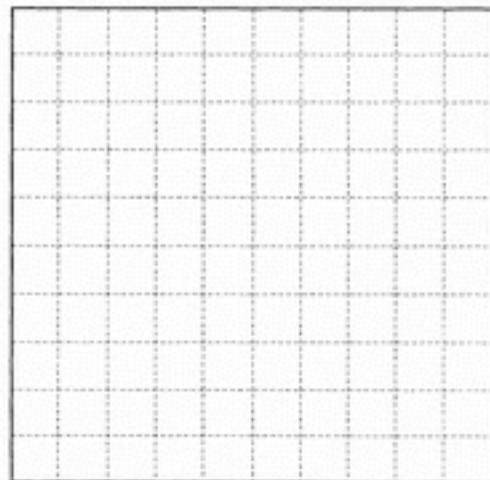
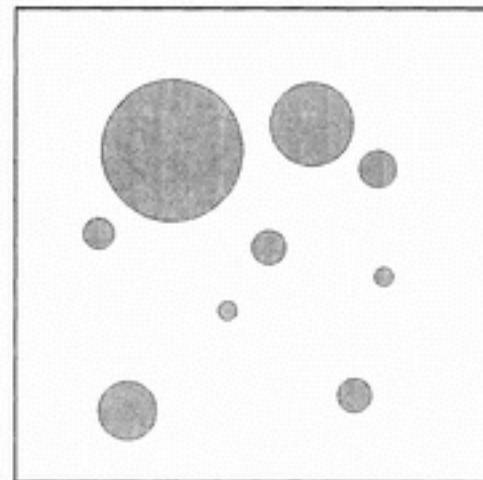


