **296**, 2158 (2002);
DOI: 10.1126/science.1063699

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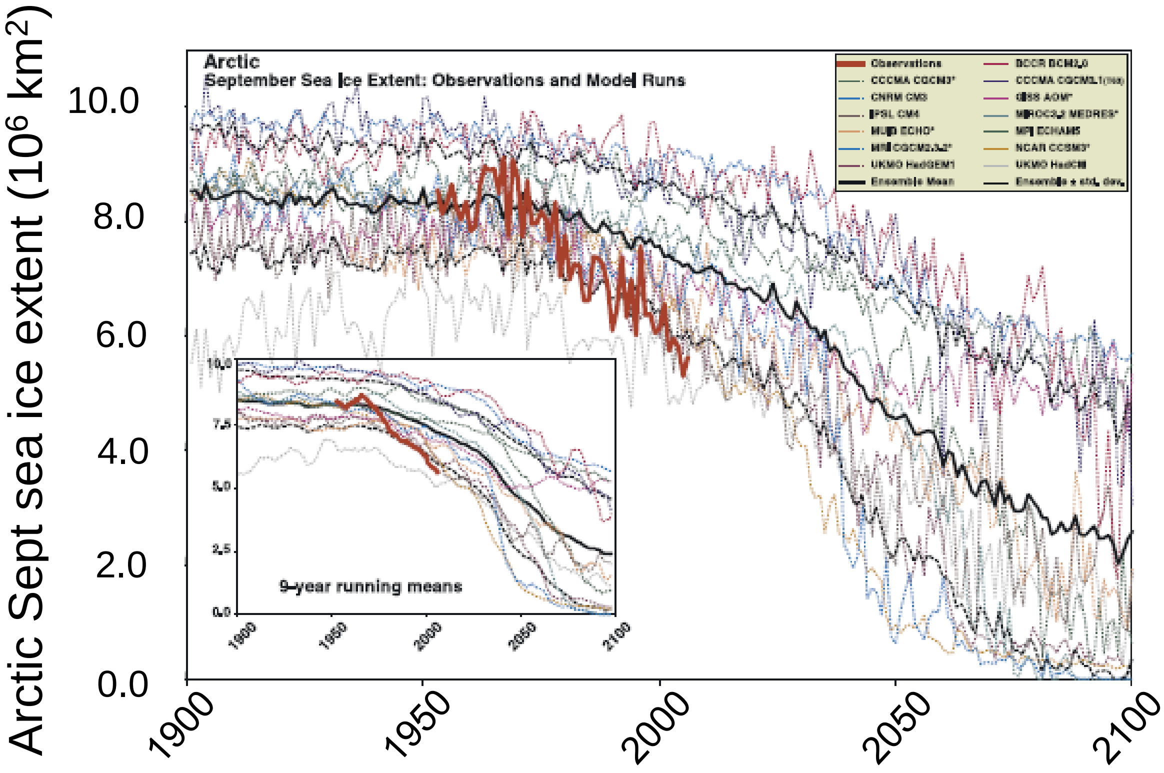


Stroeve *et al.* (2007), Geophys. Res. Lett.

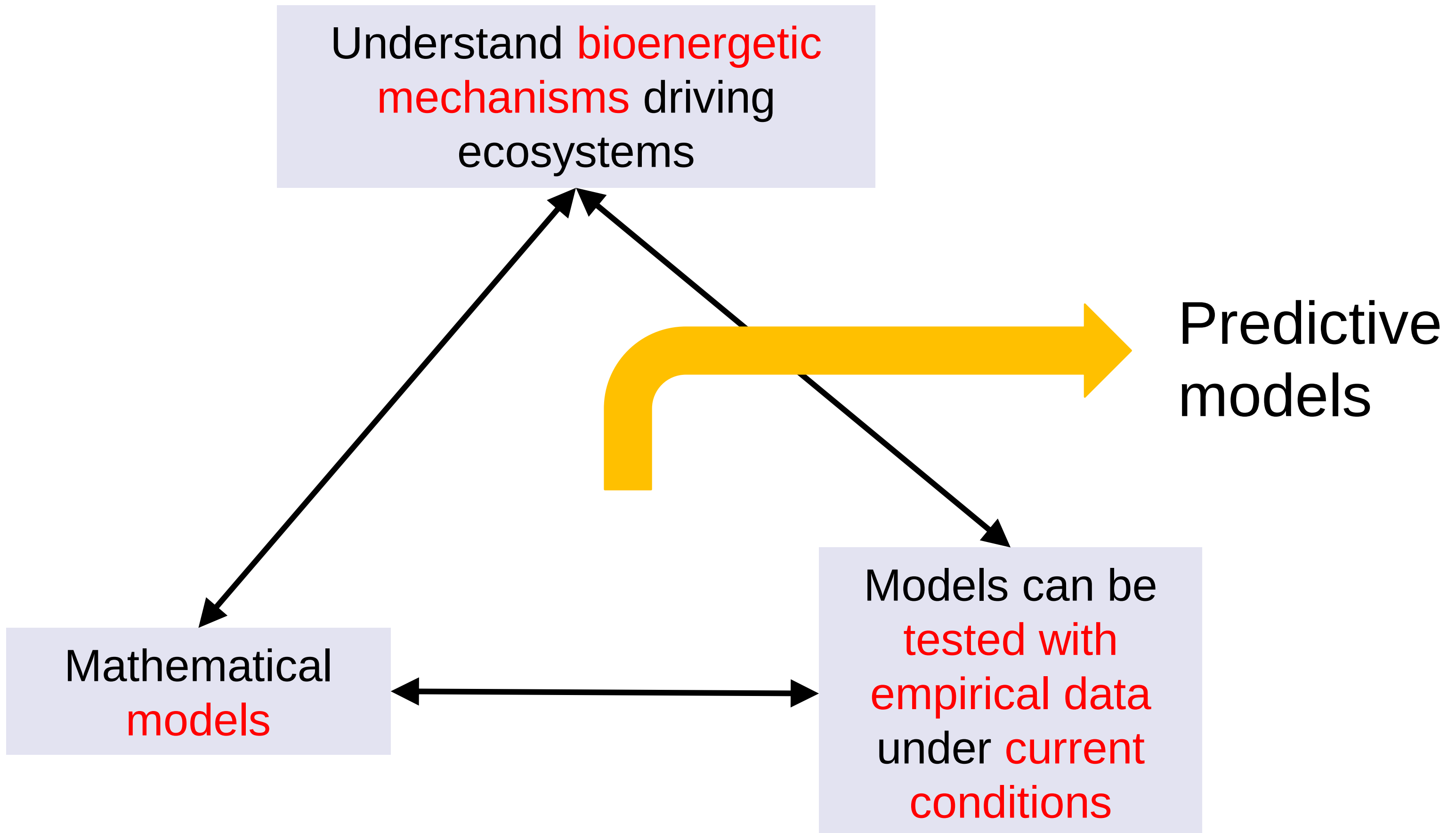
How can the response of ecosystems be predicted with confidence if they have never been observed under future conditions?

Ecological Impacts of Climate Change

Predictive framework needed

Bioenergetic (mechanistic) approach

(the laws of thermodynamics will NOT change)

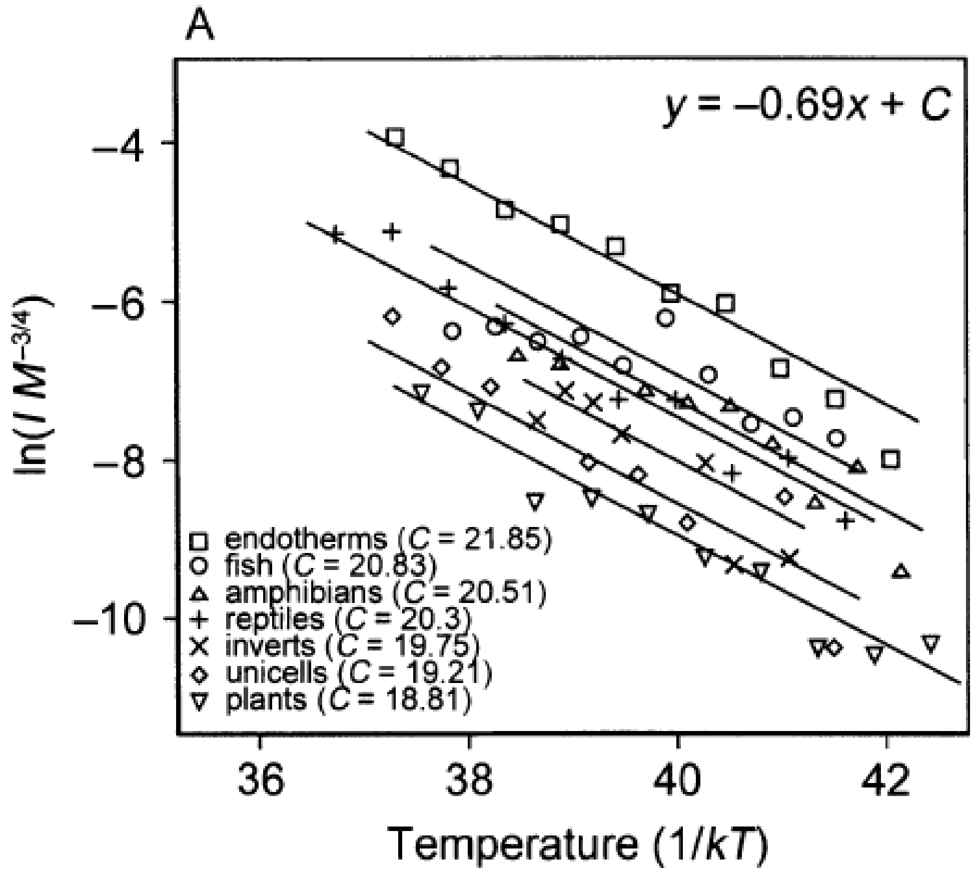


I. Metabolic Theory of Ecology (MTE)

- Physiological rates scale with temperature according to Arrhenius relationship and with activation energies $E \approx 0.65$ eV

Metabolic rate

$$I(T) = i_0 e^{\frac{E}{k}\left(\frac{1}{T} - \frac{1}{T_0}\right)}$$



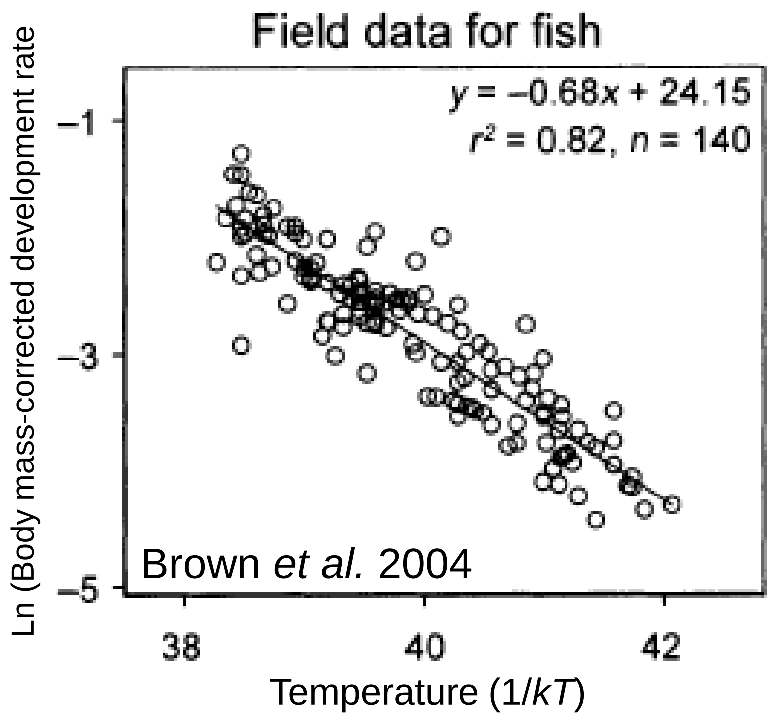
Brown *et al.* (2004), Ecology

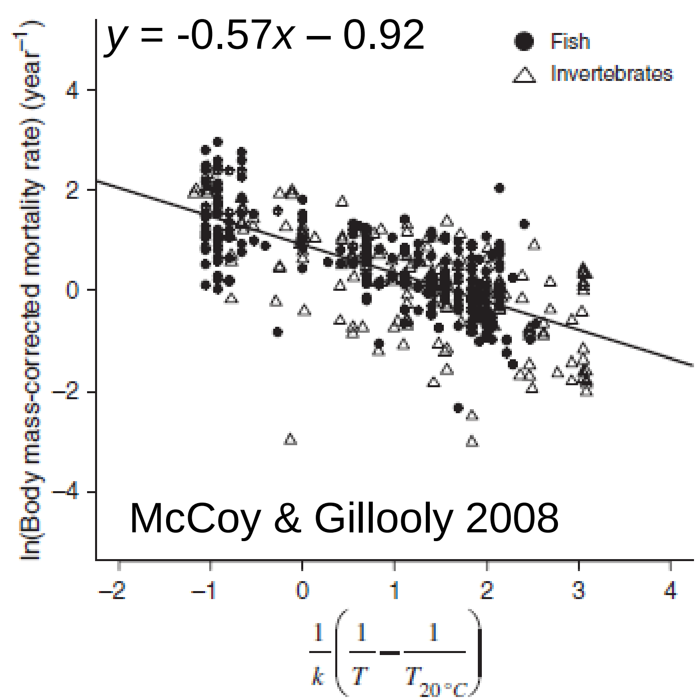
Development rate

$$\tau(T) = \tau_0 e^{-\frac{E}{k}\left(\frac{1}{T}-\frac{1}{T_0}\right)}$$

Mortality rate

$$\mu(T) = \mu_0 e^{-\frac{E}{k}\left(\frac{1}{T}-\frac{1}{T_0}\right)}$$





Population growth, carrying capacity, species diversity,…

Climate Change and Parasites

Direct Effects:

Transmission season length
Parasite development rates
Changing parasite survival

Shorter generation times with warming?

Indirect Effects:

Altered host ranges – new hosts, novel pathogens, host switching?
Changing biodiversity – dilution / amplification effects?
New stresses on host populations
…

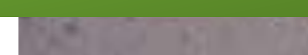
Predictive tools needed for disease management

Can we predict impacts of climate change?

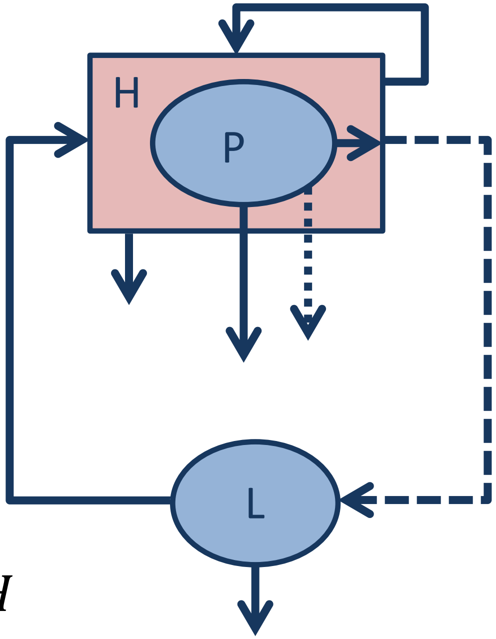
(direct: transmission season, development/generation time, mortality,...)
(indirect: host ranges, host switching, new stresses on hosts, …)

Focus on direct thermal effects first
(development time, mortality)

<u>Approach:</u> R_0 (expected lifetime reproductive output of newborn larva) under various environmental conditions



Calculating R_0



Host dynamics $$H = constant$$

Free-living infective stages $$\frac{dL}{dt} = \lambda D_L^D(T)P\big(t - \tau_L(T)\big) - \mu_L(T)L - \rho_H LH$$

Adult parasites within host $$\frac{dP}{dt} = \rho_H D_P LH(t - \tau_P) - (\mu_P + b_H)P - \alpha_H H\left(\frac{P}{H} + \frac{P^2}{H^2}\frac{k_H + 1}{k_H}\right)$$

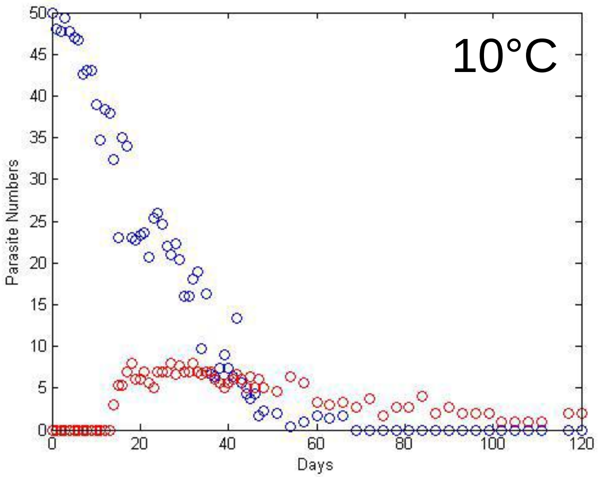
$$R_0(T) = \frac{D_L^D(T)D_P\lambda}{\alpha_H + b_H + \mu_P} \cdot \frac{\rho_H H}{\mu_L(T) + \rho_H H}$$

What are parameters of R_0?

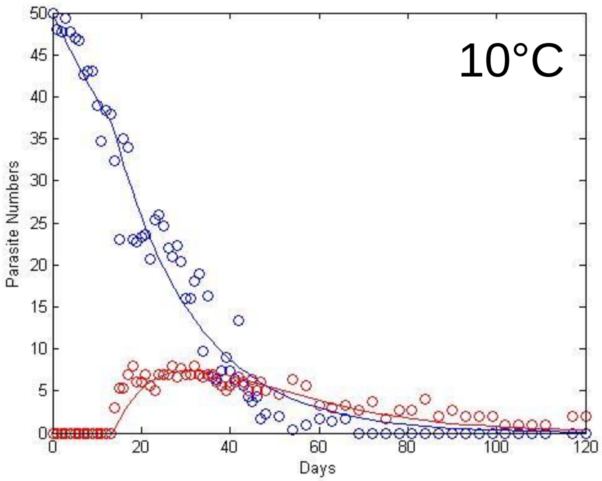
$$R_0(T) = C \cdot \frac{\exp(-\tau_L(T) \cdot \mu_L(T))\rho H}{\mu_L(T) + \rho H}$$

- parasite development time
- parasite mortality

One could go to the lab…



…and fit a development/ mortality model to data…

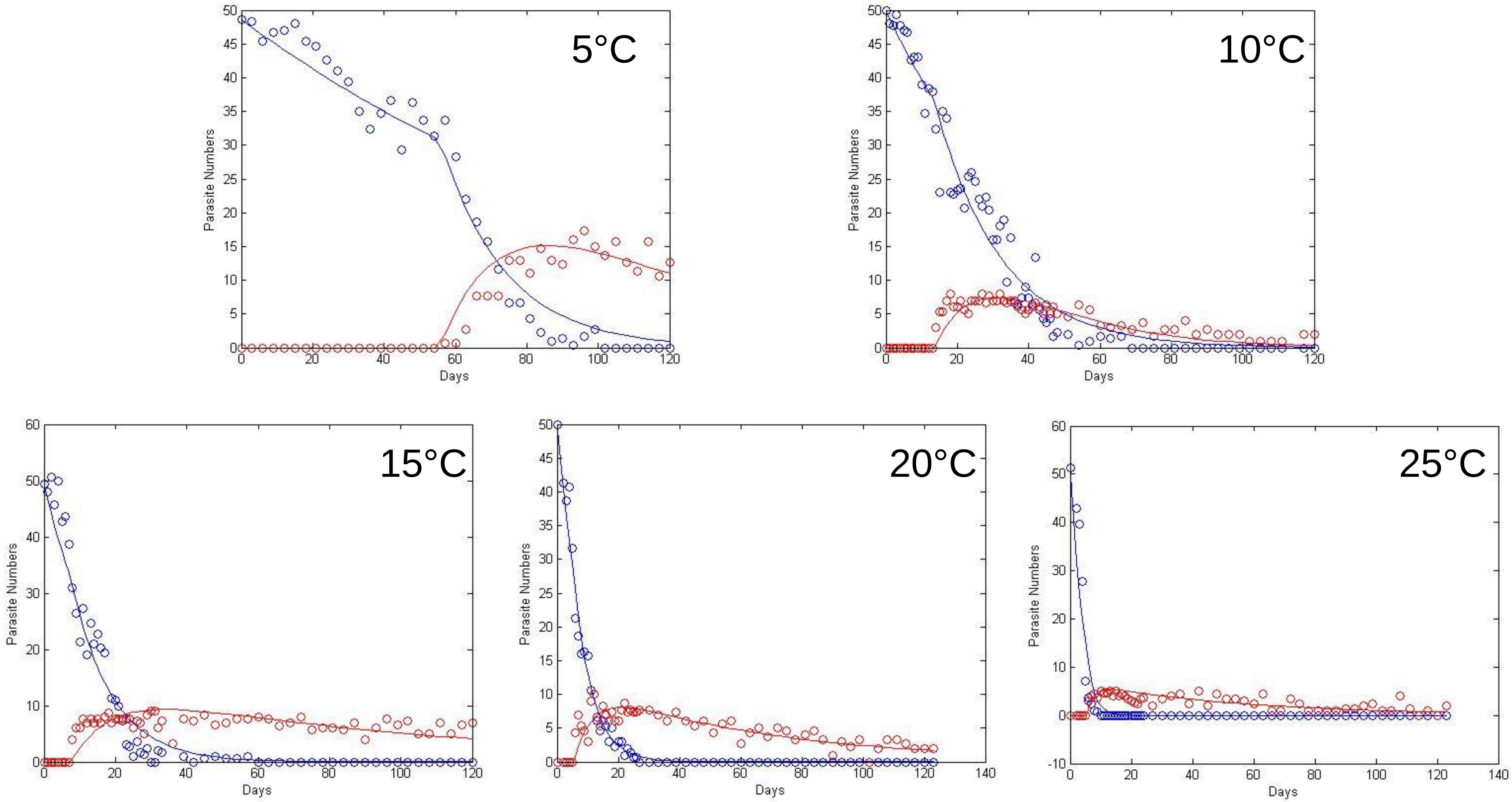


Cohort data:

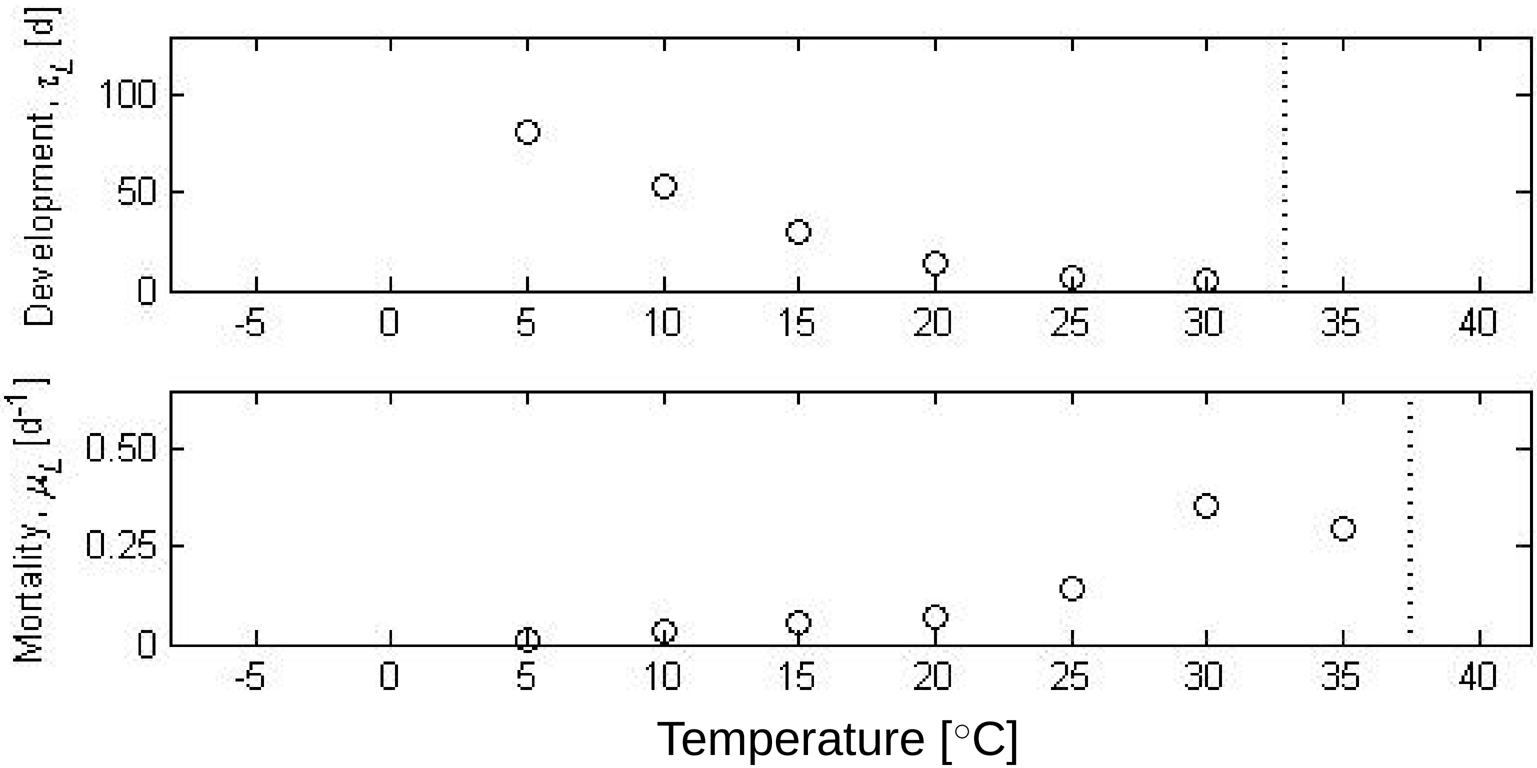
Pre-infective stages

Infective stage

… to estimate development and survival as a function of temperature…



… and we have done that.