Population dynamics on discrete patches: metapopulations

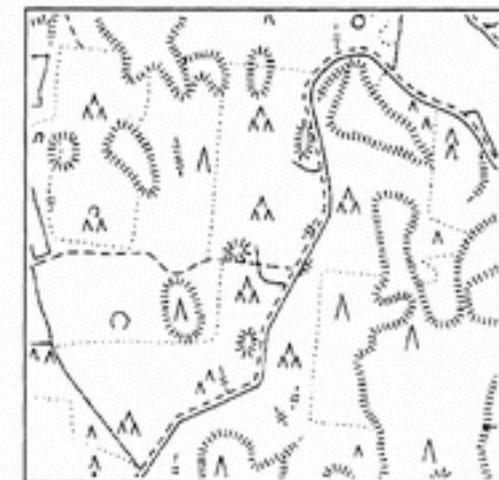
Theoretical
ecology



Metapopulation
ecology



Landscape
ecology



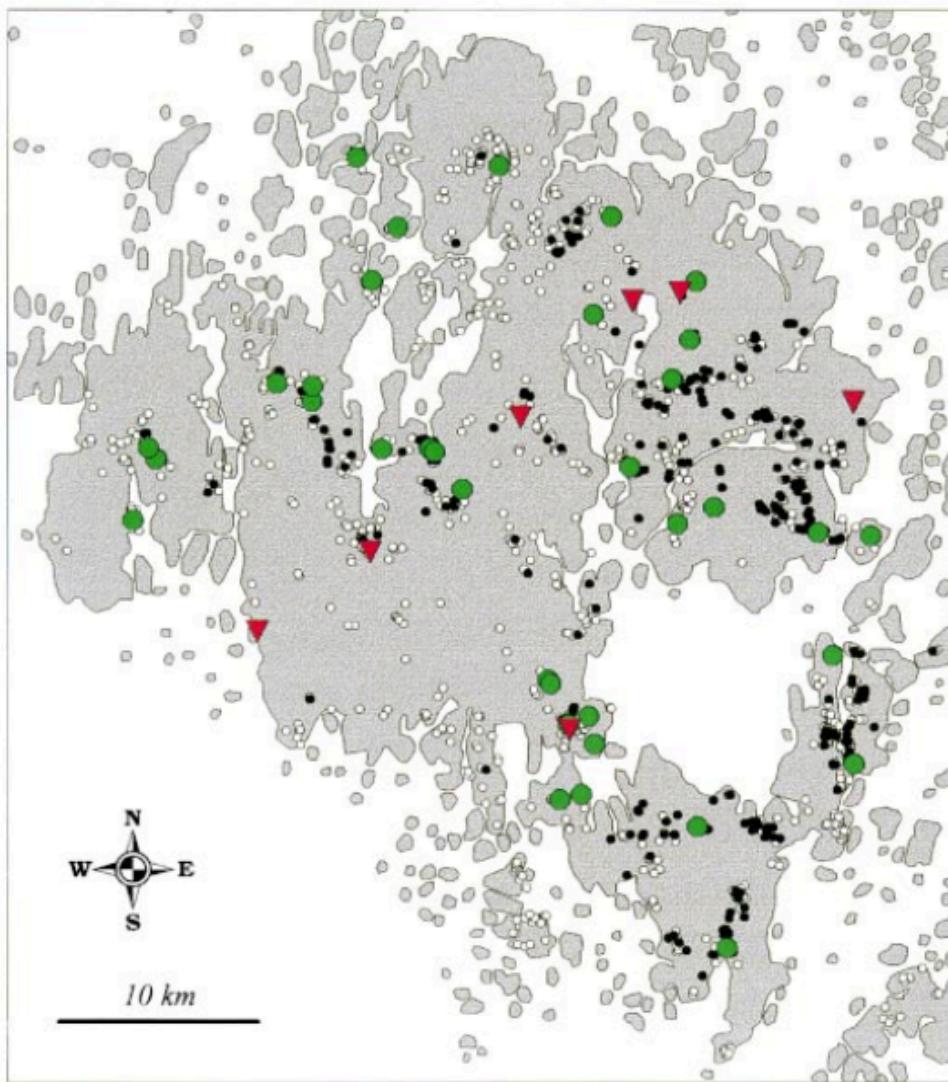


Figure 1 Map of Åland in southwestern Finland showing the locations of the 42 local populations from which adult female butterflies were sampled in summer 1996 (large symbols). All known suitable meadows are shown as small circles, with meadows in which Glanville fritillary larvae were present in autumn 1995 indicated by black circles (and large symbols), and unoccupied meadows by white circles. Of the 42 local populations sampled, the 35 that survived to autumn 1996 (green circles) are distinguished from the seven that went extinct (red triangles).

Saccheri et al. 1998. Nature 392: 491-494

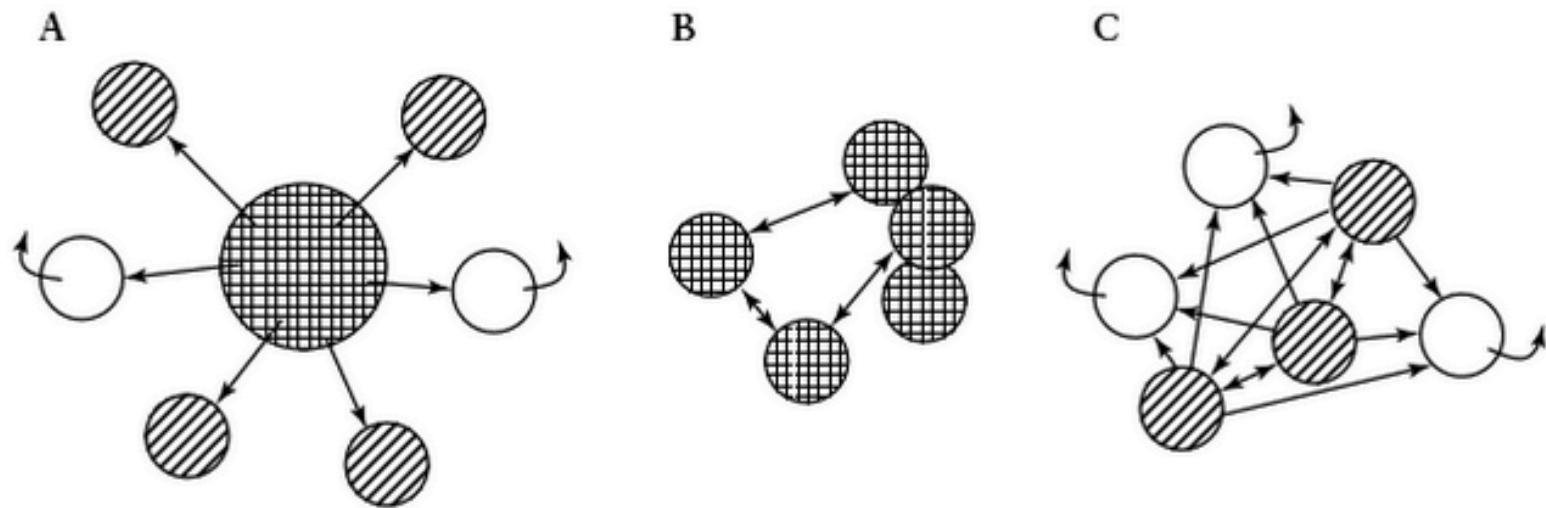


FIGURE 5.15. Simplified classification of spatially structured dynamics (modified after Harrison 1991 and Harrison and Taylor 1997). Circles with diagonal lines represent populations that are destined for extinction (e.g., because their habitat does not offer a full complement of what the population needs to survive) and thus will go extinct eventually. Cross-hatched circles represent populations that are permanent in that they are not ever expected to disappear. Empty circles represent habitats from which populations have disappeared (gone extinct) and are not yet recolonized. Straight arrows indicate migration directions; curved arrows represent previous extinction events. (A) A source–sink population. (B) A panmictic population with a clumped spatial distribution. (C) A metapopulation.

Assumptions of Metapopulation Models

Six basic assumptions underlie the idea of metapopulations:

1. Suitable habitat can be conceived of as occurring in discrete patches. This assumption seems to be fairly obvious in many cases, for example, in meadows surrounded by forest or forests in an agricultural matrix.
2. The population is at least temporarily a reproductive population. For example, in a series of dry meadows in a matrix of forest in Finland, Hanski and Simberloff (1997) found that 60%–80% of the butterflies spend their whole lives in their natal patch, providing strong evidence that a patch does not contain just an ephemeral aggregation.

3. Subpopulations have a substantial risk of extinction. In the Finland butterfly example, the largest population had only about 500 individuals (out of 377 populations), and populations with several hundred individuals have been recorded as going extinct.
4. The subpopulations are not so isolated that recolonization of empty patches is impossible. Using the Finland butterfly example again, the mean nearest-patch distance was 240 meters and the median distance moved by migrating butterflies was 330 meters, more than sufficient to allow colonization to balance extinction. On the other hand, it may be that many fragmented populations are in a state such that colonization rates will not be high enough to sustain true metapopulation dynamics.
5. The dynamics are not synchronized across subpopulations. This is a major concern in applying metapopulation theory to conservation. If extinctions are correlated among patches, a uniform dispersal rate may not be able to compensate for the peaks in extinctions.
6. All patches are alike (i.e., equally suitable) both in terms of probability of extinction and colonization and as a source of colonists. Harrison and Taylor (1997) argue that variation among patches is really the case and that it is likely that most metapopulations are closer to the source-sink model (a source, by definition, has a zero probability of going extinct and also serves as the sole source of propagules) than the classic metapopulation.

Population dynamics in continuous space



This reading is on the D2L

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Spread of invading organisms

D.A. Andow¹, P.M. Kareiva², Simon A. Levin³ and Akira Okubo⁴

What do we need to know?

1. What do the terms in the reaction diffusion equation mean?
2. What are the variables and parameters?
3. What are the assumptions of a reaction diffusion model for spatial population dynamics?
4. How are the parameters estimated?
5. What does the models predict?
6. How did the models perform when tested against data?