Unfeasible to do for all existing and emerging parasites of humans and wildlife…

MTE to the Rescue…

Development time

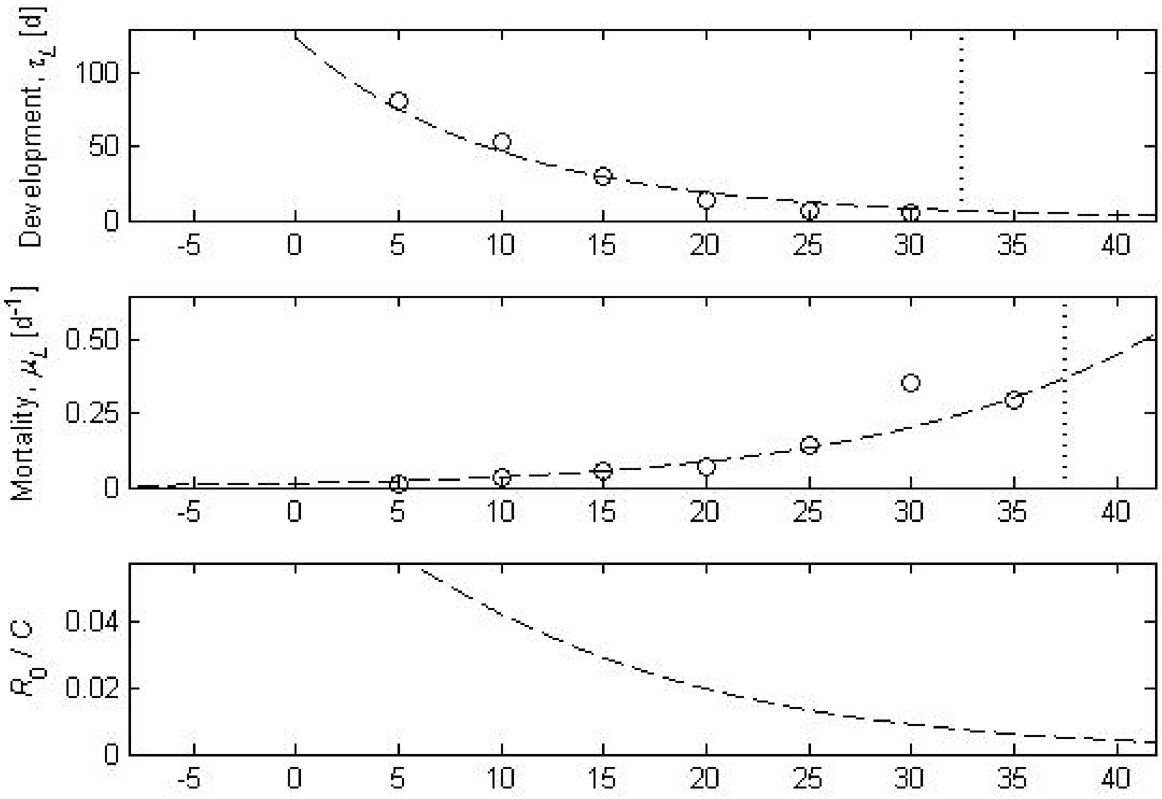
$$\tau(T) = \tau_0 e^{\frac{E_\tau}{k}\left(\frac{1}{T}-\frac{1}{T_0}\right)}$$

Mortality rate

$$\mu_L(T) = \mu_0 e^{-\frac{E_\mu}{k}\left(\frac{1}{T}-\frac{1}{T_0}\right)}$$

with $E_\tau \approx E_\mu \approx 0.65$ eV

Predictions using Metabolic Theory



- Predicts data quite well, but…
- … resulting R_0 is unrealistic at temperature extremes.

Modification – Sharpe-Schoolfield model for development

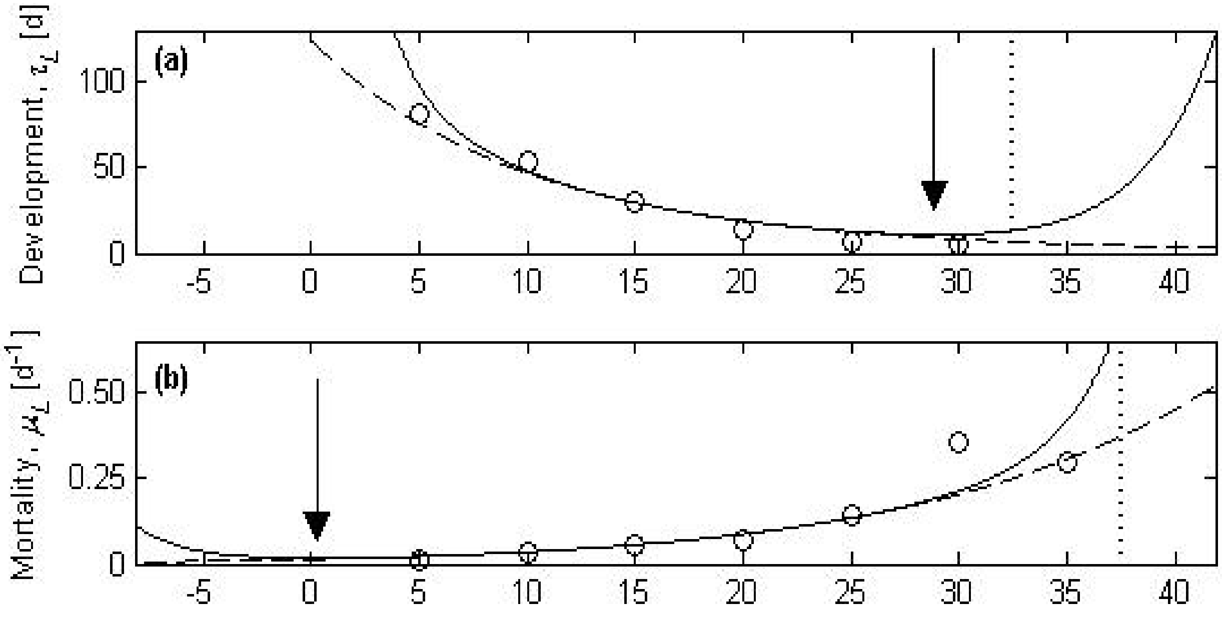
Assumes reversible inactivation of enzymes at temperature extremes, slowing or stopping development:

$$\tau(T) = \tau_0 e^{\frac{E_\tau}{k}\left(\frac{1}{T}-\frac{1}{T_0}\right)} \cdot \left(1 + e^{\frac{E_\tau^L}{k}\left(\frac{1}{T}-\frac{1}{T_L}\right)} + e^{\frac{E_\tau^H}{k}\left(-\frac{1}{T}+\frac{1}{T_H}\right)}\right)$$

A similar modification for mortality:

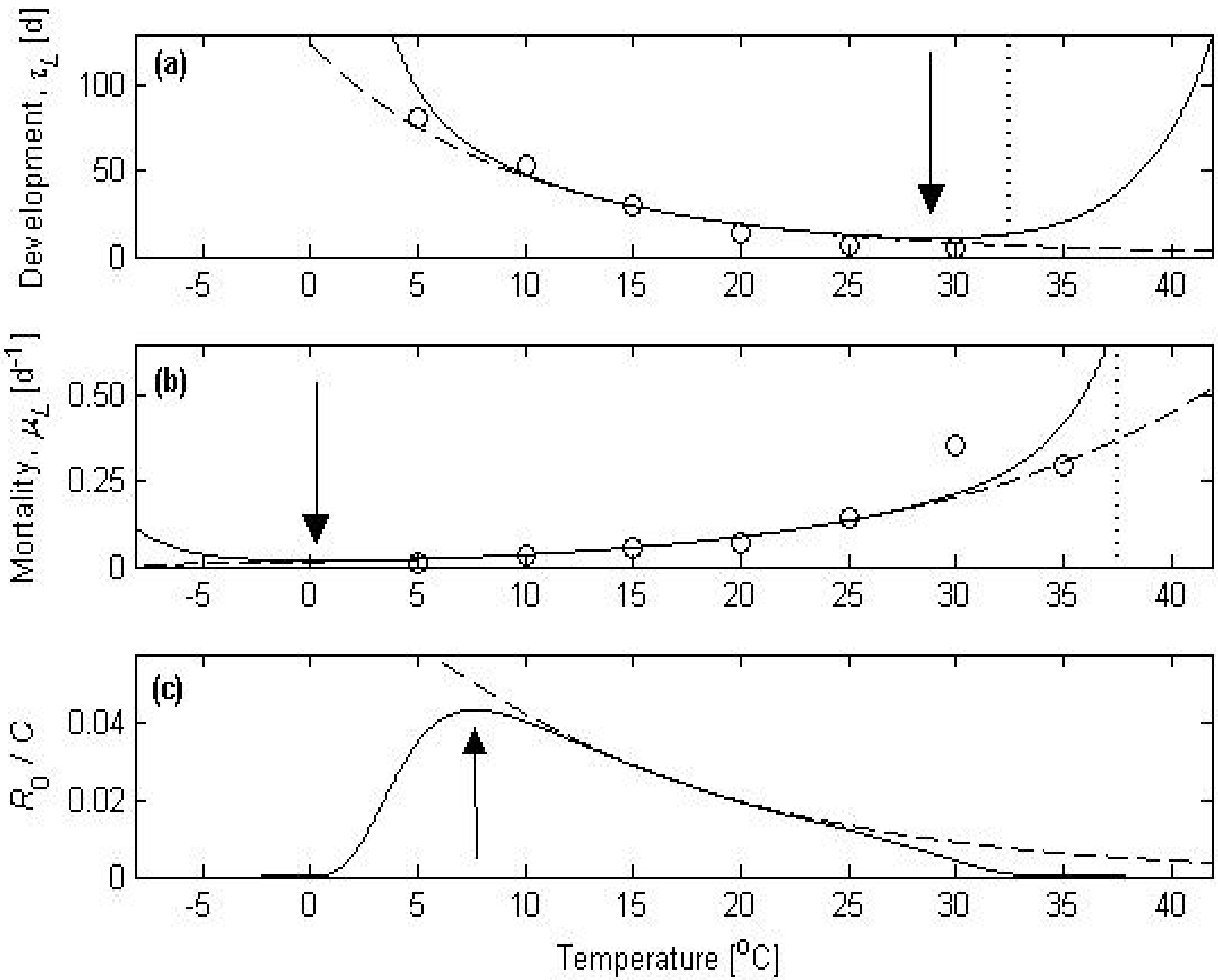
$$\mu_L(T) = \mu_0 e^{-\frac{E_\mu}{k}\left(\frac{1}{T}-\frac{1}{T_0}\right)} \cdot \left(1 + e^{\frac{E_\mu^L}{k}\left(\frac{1}{T}-\frac{1}{T_L}\right)} + e^{\frac{E_\mu^H}{k}\left(-\frac{1}{T}+\frac{1}{T_H}\right)}\right)$$

Predictions of modified model



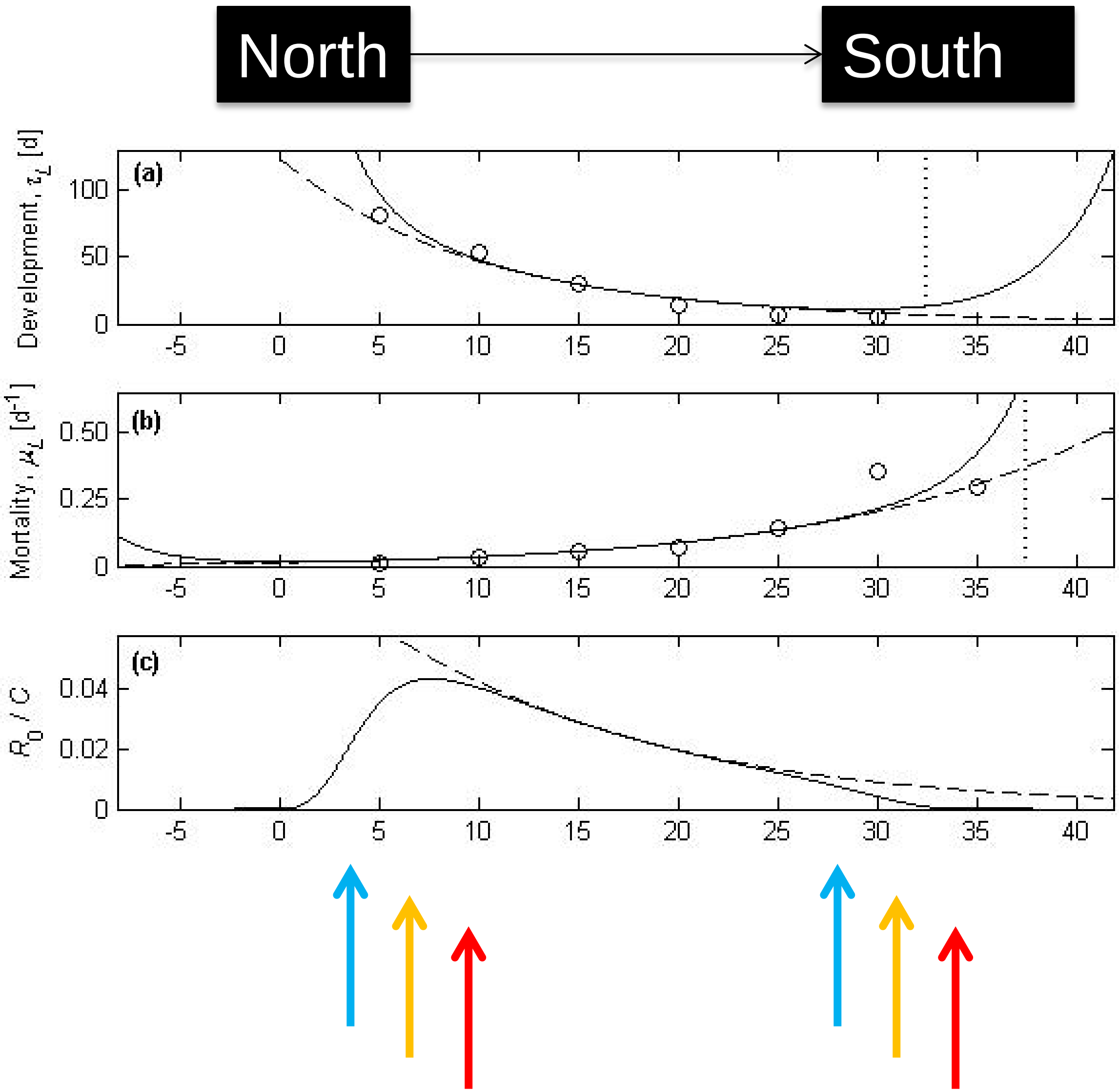
- Captures development & survival thresholds

Predictions of modified model



- Captures development & survival thresholds
- R_0 is unimodal
- Optimal temperature is weighted mean of development & survival optima

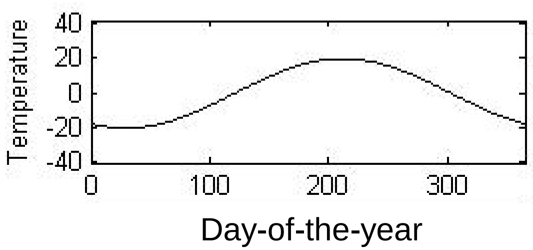
A geographical perspective



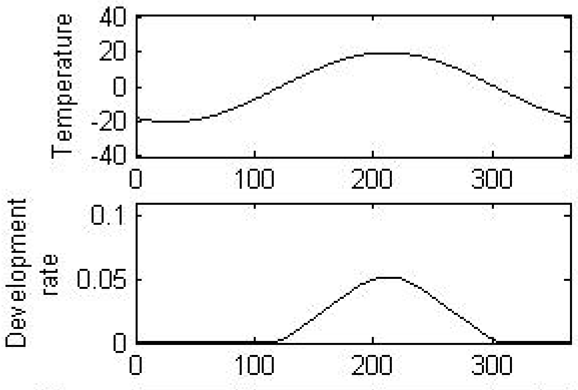
- Impacts will vary geographically
- Depending on “baseline” temperature climate change may have positive or negative effects
- Opportunity to predict range shifts

even warmer

A seasonal perspective



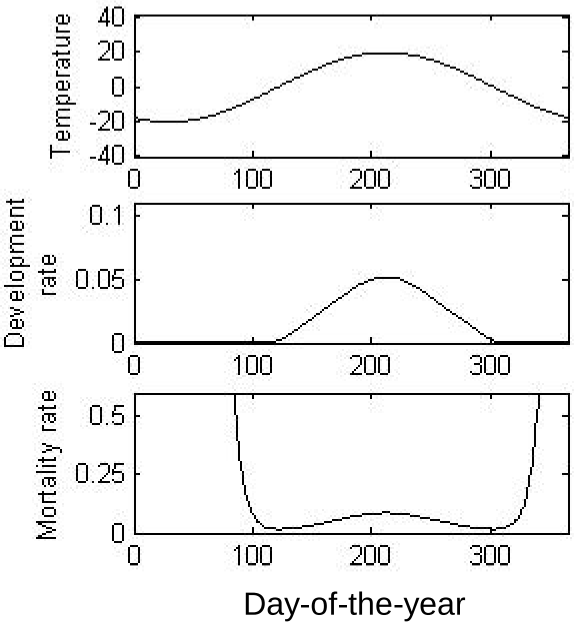
A seasonal perspective



Day-of-the-year

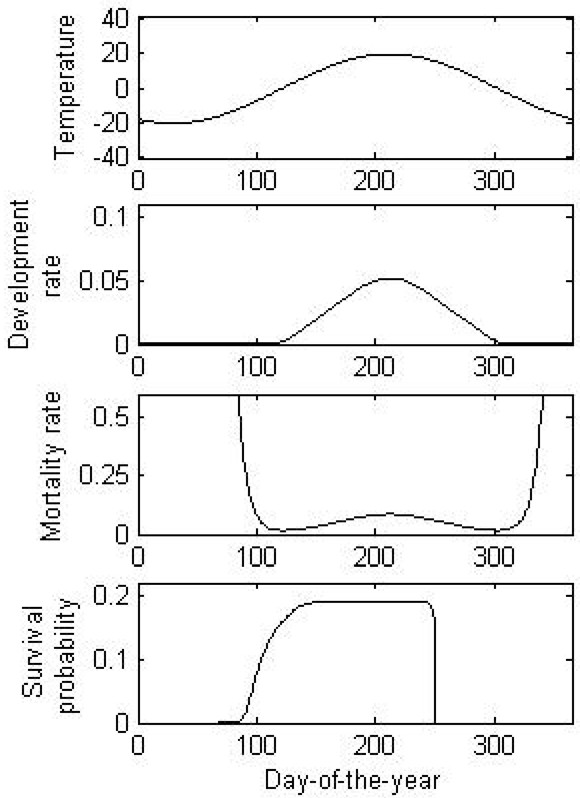
Development peaks in summer

A seasonal perspective



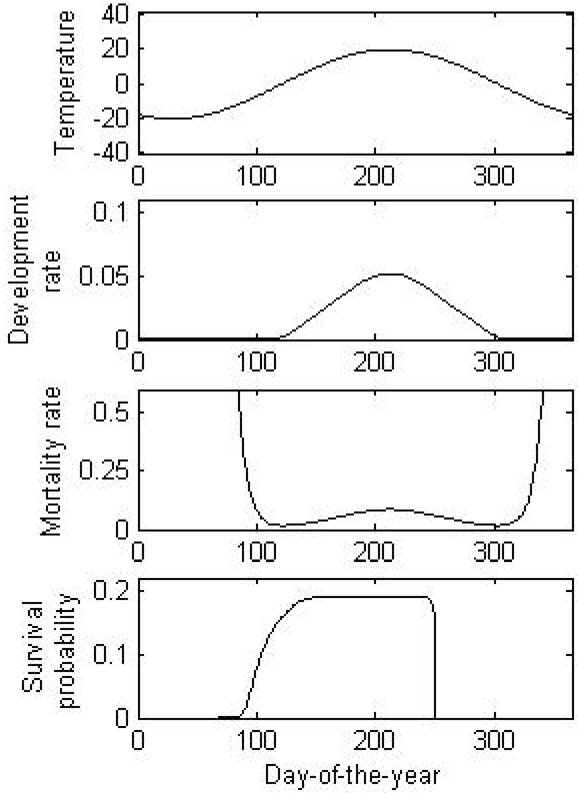
Mortality lowest in spring & fall

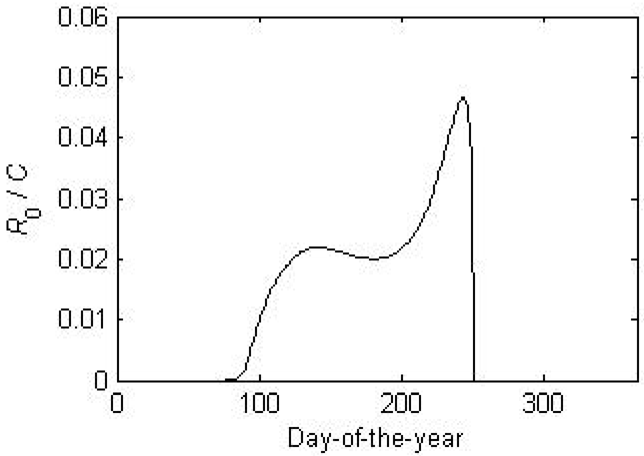
A seasonal perspective



Probability to survive to infective stage highest in summer

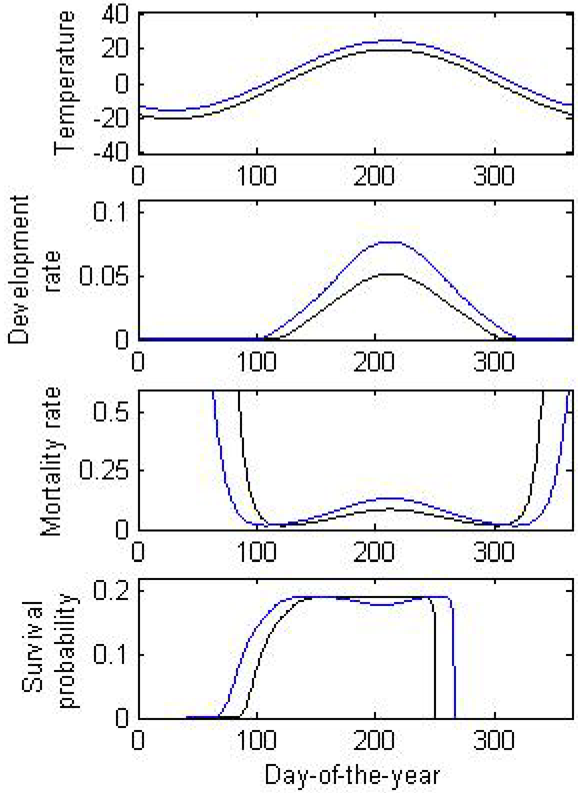
A seasonal perspective

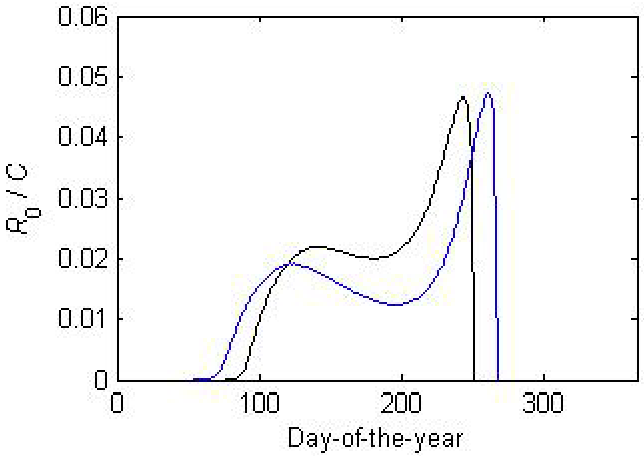




R_0 as a function of parasite 'birth' date

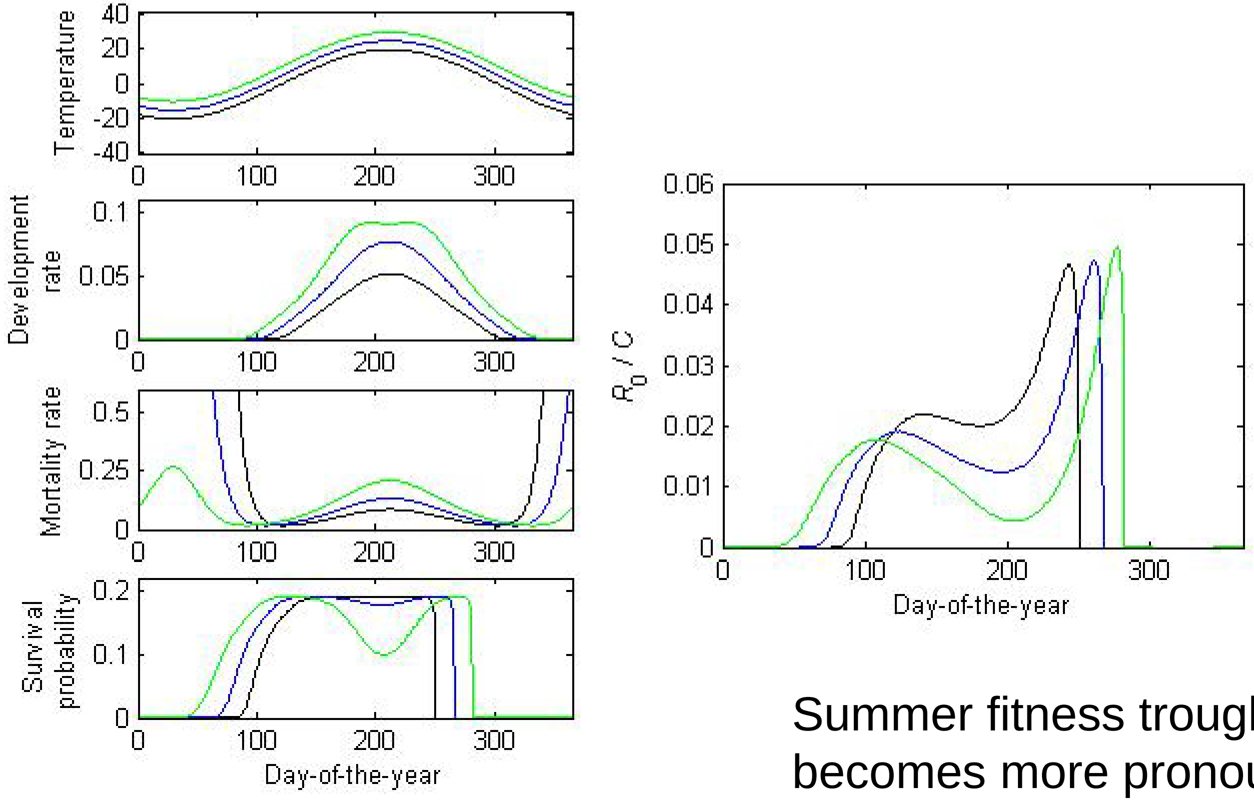
A seasonal perspective





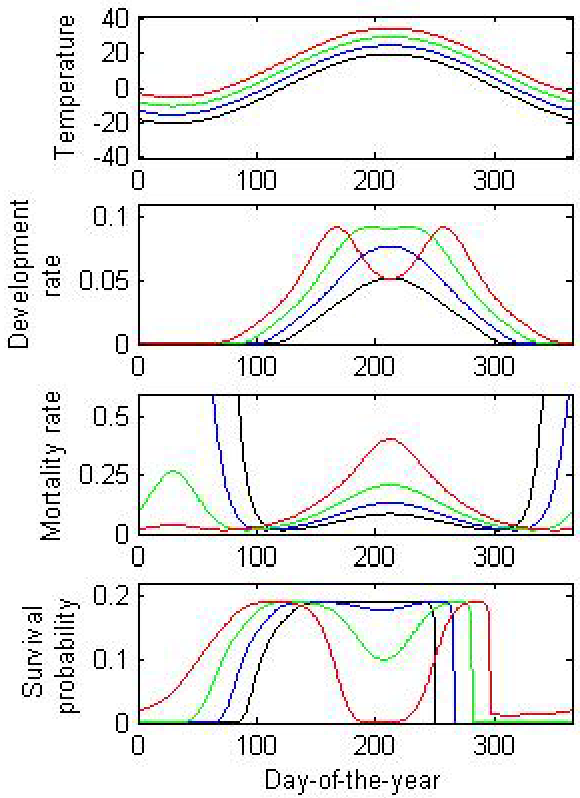
Phenological shifts

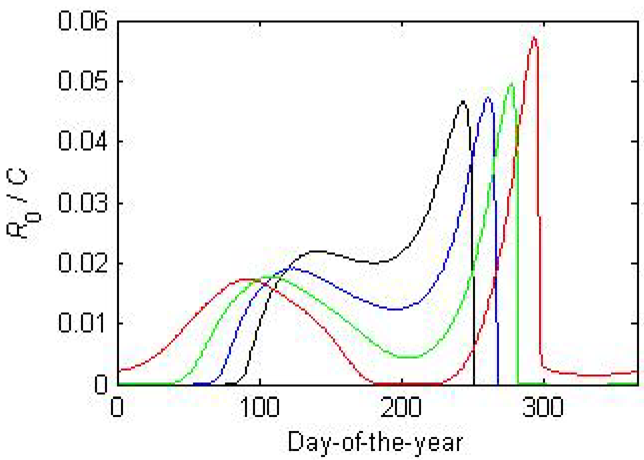
A seasonal perspective



Summer fitness trough becomes more pronounced

A seasonal perspective





- Transmission season splits into 2 separate seasons
- 'Wraps-around', allowing some winter transmission

Molnár *et al.* (*in press*) – Ecol. Lett.

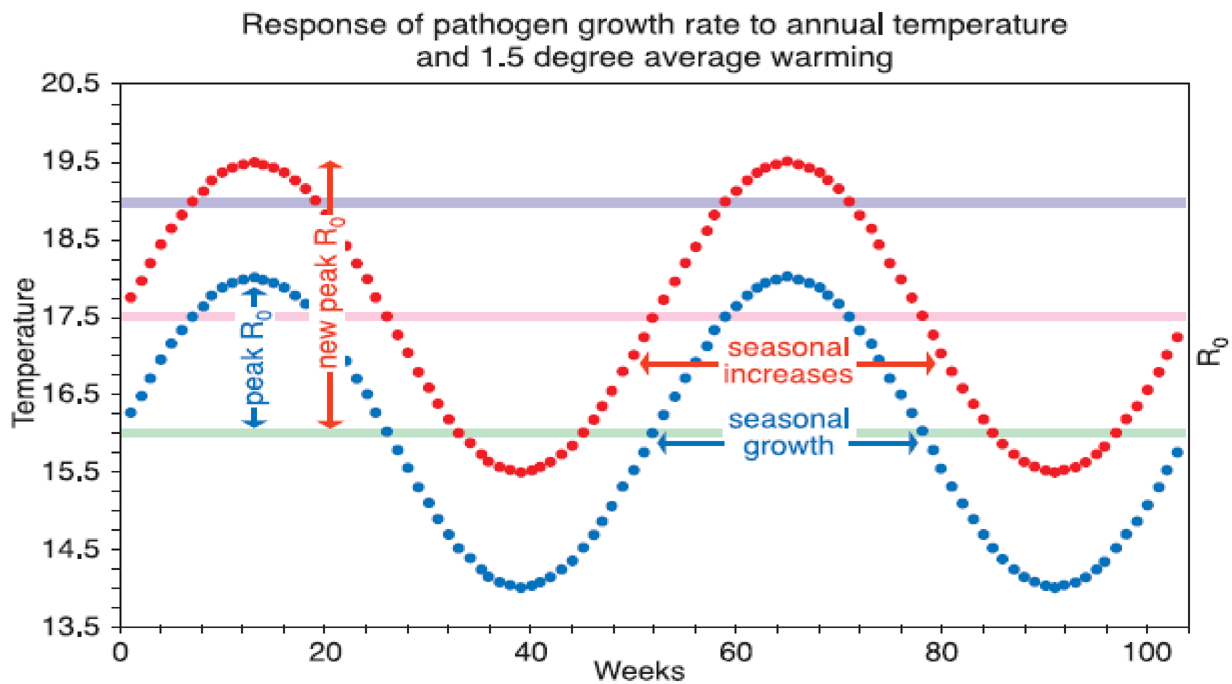


Fig. 2. The influence of an average 1.5° rise in temperature on the basic reproductive number R_0 of a hypothetical pathogen. When R_0 is above 1, a pathogen will increase. The lower blue line illustrates the average weekly temperature before climate change; the upper red line illustrates average weekly temperature after an average 1.5° temperature increase. The lower green line corresponds to $R_0 = 1$; below this temperature the pathogen declines in abundance. The pathogen increases at temperatures above this, and we assume that disease problems become severe when temperature exceeds the pink line and epidemic above the purple line. The figure illustrates that increases in temperature not only allow the peak value of R_0 to increase, but also lead to an increased annual duration of the period during which the pathogen is a problem.

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Science **296**, 2158 (2002);
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APD – suggested and drew this figure..!

Some Conclusions

The framework allows…

- synthesizing (nonlinear) climate impacts on different life history components into single measure of fitness (contrast with *degree-day models*)

How?

- straightforward extension to other host-parasite systems, parasite life cycles, environmental covariates (e.g., moisture), …

Who?

- predicting temporal and geographical impacts of climate (*fundamental* niche)

Where?

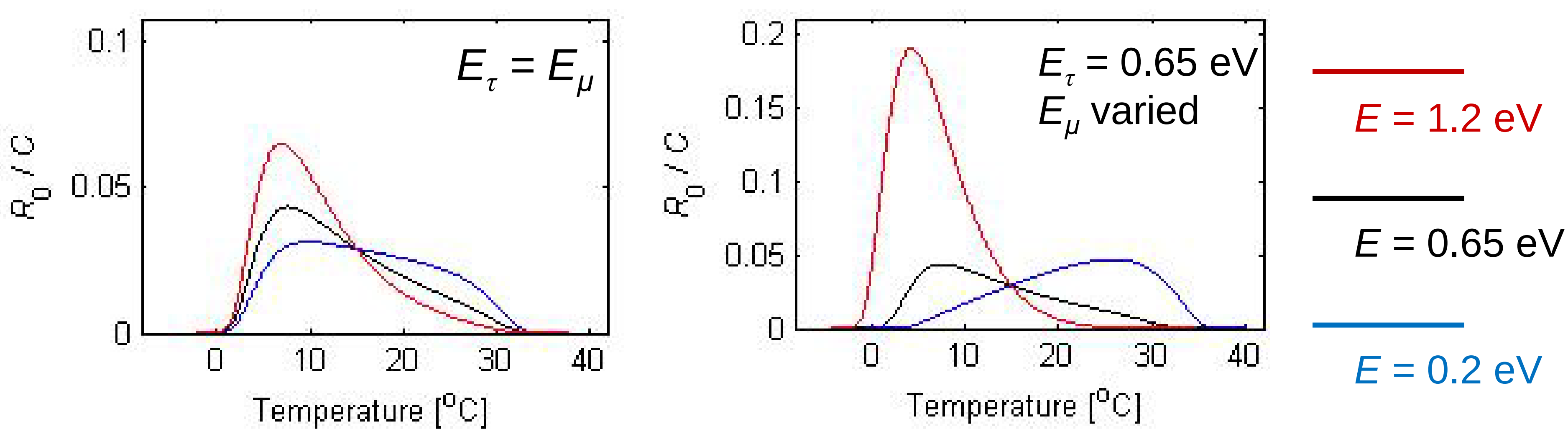
- potential extensions to include indirect effects (*realized* niche)

- *a priori* estimation of model parameters (even in data-poor systems)

So how about other species?

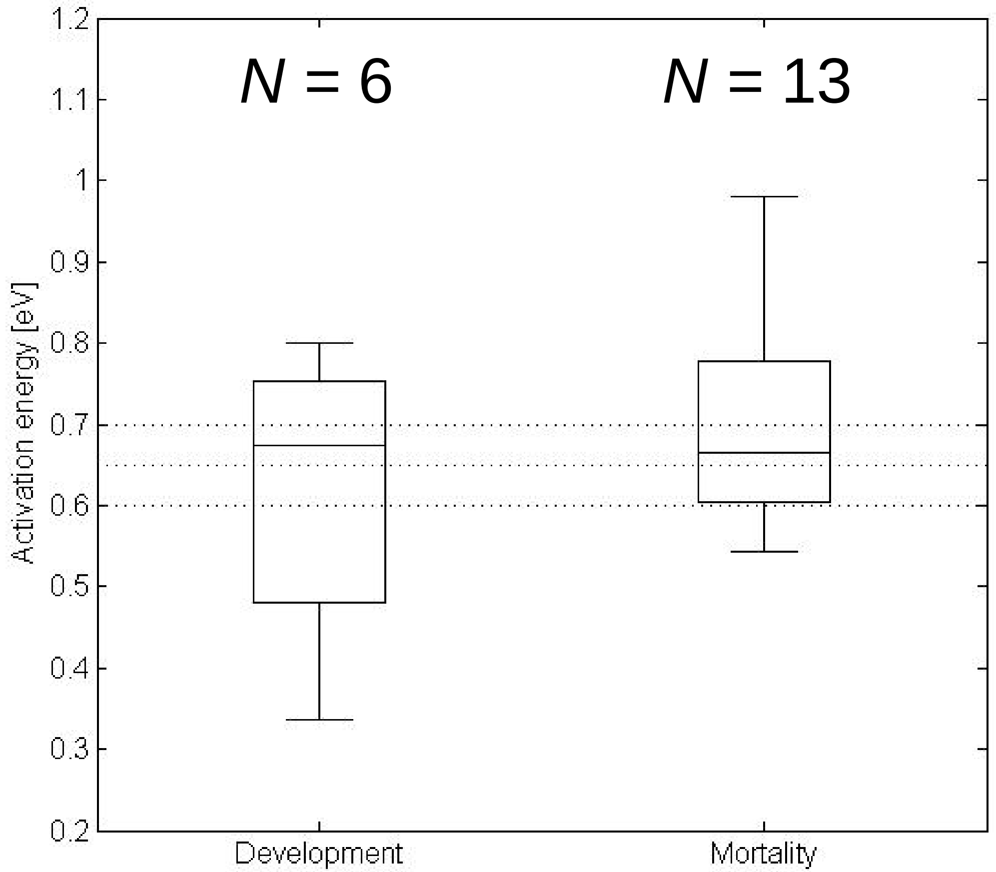
The generality of the framework

- $R_0(T)$ unimodal regardless of parameter values
- Location of optimal temperature, skewness, temperature range where $R_0 > 1$ insensitive to almost all model parameters
- Key parameters are the activation energies



- How much do parameters vary between species?

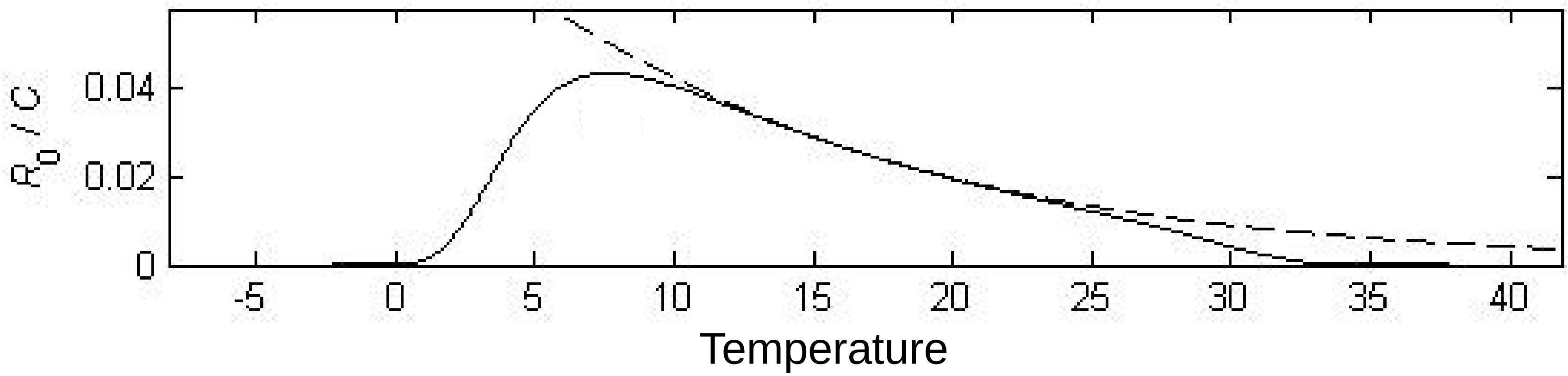
Metabolic Theory predicts $E_\tau = E_\mu = 0.65$ eV

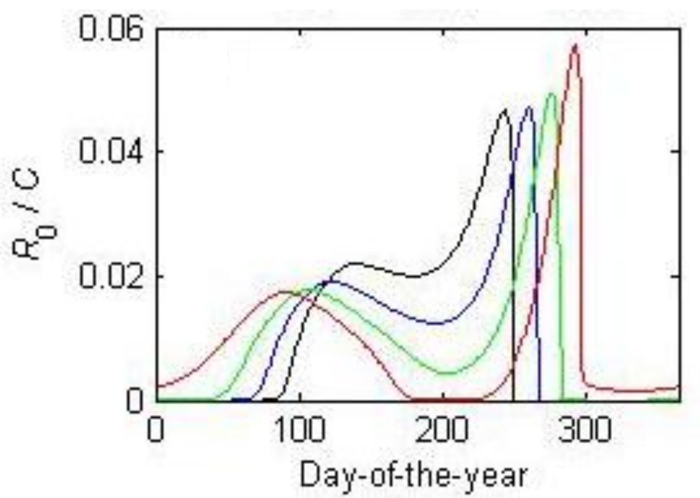


Metabolic Theory needs to be tested further for parasites!

Quo vadis, parasite?

Persistence / Establishment





Persistence / establishment depends on whether

$$R_0^{total} \geq 1$$

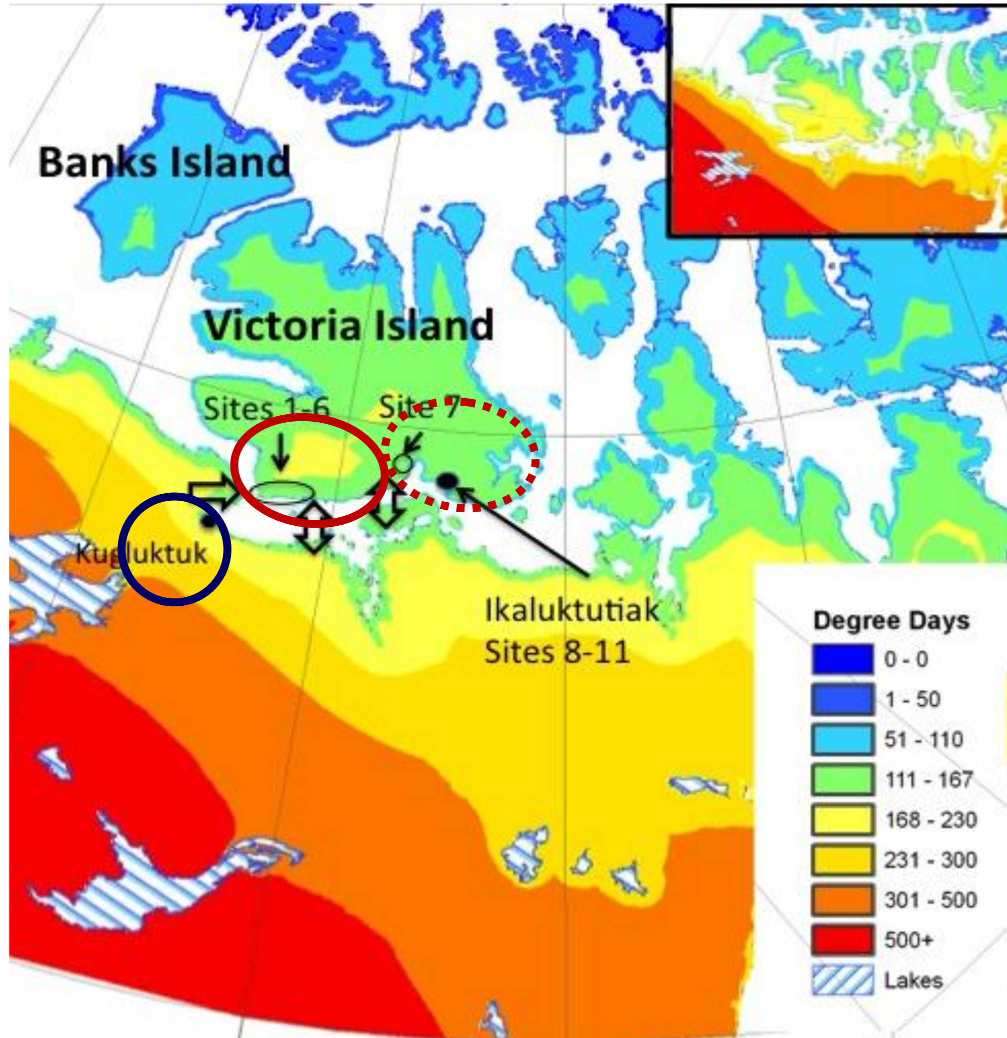
R_0-theory needs to be extended

Daily temperature fluctuations, stochastictity

Application to Specific Systems

To what degree can parasite range expansion be explained/predicted by climate change?

Temperature-dependent host-parasite reaction-diffusion models



Kutz *et al.* (in review)

Climate Change Impacts on Hosts?

Climate may affect…

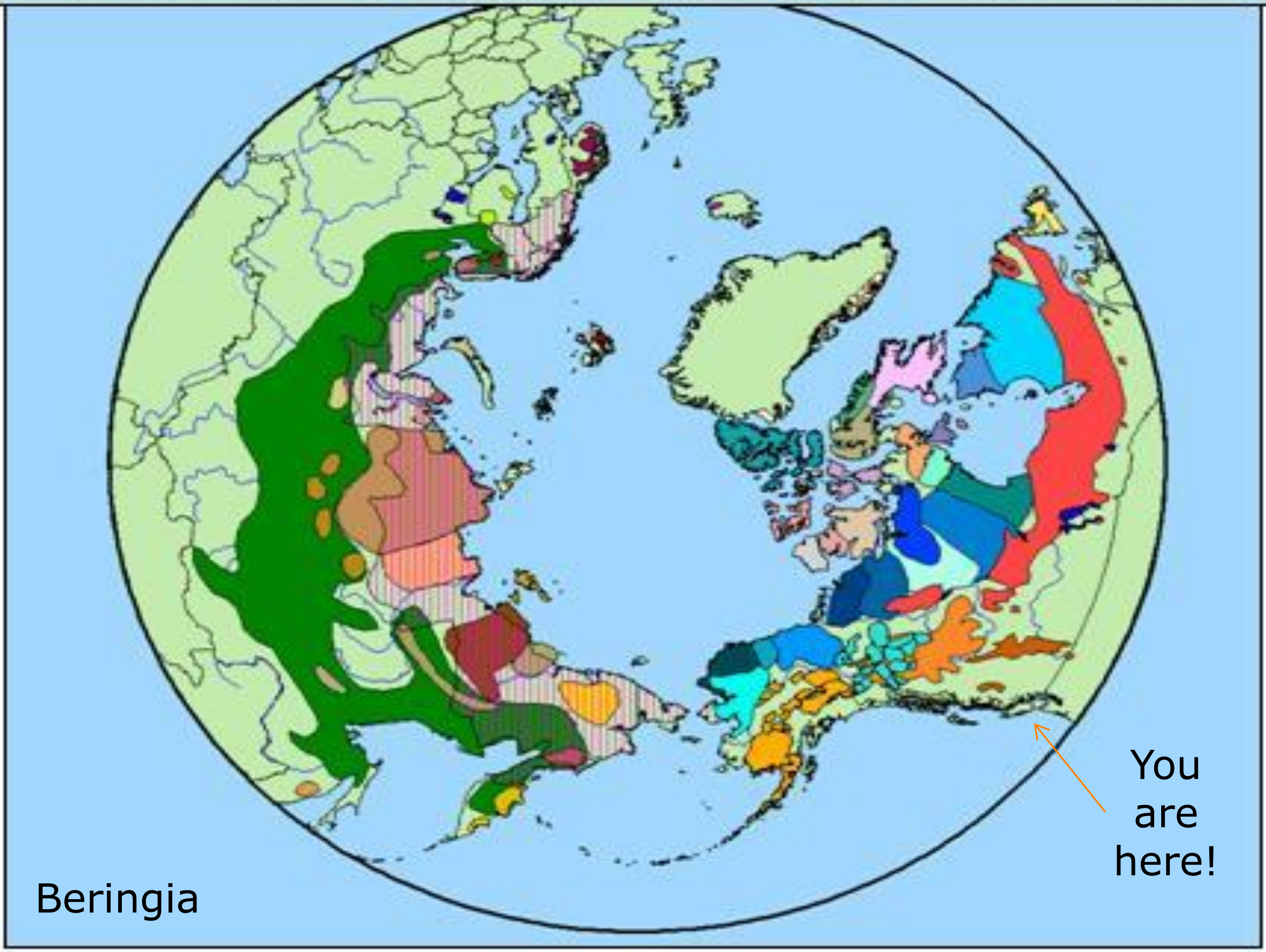
- host condition (immunity)
- host survival / reproduction
- host density
- host ranges
- community composition / biodiversity

Each of these can be treated within energetic framework

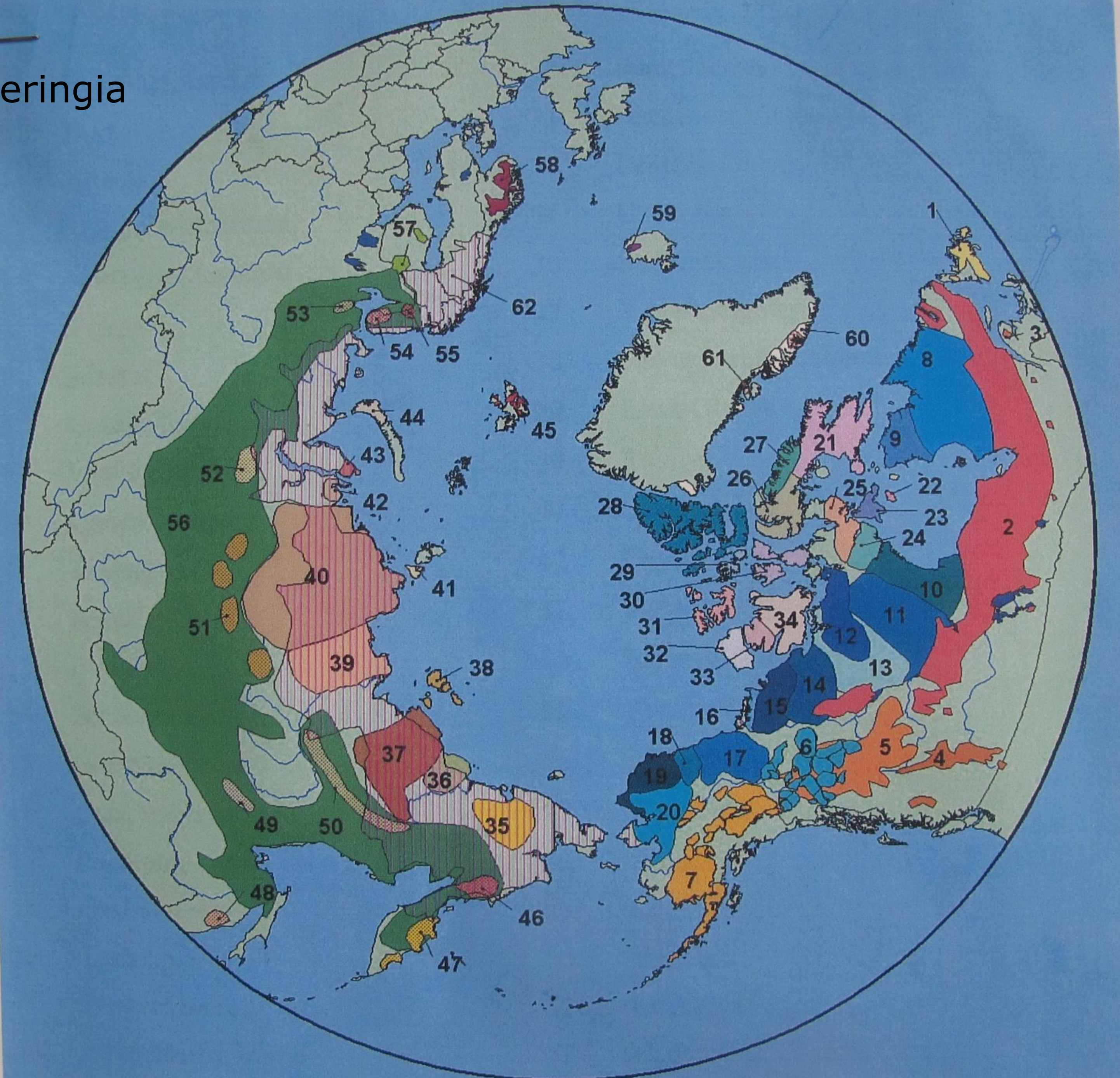
DEBs more appropriate (endotherms / supply-side problems)

Bot flies as caribou parasitoids….

Circumpolar distribution of reindeer and caribou



Beringia



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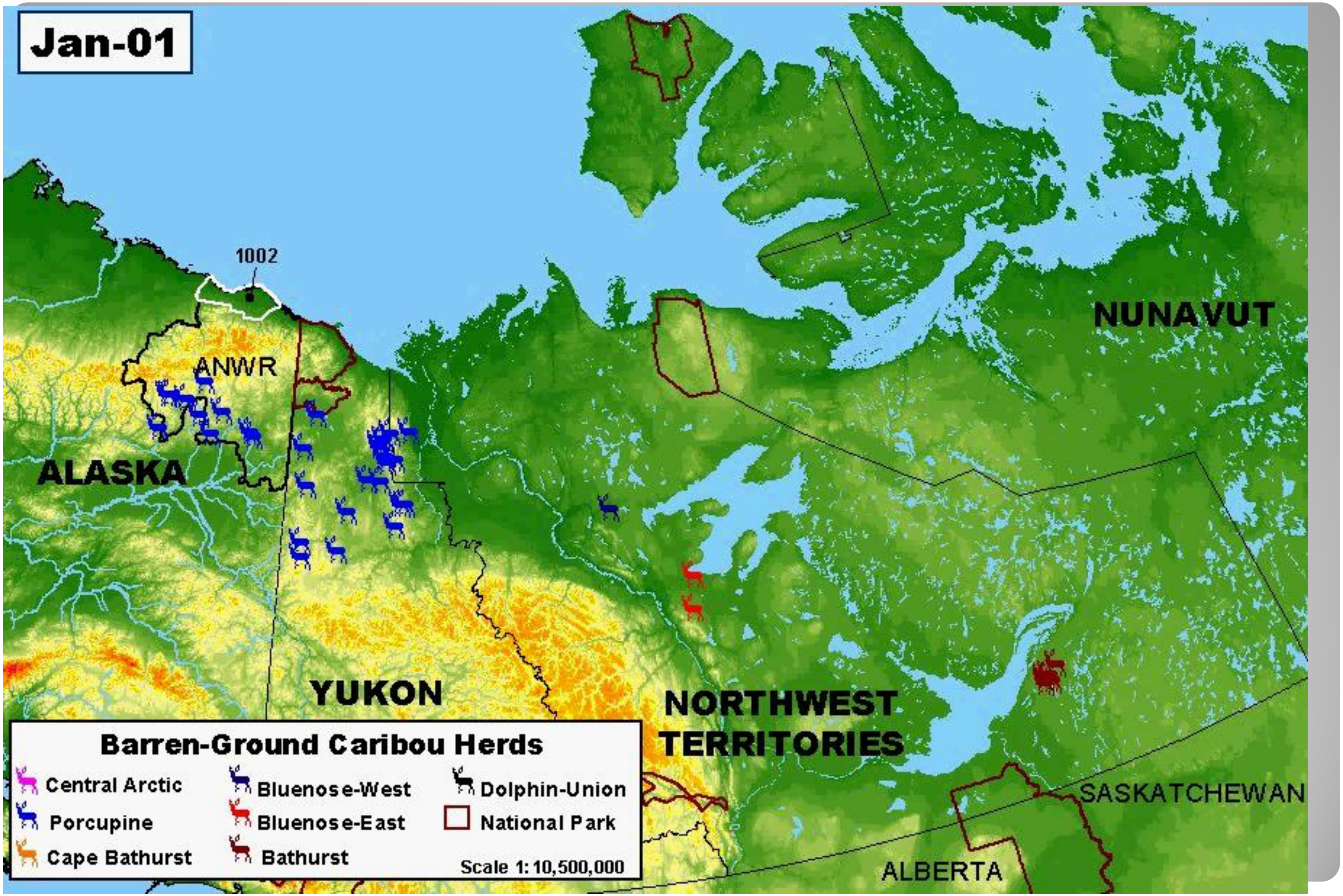
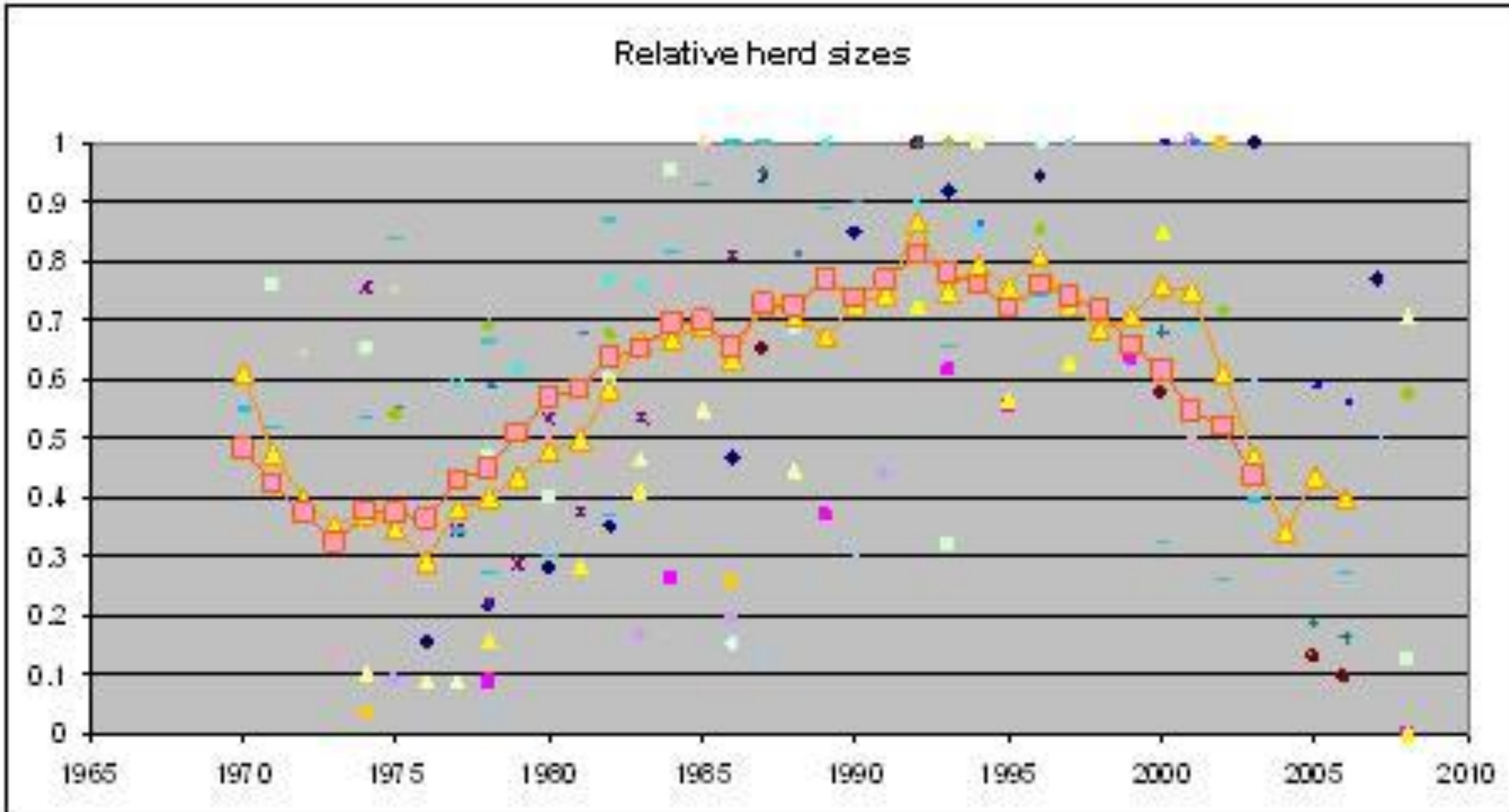
Caribou and reindeer are central to the welfare and economies of Arctic peoples

Caribou are like Wildebeest….



Caribou migration movie



The relative size of tundra dwelling wild Rangifer herds. The large triangles represent the three year running average and the large squares, the 6 year running average.

Dynamics of large herbivores in deserts: kangaroos and caribou

Graeme Caughley and Anne Gunn

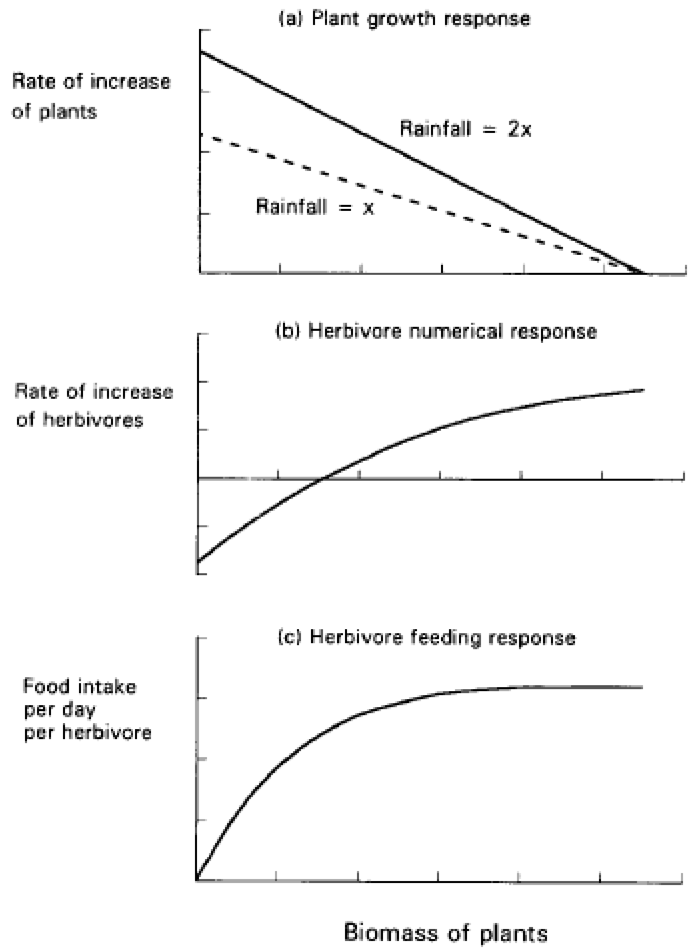
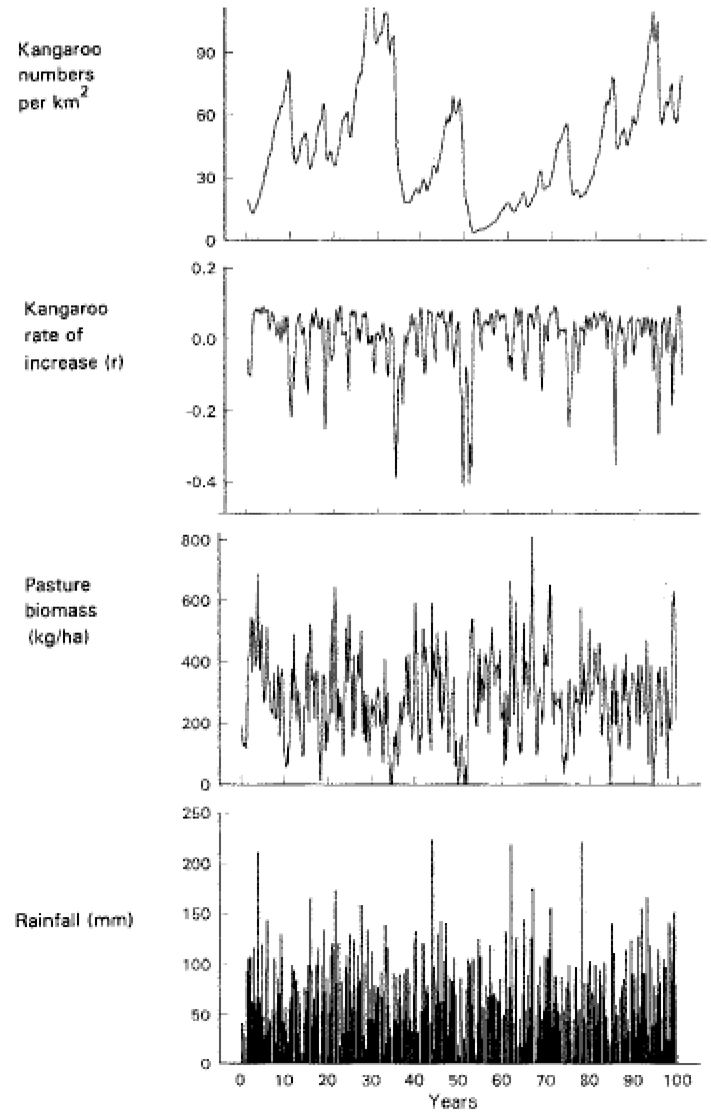
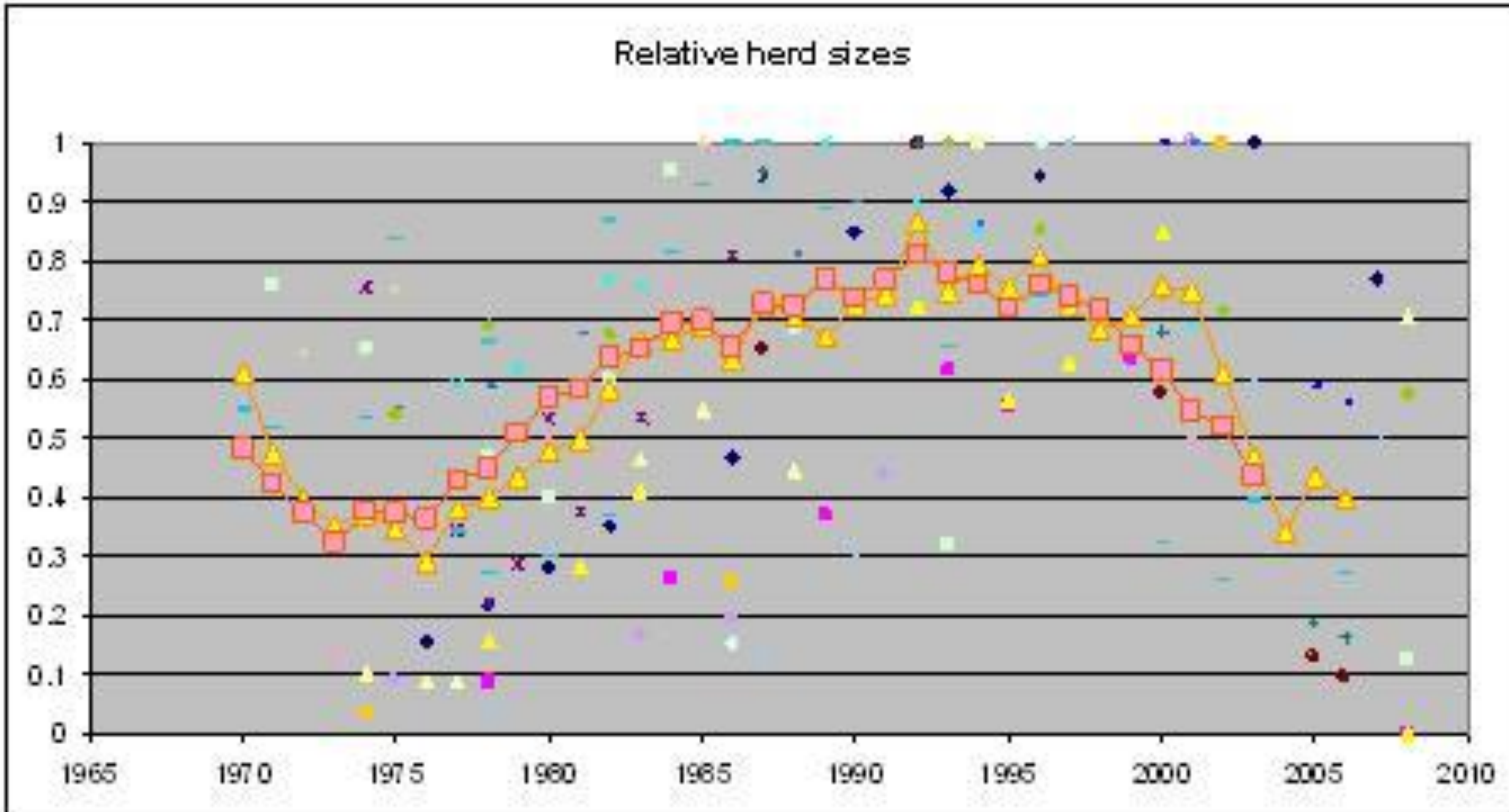


Fig. 1. A possible configuration of response functions of a plant-herbivore system, each of which is graphed against the biomass of available forage per unit area.





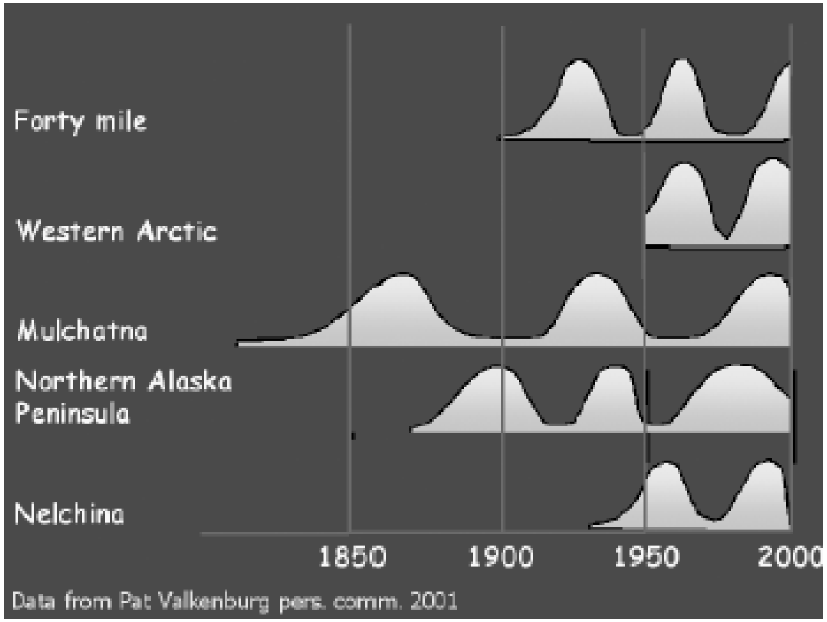
The relative size of tundra dwelling wild Rangifer herds. The large triangles represent the three year running average and the large squares, the 6 year running average.

Voles, lemmings and caribou - population cycles revisited?

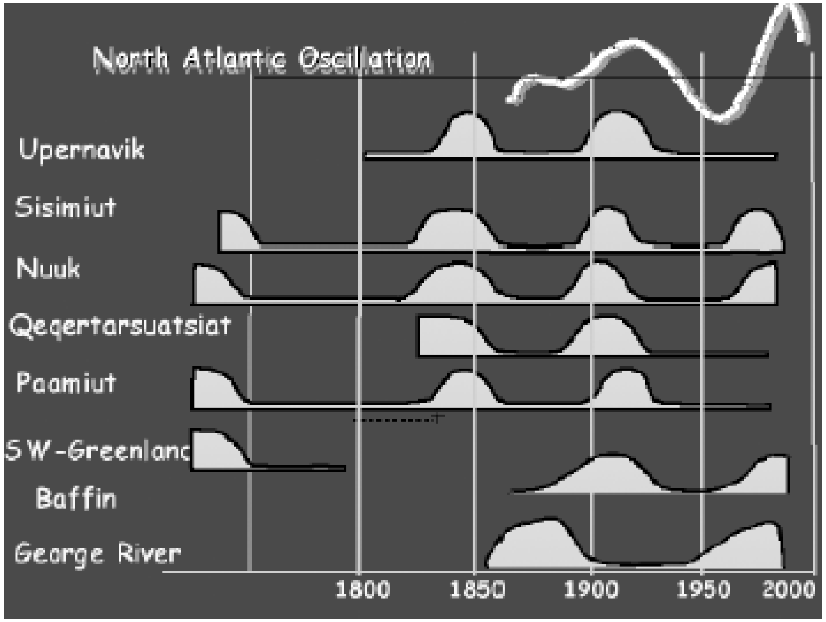
Anne Gunn

Key words: Rangifer tarandus, abundance, decadal climatic variation, cohort memory.

Rangifer, Special Issue No. 14: 105-111



(a)



(b)

Fig. 1. Standardized fluctuations in caribou abundance in (a) Alaska and (b) Greenland and eastern North America .



Do Bot-flies and warbles play any role in migration and population cycles?

Bot fly larvae under skin of caribou

Fig. 14.79. Ventral view of third-instar *Gyrostigma rhinocerontis* (bar = 1 cm).

Fig. 14.80. Lateral view of third-instar *Gyrostigma rhinocerontis* (bar = 1 cm).

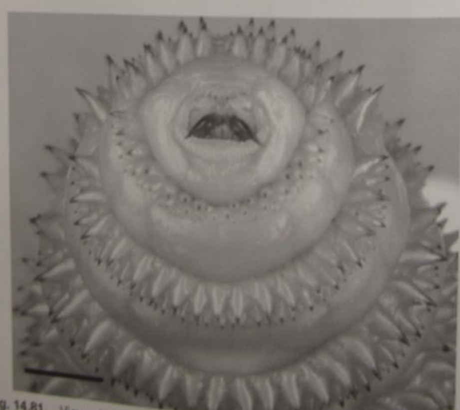
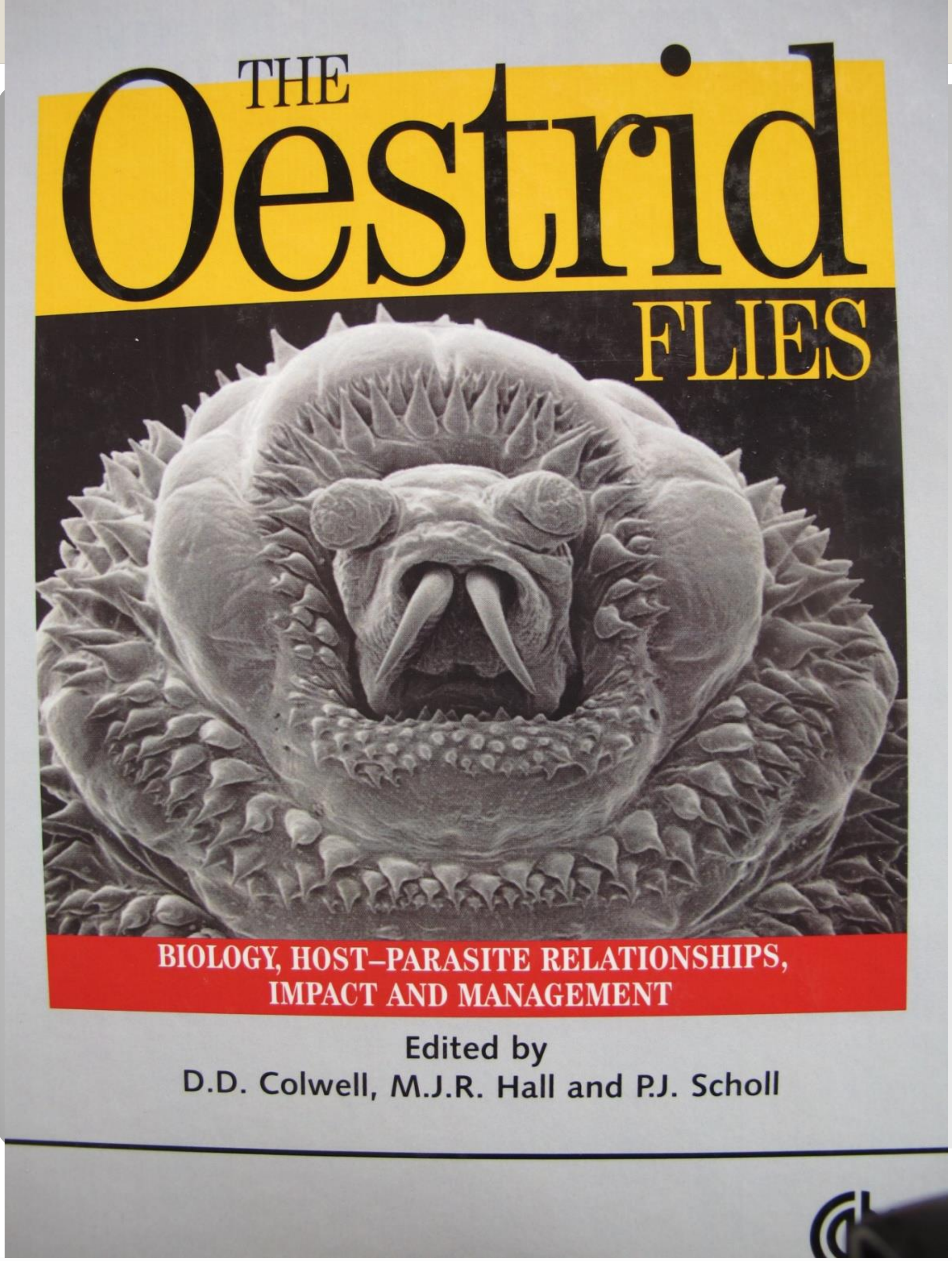


Fig. 14.81. View of the cephalic and thoracic segments of third-instar *Gyrostigma rhinocerontis* (bar = 0.5 cm).

Fig. 14.73. Ovipositing *Gasterophilus intestinalis*. Note eggs already attached to host hair (white arrows) (bar = 0.5 cm).

Fig. 14.74. Third-instar *Gasterophilus intestinalis* (bar = 0.5 cm). (Lateral view, cephalic segment to the right.)

Fig. 14.75. Third-instar *Gasterophilus nasalis* (bar = 0.5 cm). (Lateral view, cephalic segment to the right.)



Definitive guide to bot-flies and warbles

Seasonal Changes in Scar and Hole Counts

The numbers of breathing holes of warble fly larvae in museum hides, per month, are shown in Figure 2 as a percentage of the total count of holes and scars. There are no data

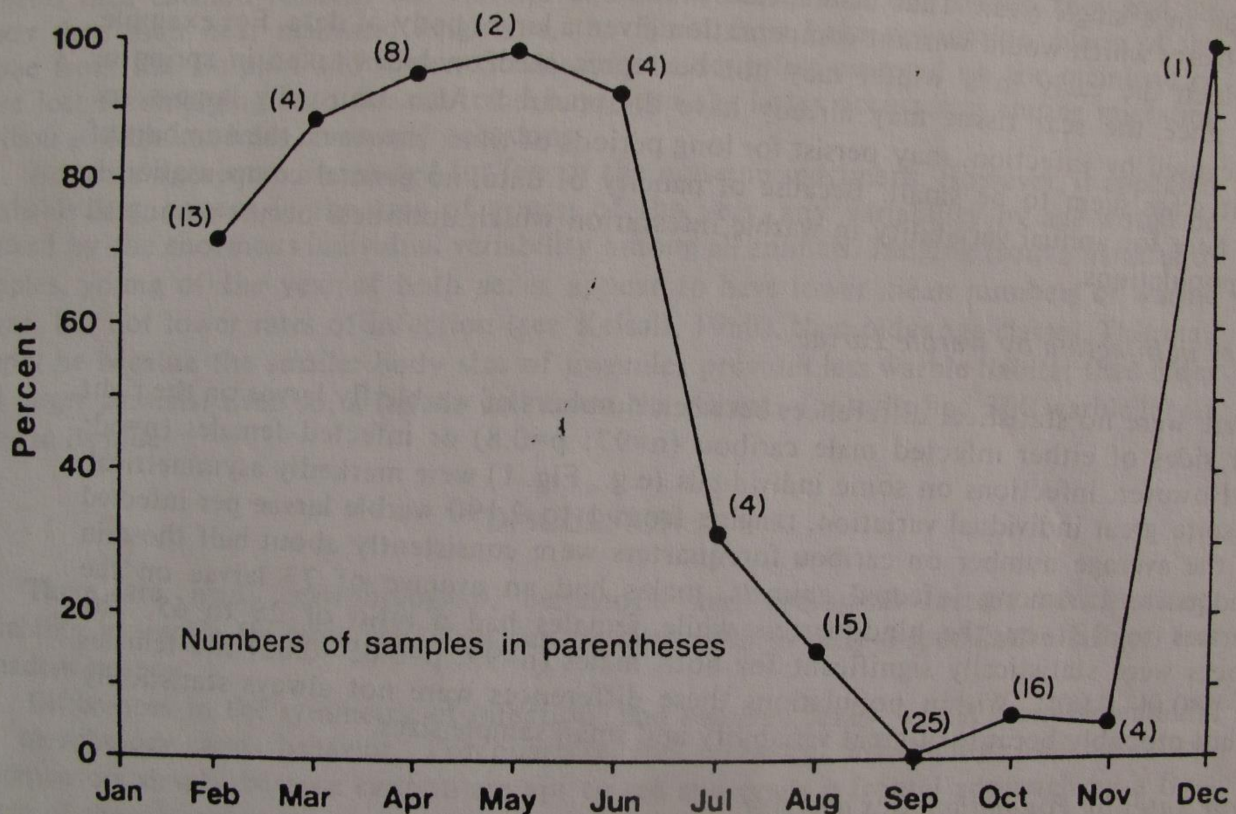


Fig. 2.—Warble larvae holes, as a per cent of holes plus scars on caribou hides, by month of collection.

The timing and departure rate of larvae of the warble fly *Hypoderma* (= *Oedemagena*) *tarandi* (L.) and the nose bot fly *Cephenemyia trompe* (Modeer) (Diptera: Oestridae) from reindeer

Arne C. Nilssen & Rolf E. Haugerud

Zoology Department, Tromsø Museum, N-9006 Tromsø, Norway

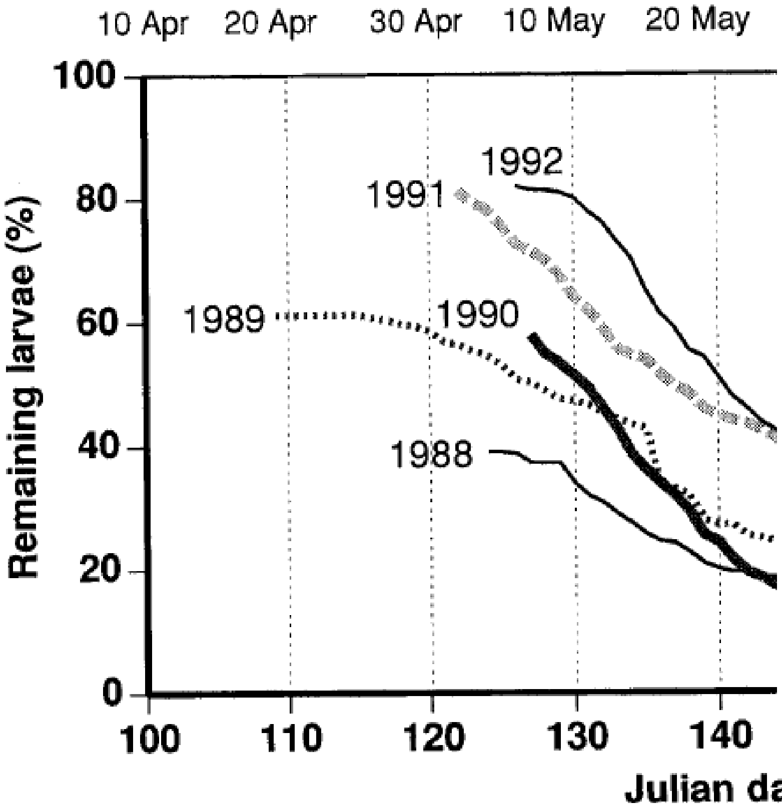


Fig. 3. Larvae of *H. tarandi* remaining in the host as a function of date from 5 years of investigation. (Sample sizes, see Table 1). 100 % is based on counting of larval scars at autopsy.

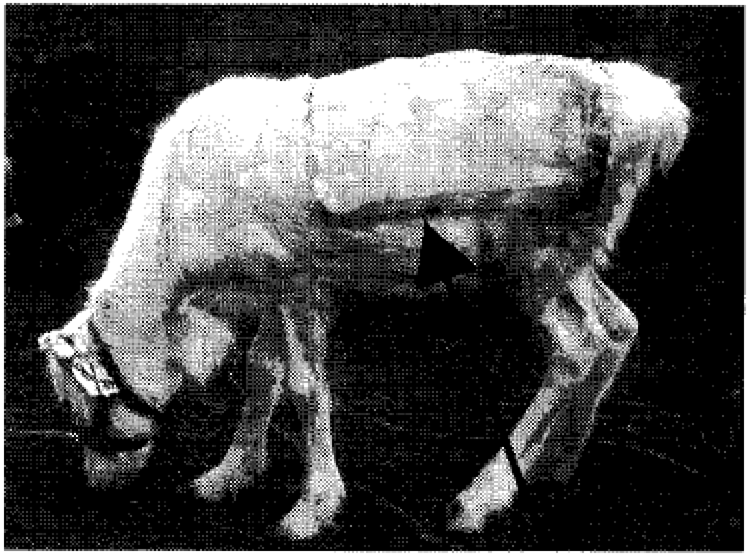
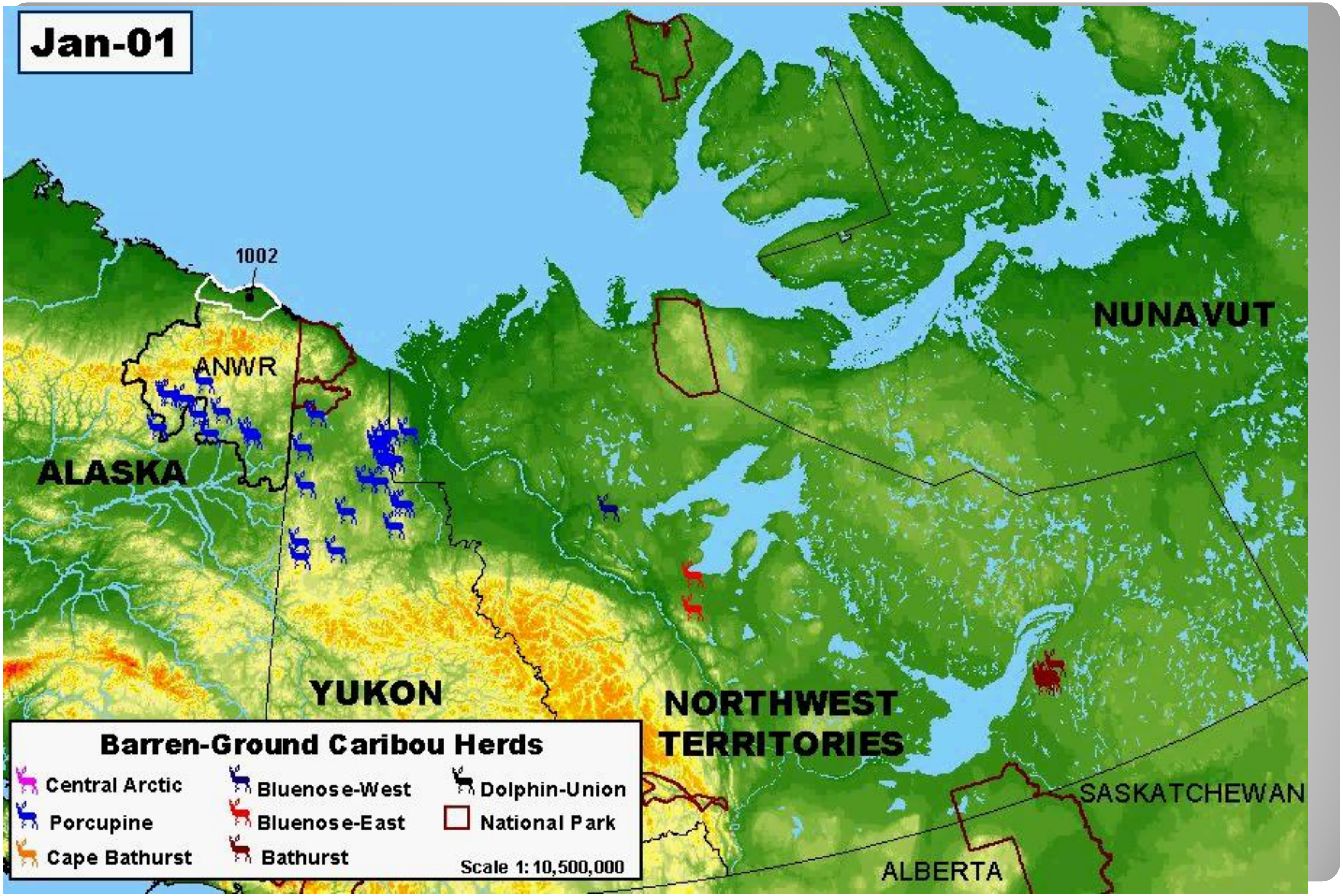


Fig. 2. The «collection cape technique» was used in 1988 and 1989 to collect *H. tarandi* larvae. The collection cape consisted of a nylon mesh fastened over the back of each animal. The mesh made a transparent bag into which the larvae collected when they emerged. The arrow points at one dropped larva.



Caribou migration movie

The timing and departure rate of larvae of the warble fly *Hypoderma* (= *Oedemagena*) *tarandi* (L.) and the nose bot fly *Cephenemyia trompe* (Modeer) (Diptera: Oestridae) from reindeer

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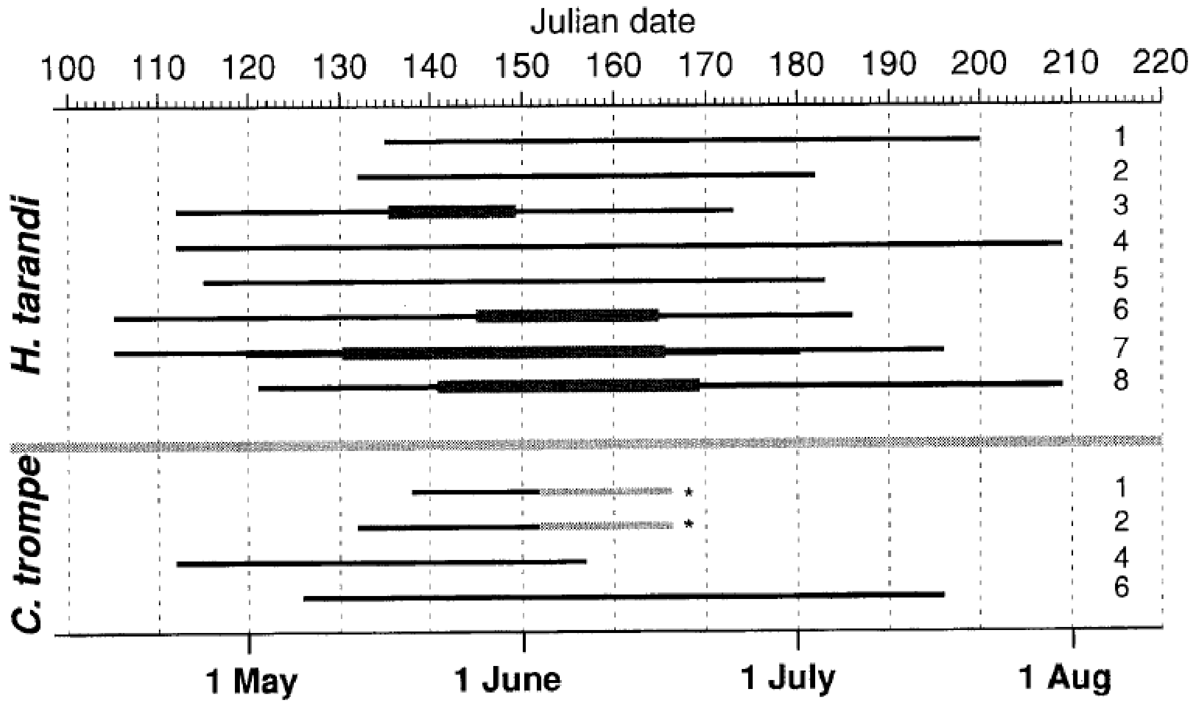

Fig. 1. Summary of published records of dropping periods of larvae of *H. tarandi* and *C. trompe*. Thicker portions of the lines denote mass departure of larvae. *: End of dropping not given. The number after each line refers to: 1: Bergmann 1917 (Sweden). 2: Hadwen & Palmer 1922 (Alaska). 3: Palmer 1929 (Alaska). 4: Sdobnikov 1935 (Russia, Alaska). 5: Breyev & Karazeeva 1954 (NW Soviet Union). 6: Gomoyunova 1976 (Tsjuktsjer peninsula in Russia). 7: Solopov 1989 (various parts of northern Russia). 8: Nordkvist 1960 (Sweden).

Table 5. Numbers of warble larvae under the skin of pregnant and non-pregnant, female, barren-ground caribou sampled in December (1982-86) and March (1980-87).

Age class (yr)	Month	Pregnant $\bar{x}$	Pregnant SE	Pregnant n	Not pregnant $\bar{x}$	Not pregnant SE	Not pregnant n
2	Dec	20.0	16.0	2	24.0	4.4	24
3	Dec	11.3	2.5	17	17.7	6.0	13
4	Dec	4.8	1.6	29	8.0	4.3	8
<4	Dec	8.4	2.2	102	12.8	4.0	18
2	Mar	109.9	18.4	8	114.8	13.1	51
3	Mar	40.5	5.0	61	60.6	13.3	21
4	Mar	40.1	4.3	49	71.1	16.7	12
<4	Mar	31.9	2.3	297	59.3	9.3	38

*P<0.05
**P<0.01

males was consistent.

Warble fly avoidance behavior in barren-ground caribou
One observed strategy was to find escape habi-

may stand together. The warble fly is highly active only on certain days and especially on warm, sunny afternoons. By about 1800 hours (in late July-early August) the attacks cease and

Significant impacts on host

Table 1. Frequency of occurrence (percent) and mean numbers of warble larvae under the skin of caribou sampled from the Beverly herds in December (1982-86) and March (1980-87).

Sex/age (yr)	Numbers of warble larvae: December Freq. %	Mean	SE	n	March Freq. %	Mean	SE	n
F 1	100	18.8	4.1	5	100	124.7	14.1	29
M 1	100	65.3	14.0	15	100	118.7	18.3	20
F 2	92	23.7	4.1	26	100	114.2	11.6	59
M 2	100	47.6	6.4	26	100	171.1	16.1	57
F 3	87	14.1	3.0	30	98	45.7	5.1	82
M 3	95	18.4	2.8	42	99	93.1	9.4	90
F 4	61	5.8	1.5	38	97	46.2	5.0	61
M 4	100	25.9	5.2	24	100	80.8	10.3	28
F 5	84	12.2	7.2	25	98	28.3	3.8	56
M 5	100	77.0	22.0	10	100	145.5	43.7	20
F 6-8	76	10.5	2.5	58	97	36.1	3.8	153
F 9-11	59	4.2	1.3	22	99	37.1	4.9	91
M > 5	100	147.7	49.1	6	100	222.6	36.4	23
F > 11	61	5.4	2.4	18	97	35.9	5.5	36
F > 3	70	8.2	1.5	161	98	36.8	2.1	397
M > 3	100	56.9	11.6	40	100	144.9	18.6	71
F > 4	72	9.0	1.9	123	98	35.1	2.3	336
M > 4	100	103.5	23.7	16	100	186.7	28.4	43

Males have heavier burden then females & Not very aggregated

Parasitology (1977), **75**, 259–276
With **4** *figures in the text*

Dynamical aspects of host–parasite associations: Crofton's model revisited

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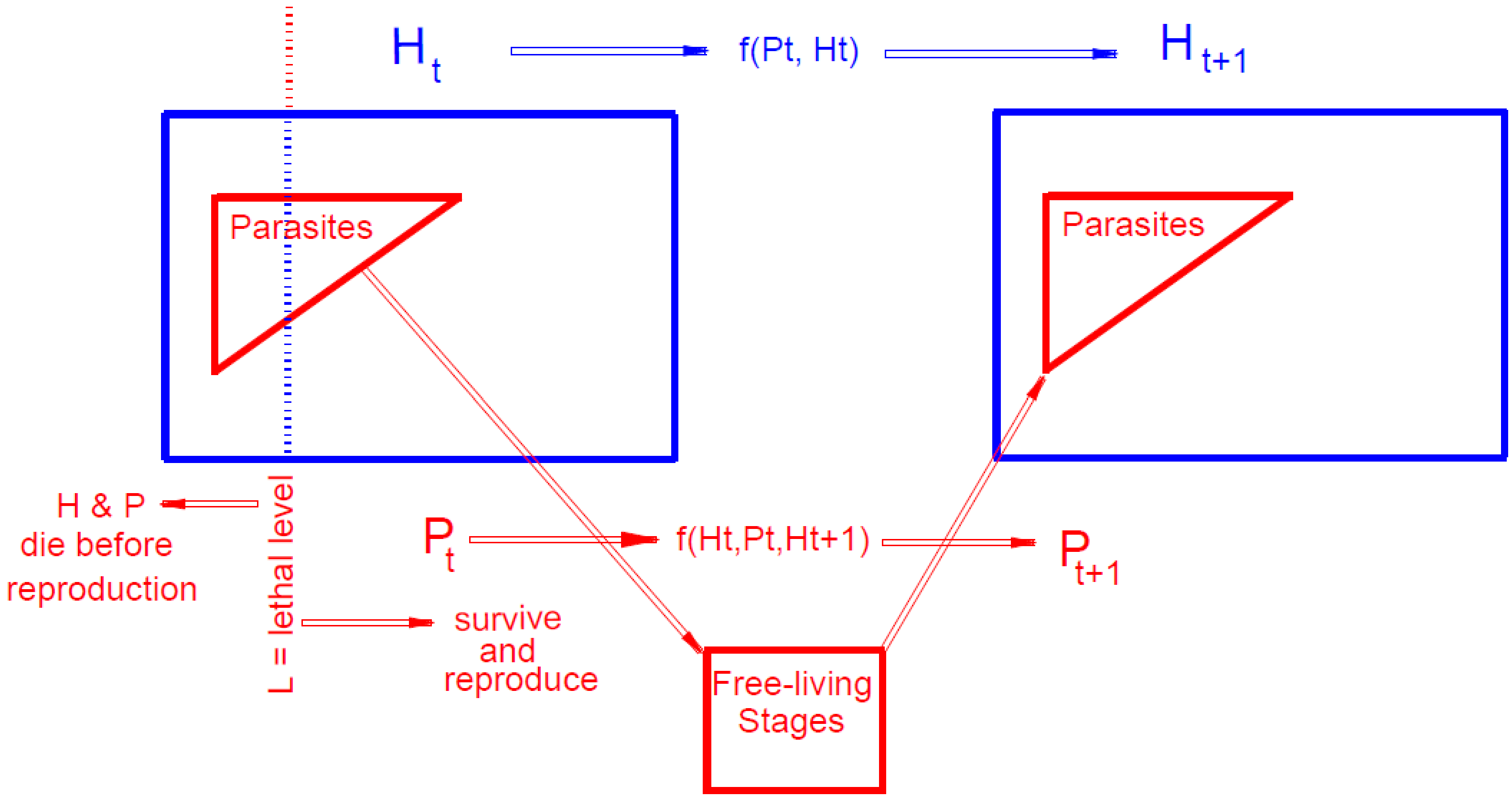
Biology Department, Princeton University, Princeton 08540, *New Jersey*

(*Received* 2 *May* 1977)

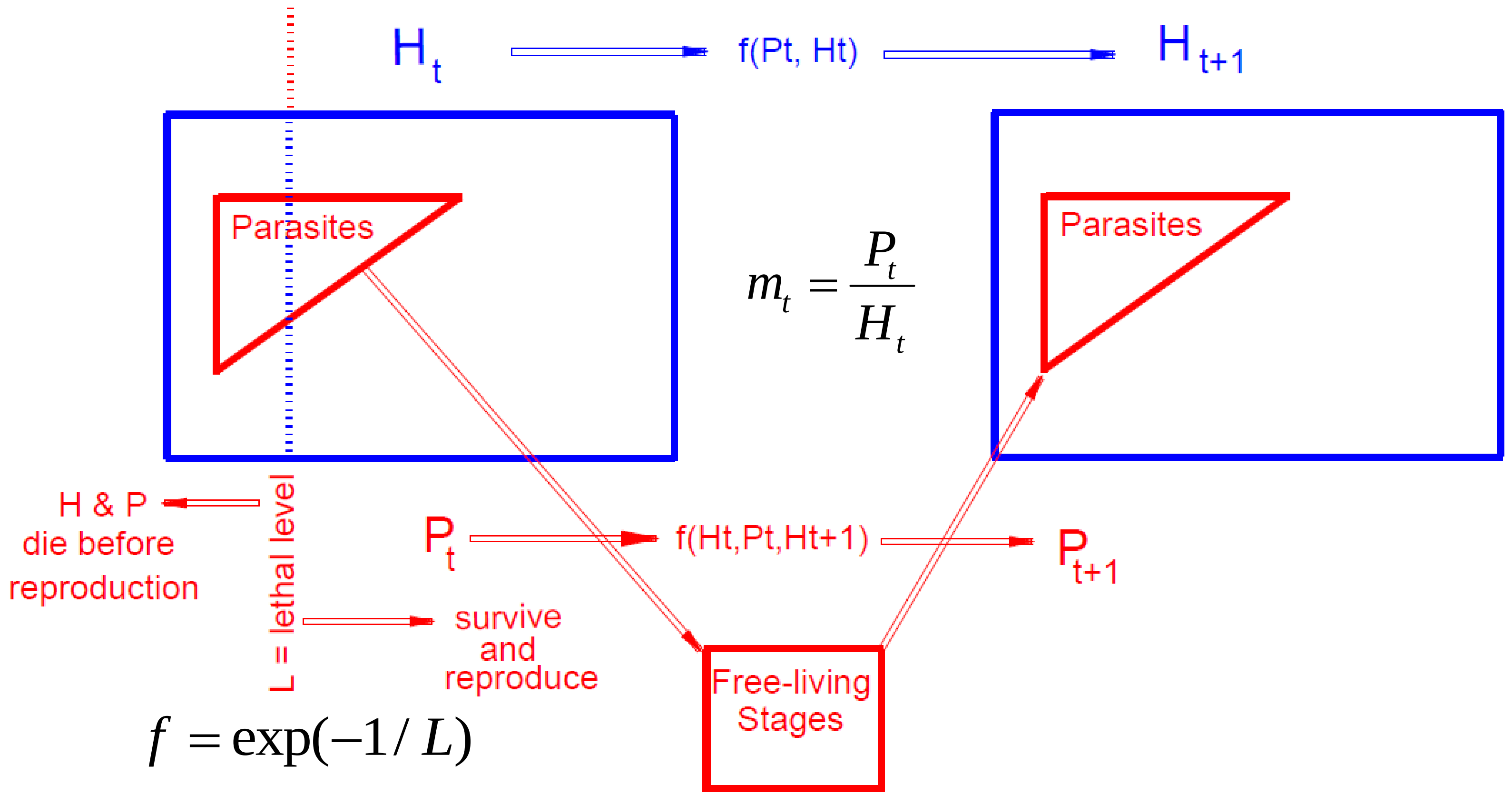
SUMMARY

Although superseded by more recent and biologically realistic studies, Crofton's (1971*b*) model of host–parasite associations remains of interest as the simplest model which captures the essentials. Even if its simplifying assumptions are all accepted, Crofton's model has two defects: the first is that its general conclusions are drawn from numerical simulations for a very restricted range of parameter values; the second is that the probability for a parasite transmission stage to succeed in establishing itself in a host is not constrained to be less than unity, as biologically it must be. The present paper remedies these two defects, by giving analytical results valid for all values of the parameters, and by demanding that the parasite transmission factor indeed saturates to unity. Some of Crofton's conclusions remain intact, others are significantly altered.

Basic May-Crofton Model

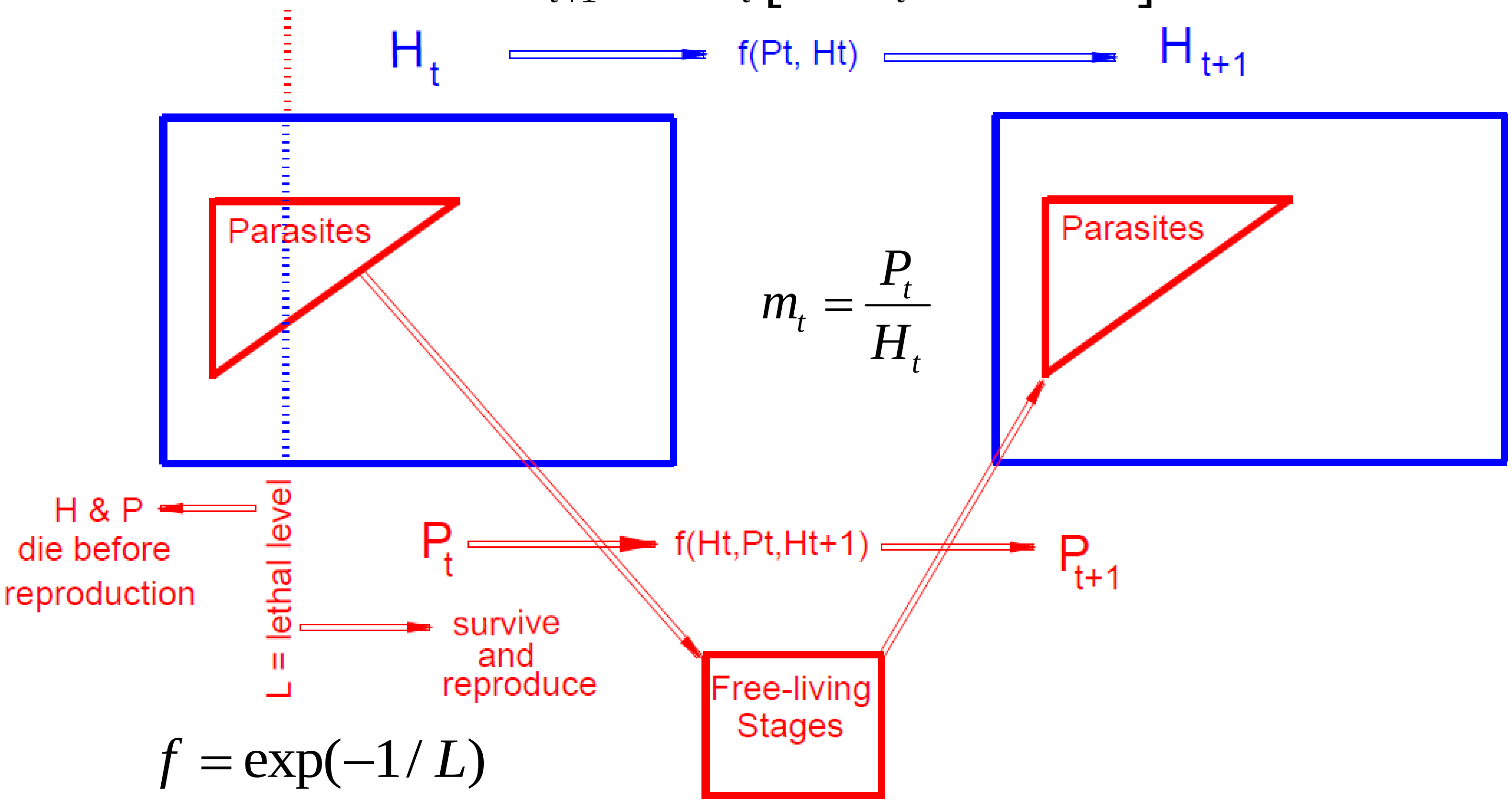


Basic May-Crofton Model



Basic May-Crofton Model

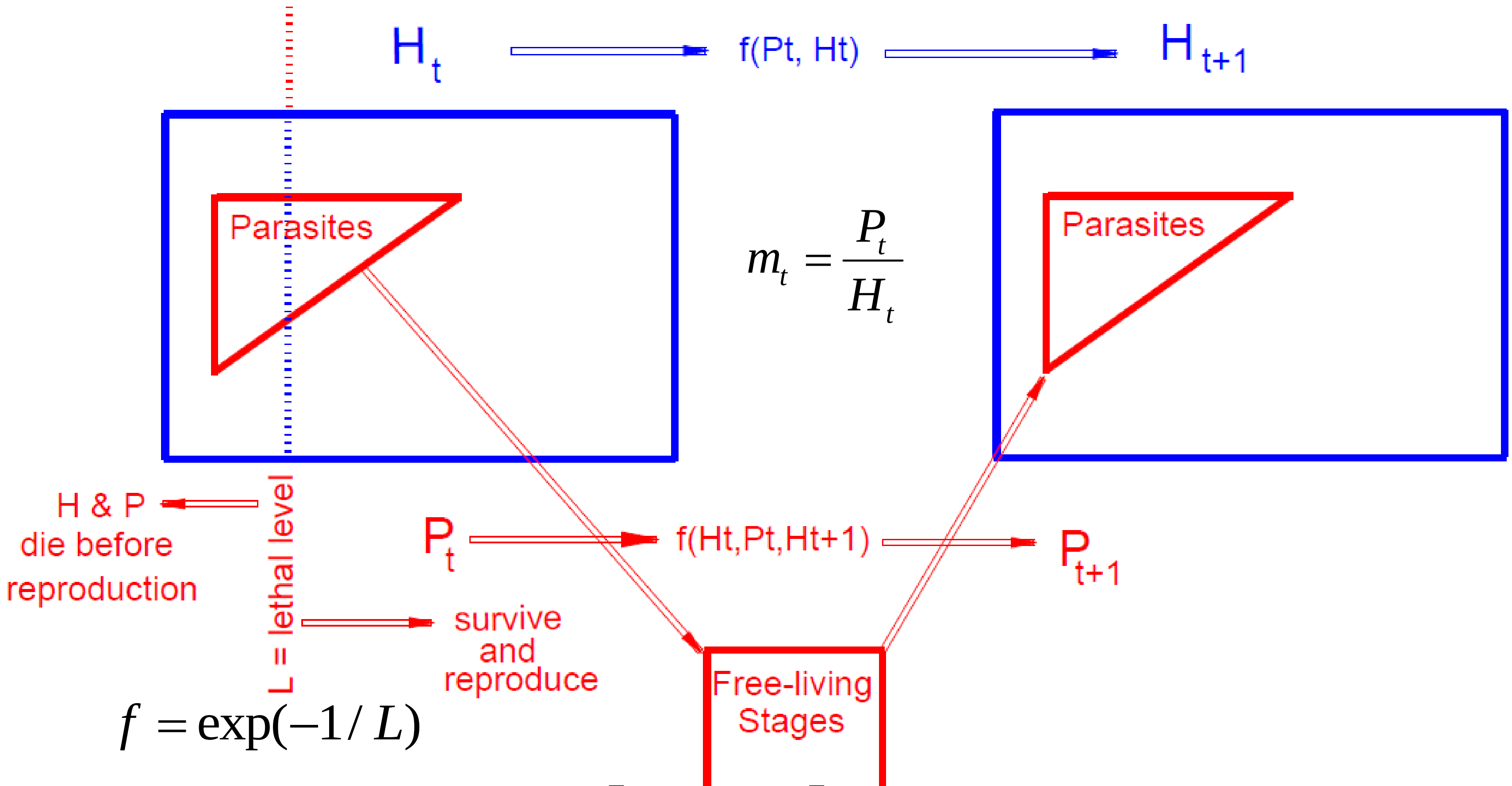
$$H_{t+1} = \lambda H_t \left[1 + m_t(1 - f)/k\right]^{-k}$$



$$f = \exp(-1/L)$$

Basic May-Crofton Model

$$H_{t+1} = \lambda H_t \left[1 + m_t(1-f)/k\right]^{-k}$$

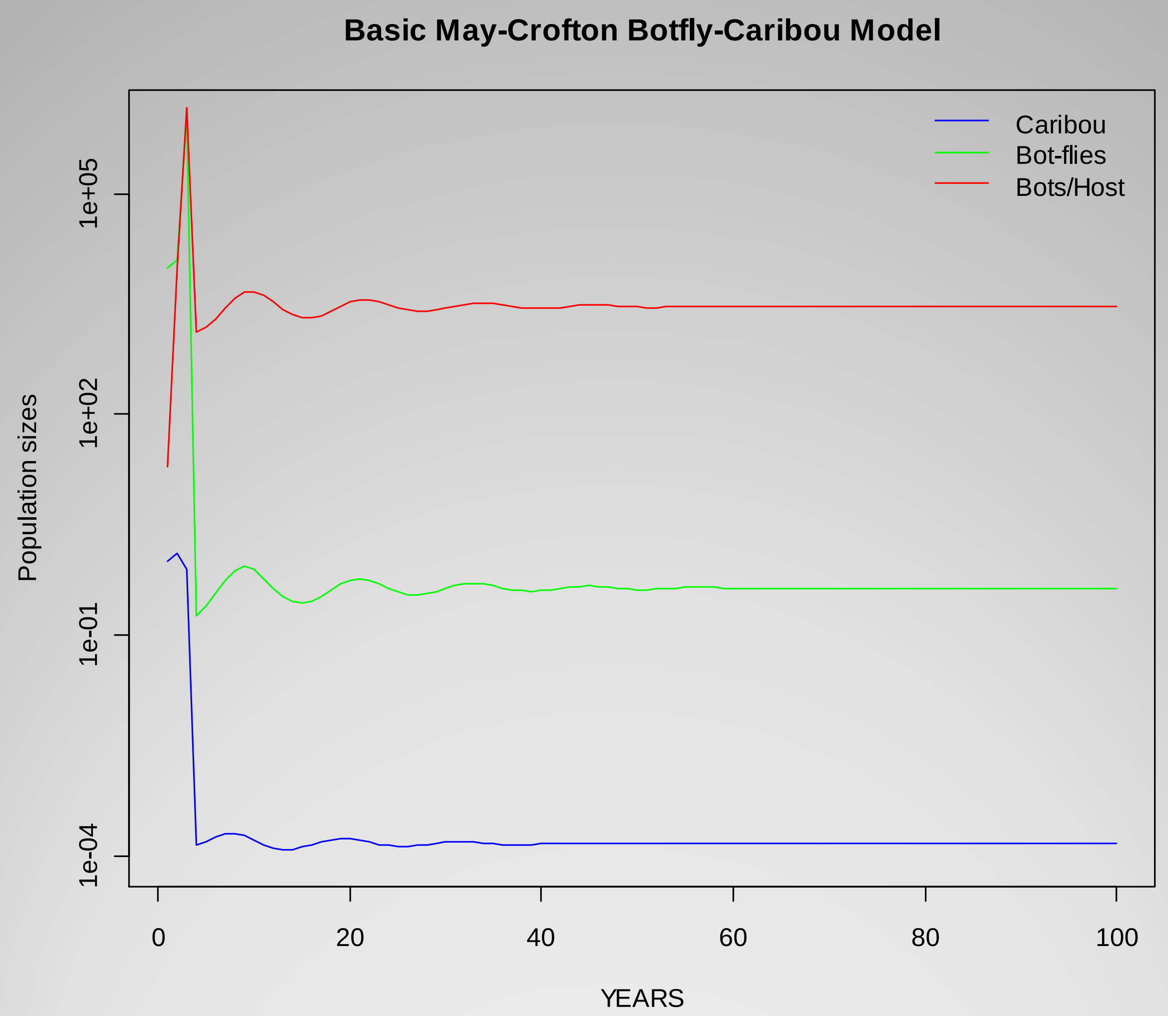


$$m_t = \frac{P_t}{H_t}$$

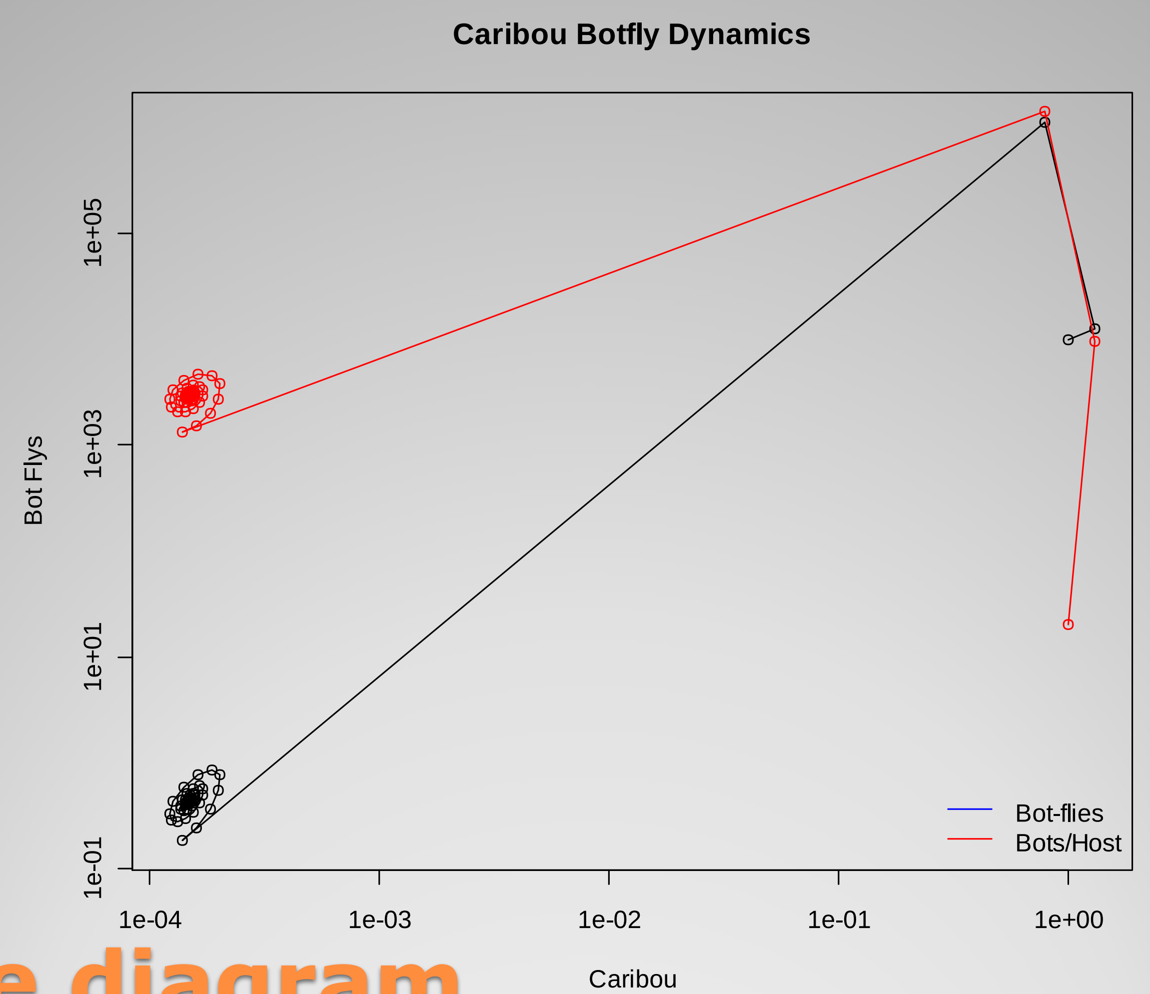
$$f = \exp(-1/L)$$

$$m_{t+1} = fAm_t \left[\frac{H_t}{(H_S + H_t)}\right]\left[1 + m_t\left(1-f\right)/k\right)\right]^{-k+1}$$

Which is a moment expansion of: $P_{t+1} = AH_t \sum_{i=0}^{\infty} i \prod \left(i \middle| m_t\right) p(i)$ to handle differential death rates



Caribou bot-fly – no age structure



Phase diagram
Caribou abundance x bot flys

Add age-structure to Caribou

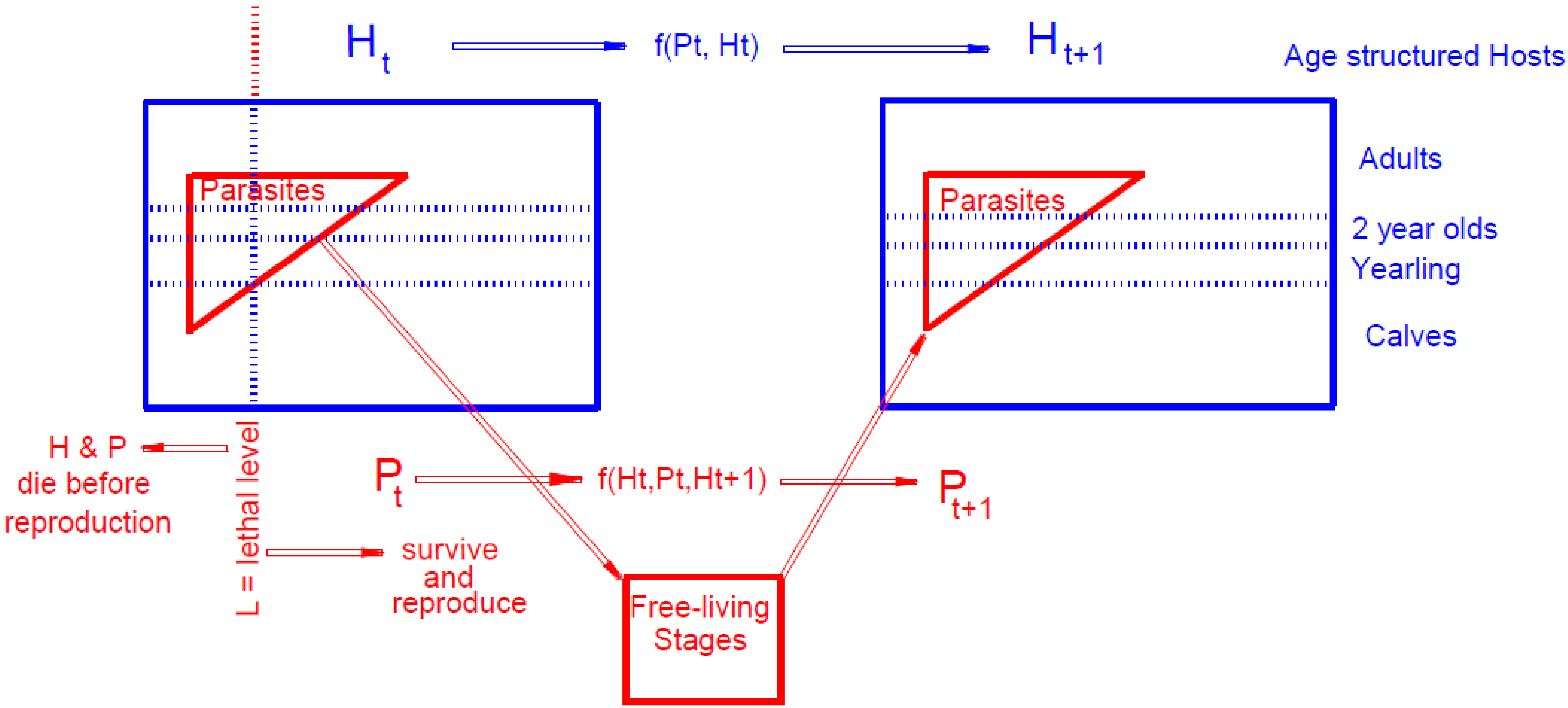
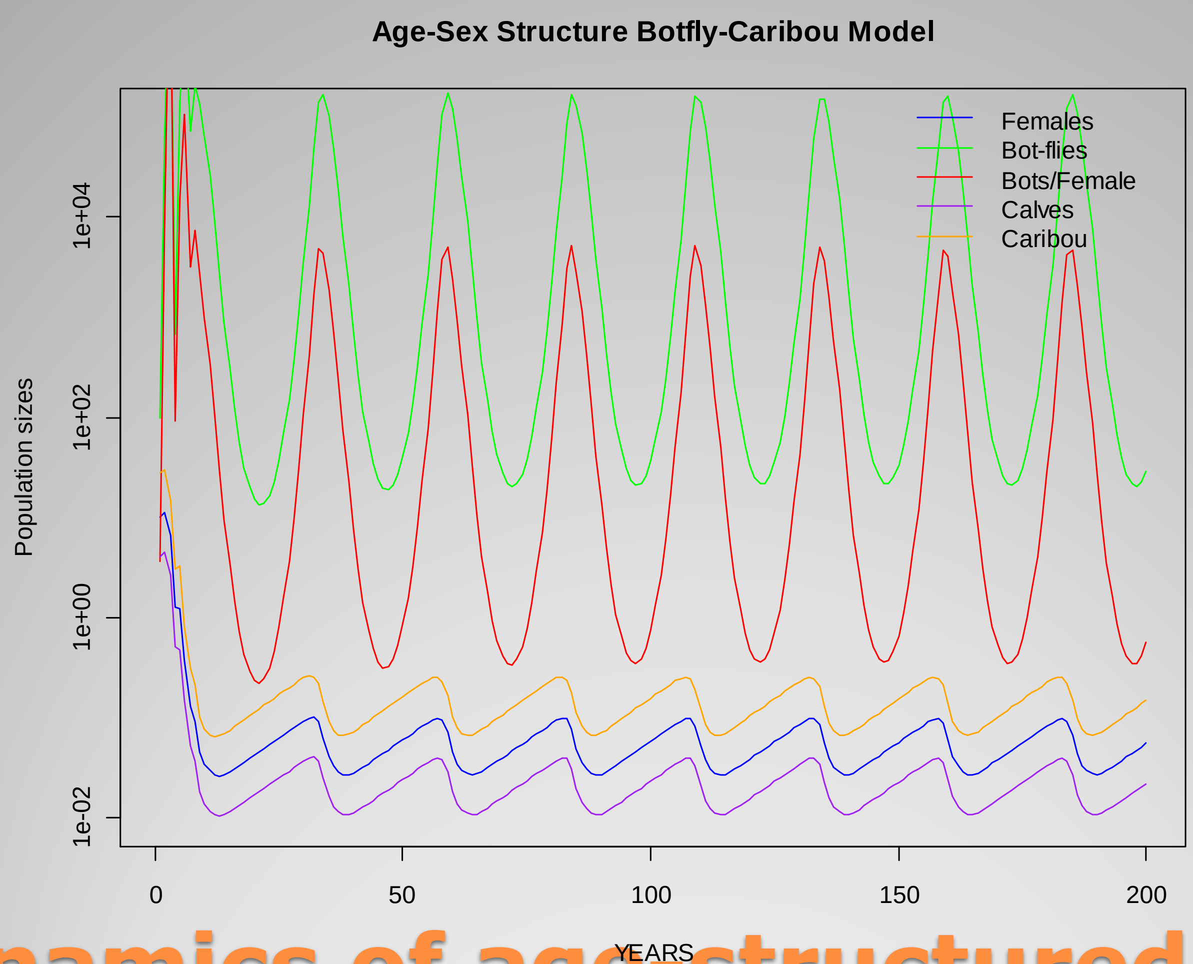


Table 1. Contracted life table for female caribou >1.5 years old that were collected from the Beverly herd from 1980 through 1987.

Age[a] (yr) x	Observed frequency Feb 21 of_x	Frequency from Quadratic[b] Feb 21 f_x	June 8 f_x	Survival[c] l_x	Mortality[d] d_x	Mortality rate[e] q_x	Survival rate[f] p_x
2		135.5	131.3[e]	100.0	10.6	10.6	89.4
3	120	121.4	117.4	89.4	10.0	11.3	88.7
4	109	107.9	104.2	79.4	9.6	12.1	87.9
5	83	95.2	91.6	69.8	9.2	13.0	87.0
6	101	83.0	79.6	60.6	8.5	14.1	85.9
7	70	71.6	68.4	52.1	8.1	15.5	84.5
8	59	60.8	57.8	44.0	7.6	17.2	82.8
9	52	50.6	47.8	36.4	7.1	19.4	80.6
10	45	41.2	38.5	29.3	6.5	22.4	77.6
11	21	32.3	29.9	22.8	6.1	26.6	73.4
12	31	24.2	21.9	16.7	5.6	33.3	66.7
13	12	16.7	14.6	11.1	5.0	45.4	54.6
14	9	9.8	8.0	6.1	4.6	75.0	25.0
15	2	3.7	2.0	1.5	1.5	100.0	0.0
16	2						
Totals	716	853.9	813.0		100.0		

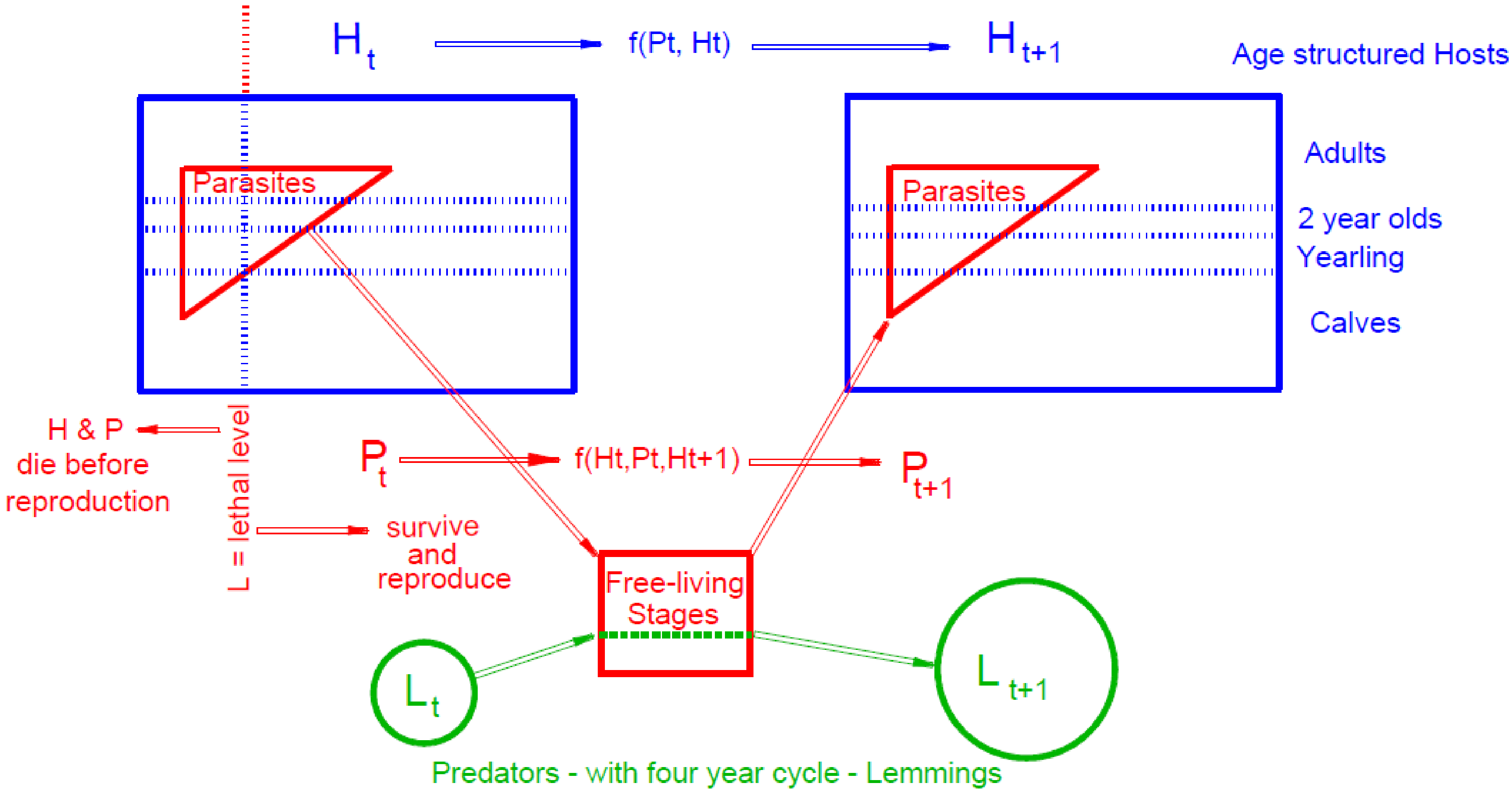
[a] Ages at June 8. Ages at February 21 are *Age — 0.29*. E.g., 1.71/2 yr.
[b] From quadratic equation: $y = 0.330x^2 - 15.558x + 161.113$ where y is frequency and x is age.
[c] Each frequency divided by 131.3 and converted to percent (X 100).
[d] Difference between survival at successive age classes.
[e] $100\ d_x/l_x$. These values were rounded from three decimal places.

Life table for caribou

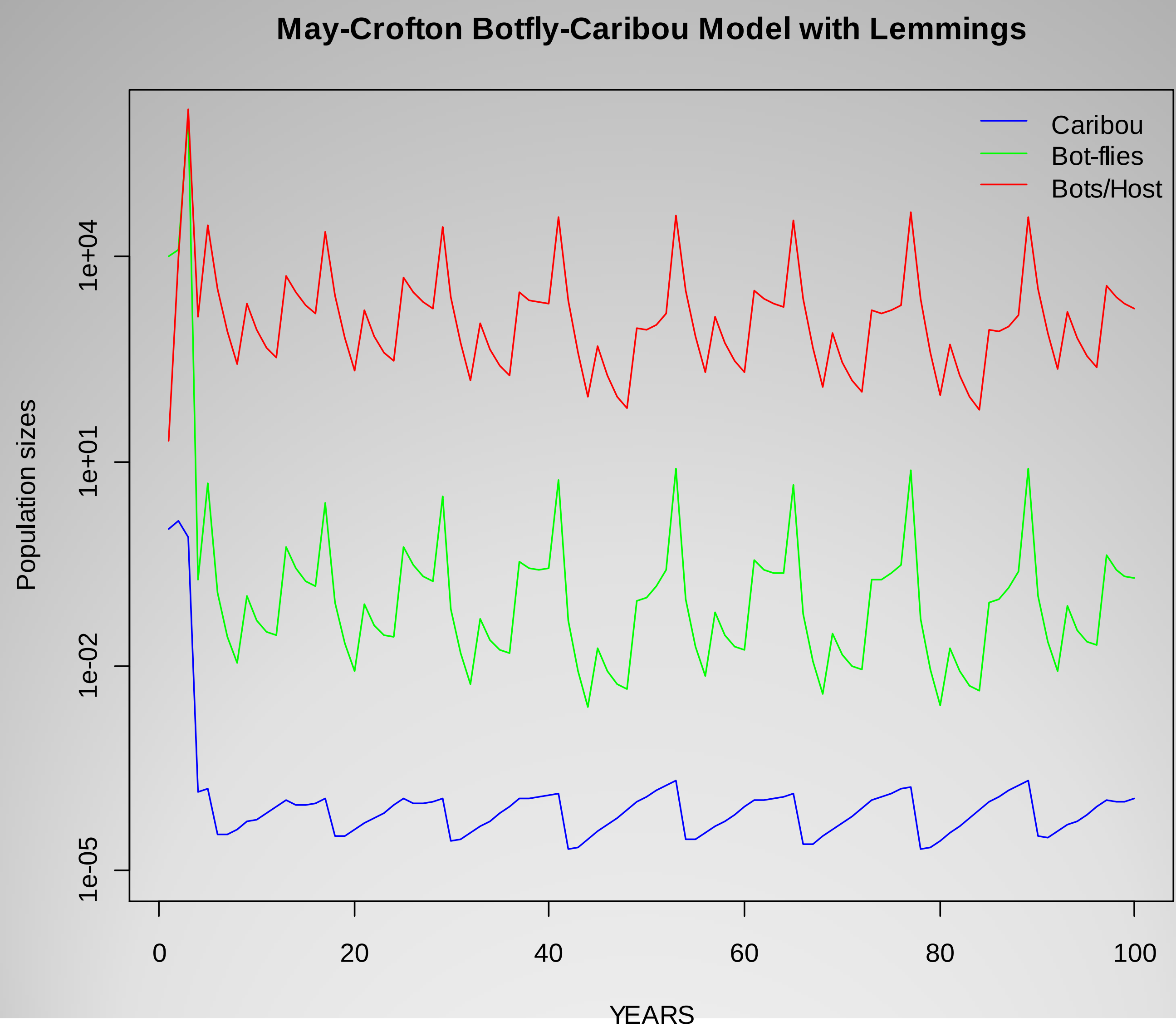


Dynamics of age-structured caribou model with botflies

Basic Crofton May with Predators on free-living stages

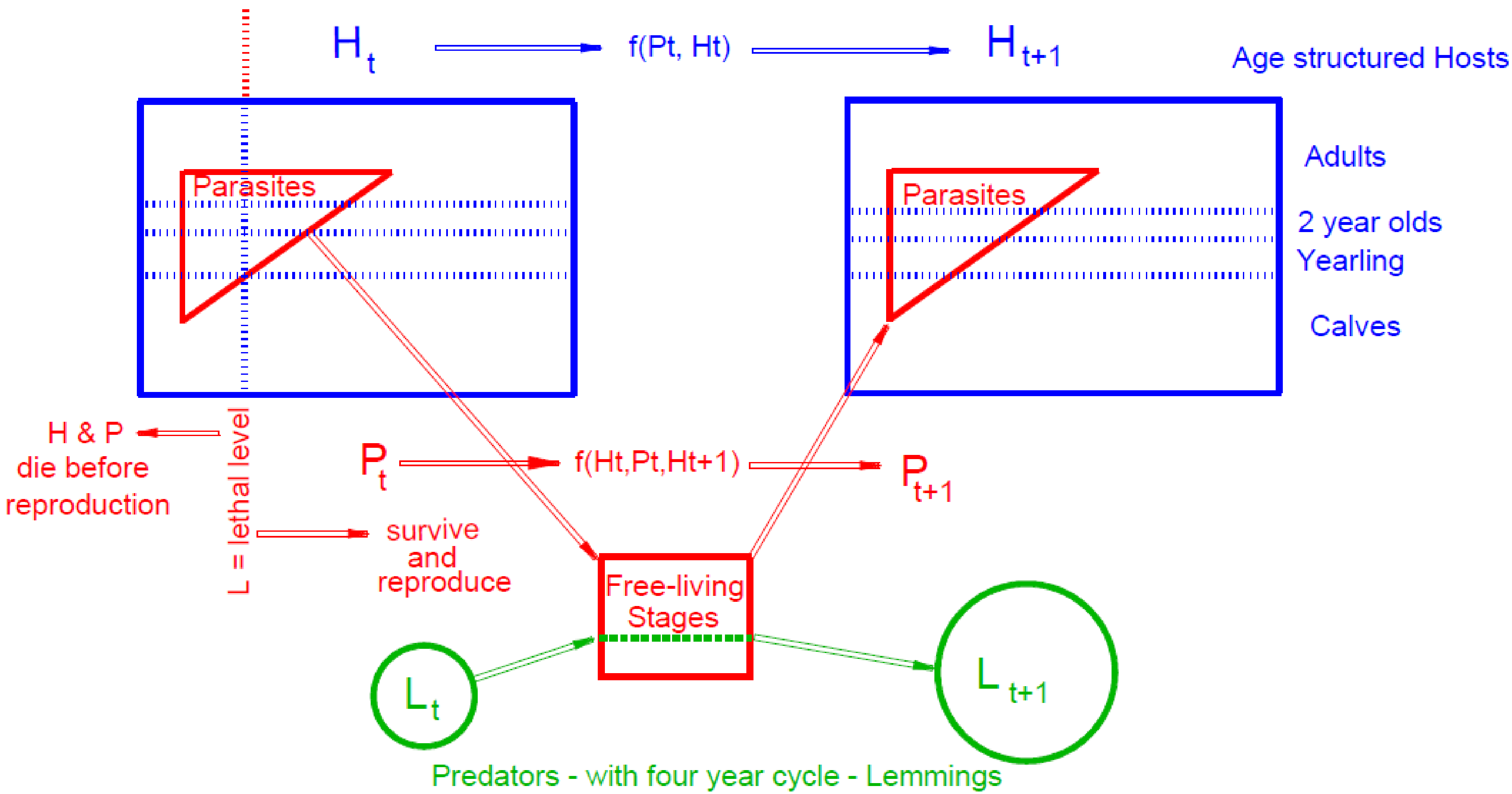


Add predators to free-living bots

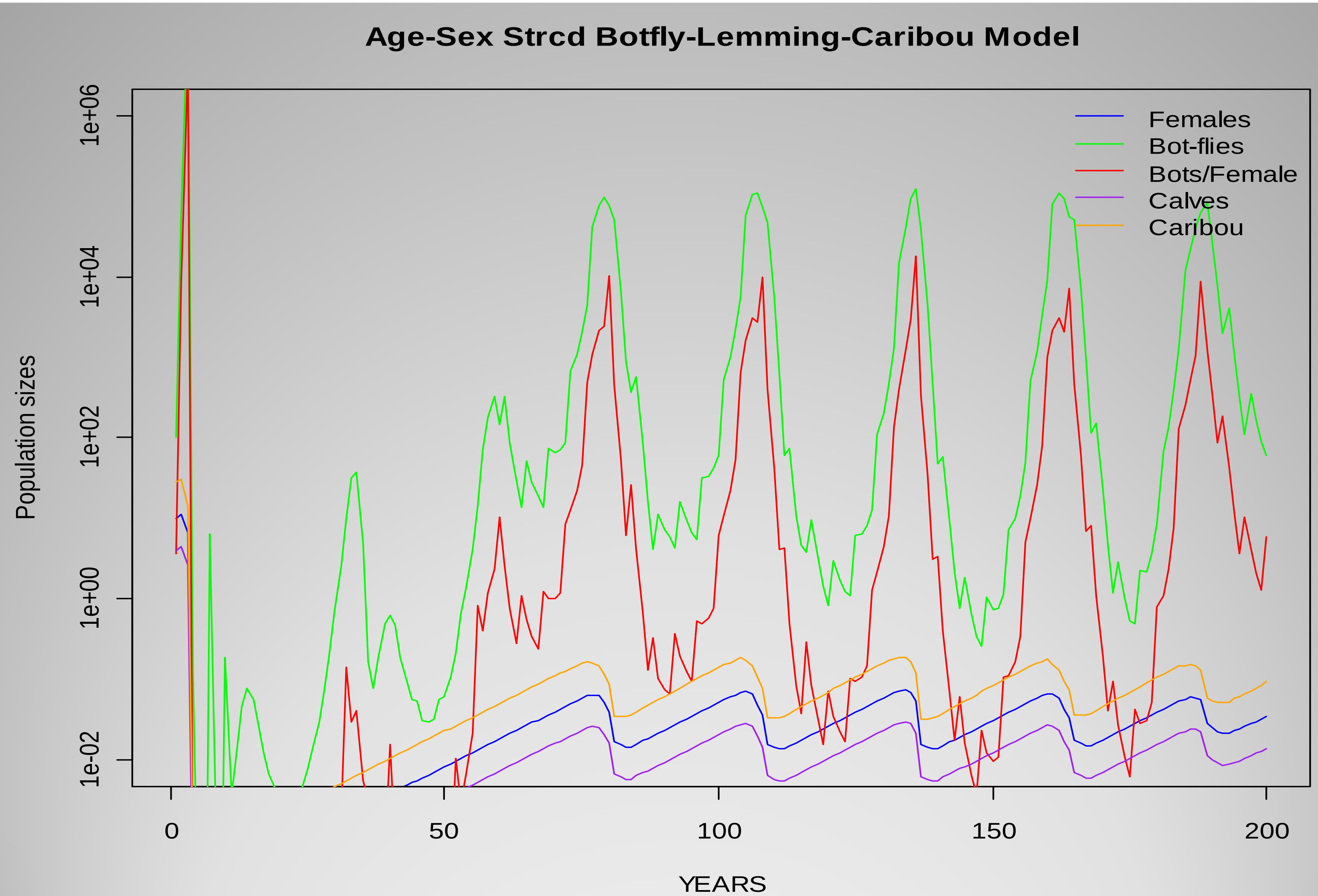


Lemmings (and others) eat bot-flies

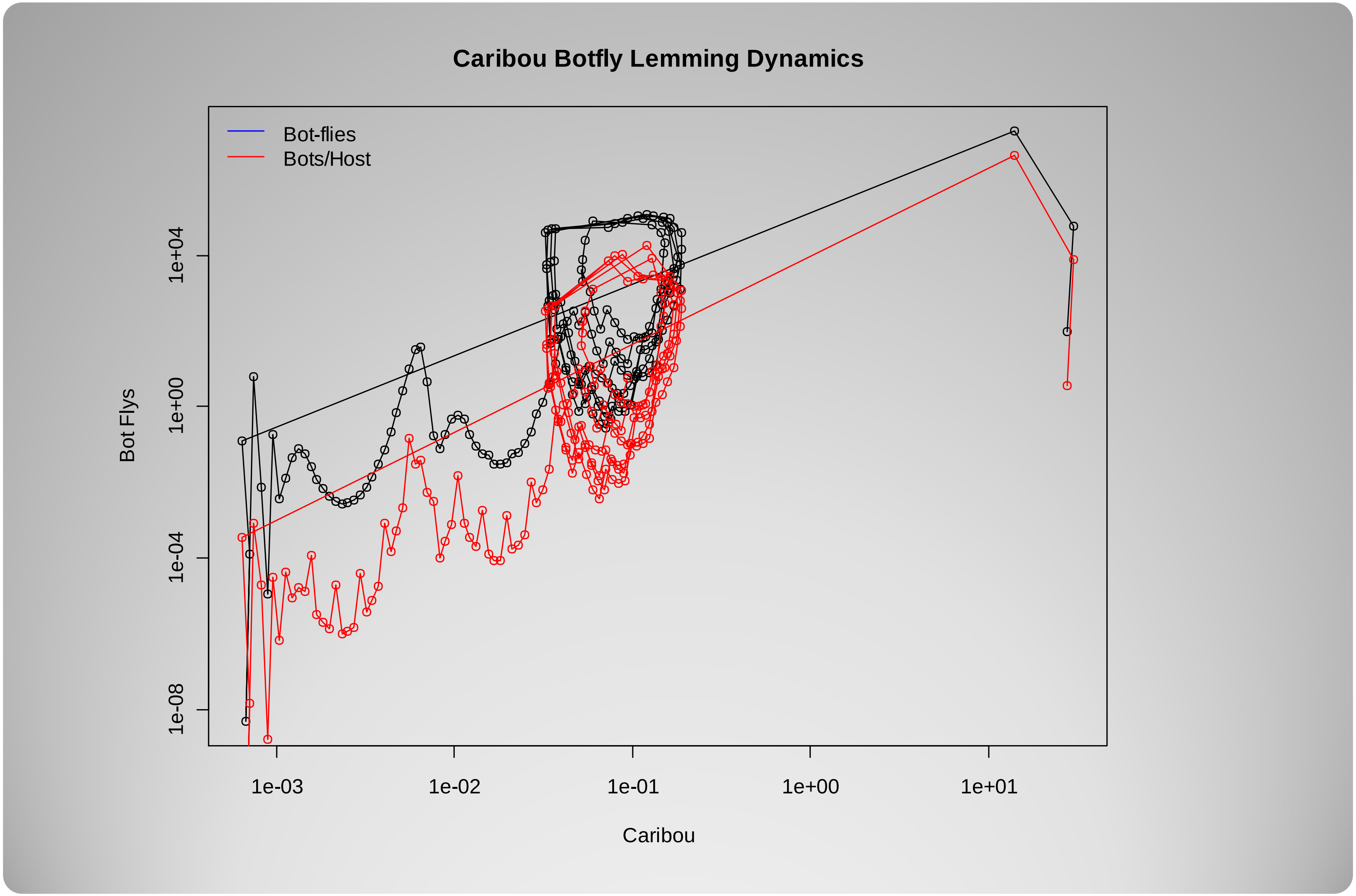
Age-structured Crofton May with predator attack on free-living stages



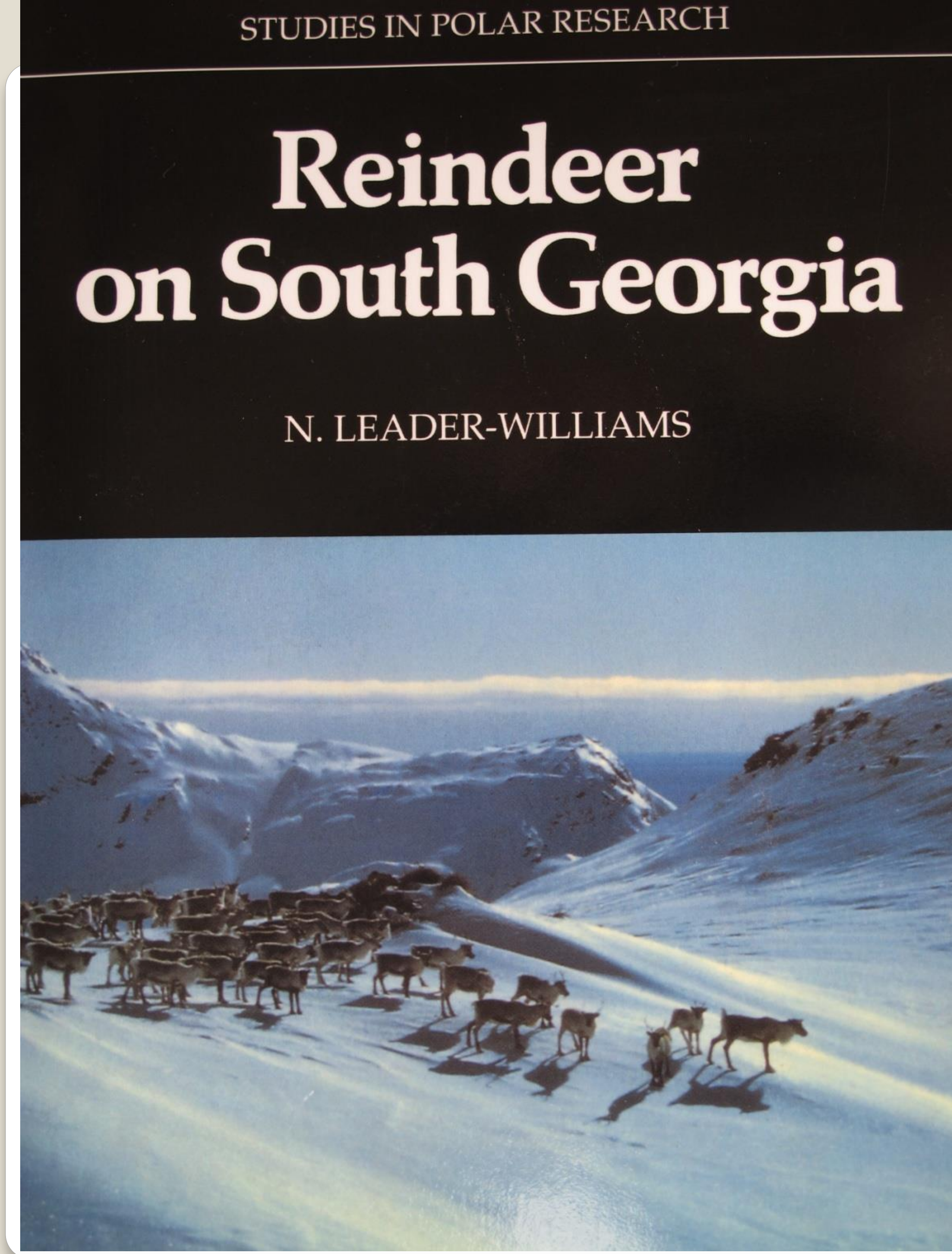
Add predators to free-living bots



Age-structured Caribou-Bot-Fly model with four year lemming cycles



Phase plot of Caribou, Botflies & Lemmings



Any evidence..?

1. Hard to design an experiment to remove bots and warble flies from thousands of caribou…

2. All populations of caribou with bot-flies / warbles show evidence of long-term cycles

3. Reindeer introduced to South Georgia and Iceland over 100 years ago, show no evidence of cycles and there are no Bots nor warbles there.

May's Crofton revisited.....

first is that its general conclusions are drawn from numerical simulations for a very restricted range of parameter values; the second is that the probability for a parasite transmission stage to succeed in establishing itself in a host is not constrained to be less than unity, as biologically it must be. The present paper remedies these two defects, by giving analytical results valid for all values of the parameters, and by demanding that the parasite transmission factor indeed saturates to unity. Some of Crofton's conclusions remain intact, others are significantly altered.

(1) Crofton (1971*b*) has presented a mathematical model which aims to exhibit some of the essential dynamical properties of host–parasite associations. The extreme biological simplicity of this model (e.g. hosts and parasites have the same generation time) makes it applicable to few real systems, and later models (Anderson & May, 1977; May & Anderson, 1977) have added many more general biological features in an effort to make contact with empirical data. Nevertheless, Crofton's model retains pedagogical value as *the* basic model.

(2) Even within its own framework of simple assumptions, Crofton's model has two defects. The first is that the general conclusions about its dynamical behaviour are drawn from numerical stimulations for a restricted, and not necessarily representative, range of parameter values. The second is that the factor describing the input of parasite transmission stages into the next generation of hosts does not saturate to unity, as its biological definition implies it must. The present paper gives an analytical account of the dynamical behaviour of Crofton's model, valid for all values of the relevant biological parameters, and with a parasite transmission factor that does saturate to unity. The ensuing conclusions are in several respects

Ecological Dynamics Across the Arctic Associated with Recent Climate Change

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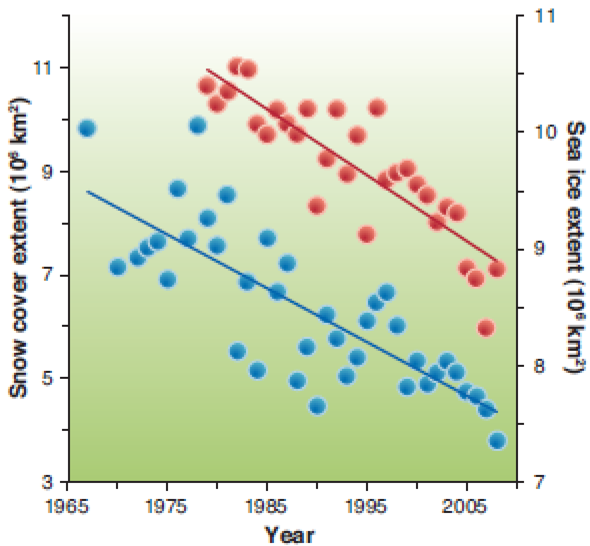

Fig. 1. Reductions in terrestrial snow cover (blue) and sea ice (red) extent during June to August over the Northern Hemisphere since the late 1960s and 1970s, respectively. Data are from the Global Snow Lab, Rutgers University, New Jersey, and the U.S. National Snow and Ice Data Center, University of Colorado, Boulder.

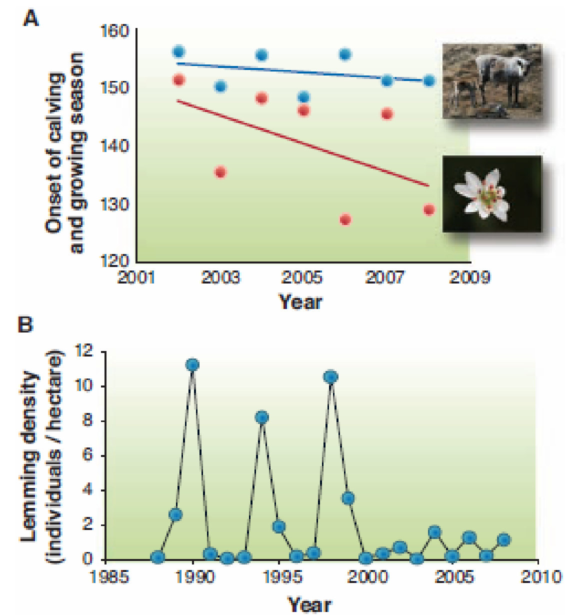

Fig. 3. Complex responses to Arctic climate change that may have broader community and ecosystem consequences. **(A)** A developing trophic mismatch between the timing of caribou calving (blue), which has not changed, and the timing of plant growth (red), which is advancing with warming in Greenland [updated from (*33*)]. **(B)** The recent observed collapse in the population cycles of small rodents, shown here for lemmings in northeast Greenland, as a result of diminished snow cover in the Arctic [from (*36*)].

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Lemmings stop cycling..?

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