Reaction diffusion equation (2 dimensional space)

$$\frac{\partial N}{\partial t} = f(N) + D \left[\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \right]$$

Diagram illustrating the components of the Reaction diffusion equation:

- Reaction term:** $f(N)$
- Diffusion term:** $D \left[\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \right]$
- Change in population size, N , at a particular point in space (x,y) :** $\frac{\partial N}{\partial t}$
- A continuous time population growth function (i.e. exponential, logistic):** $f(N)$
- Diffusion coefficient:** D
- Second partial derivatives of population size with respect to space (x and y): describe diffusive movement:** $\left[\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \right]$

Reaction diffusion equation (2 dimensional space)

$$\frac{\partial N}{\partial t} = f(N) + D \left[\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \right]$$

Variables

- $N(t,x,y)$: local population density (number per area) at time, t , at location (x,y)

Reaction diffusion equation

(1 dimensional space, with $f(N)$ as exponential growth)

$$\frac{\partial N}{\partial t} = \alpha N + D \frac{\partial^2 N}{\partial x^2}$$

Variables

- $N(t,x)$: local population density (number per area) at time, t , at location x .

Reaction diffusion equation

(1 dimensional space, with $f(N)$ as exponential growth)

$$\frac{\partial N}{\partial t} = \alpha N + D \frac{\partial^2 N}{\partial x^2}$$

Parameters

- D : diffusion coefficient
- α : intrinsic growth rate for the exponential model (i.e. $\alpha=r=b-d$, where r is the notation typically used in class)

Can you think of an instance where 1 dimensional space would be appropriate?



Photo by Mike Baird bairdphotos.com

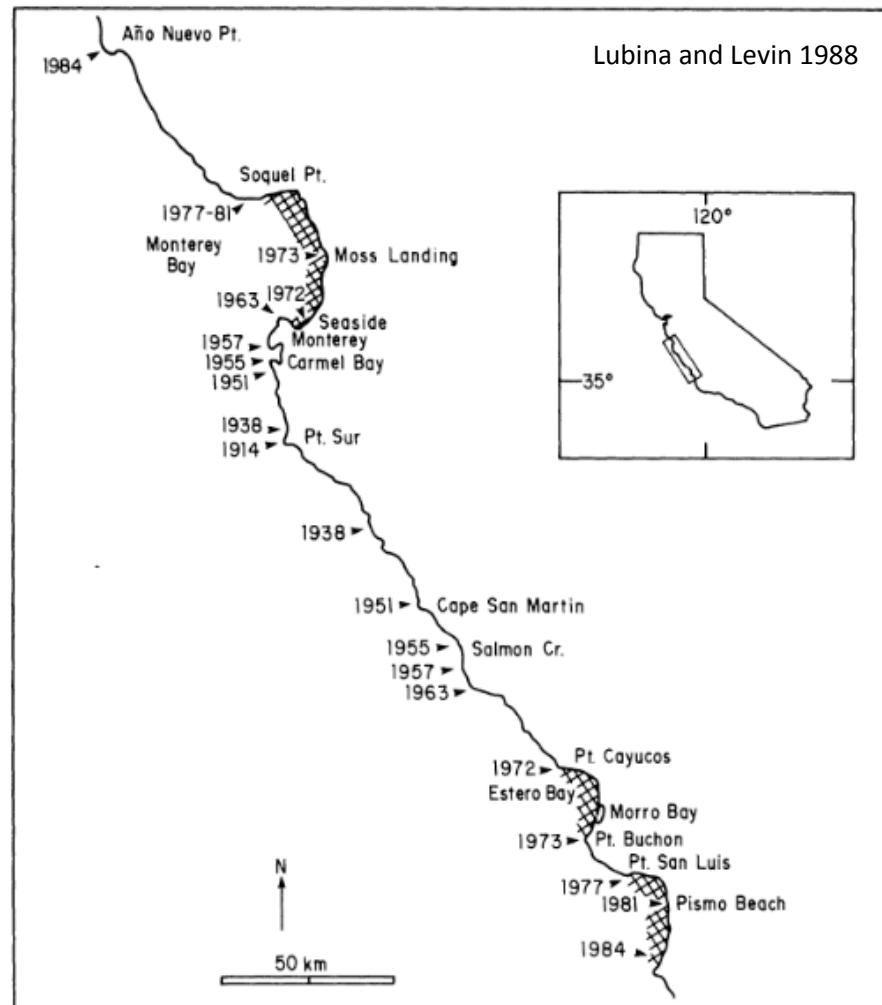
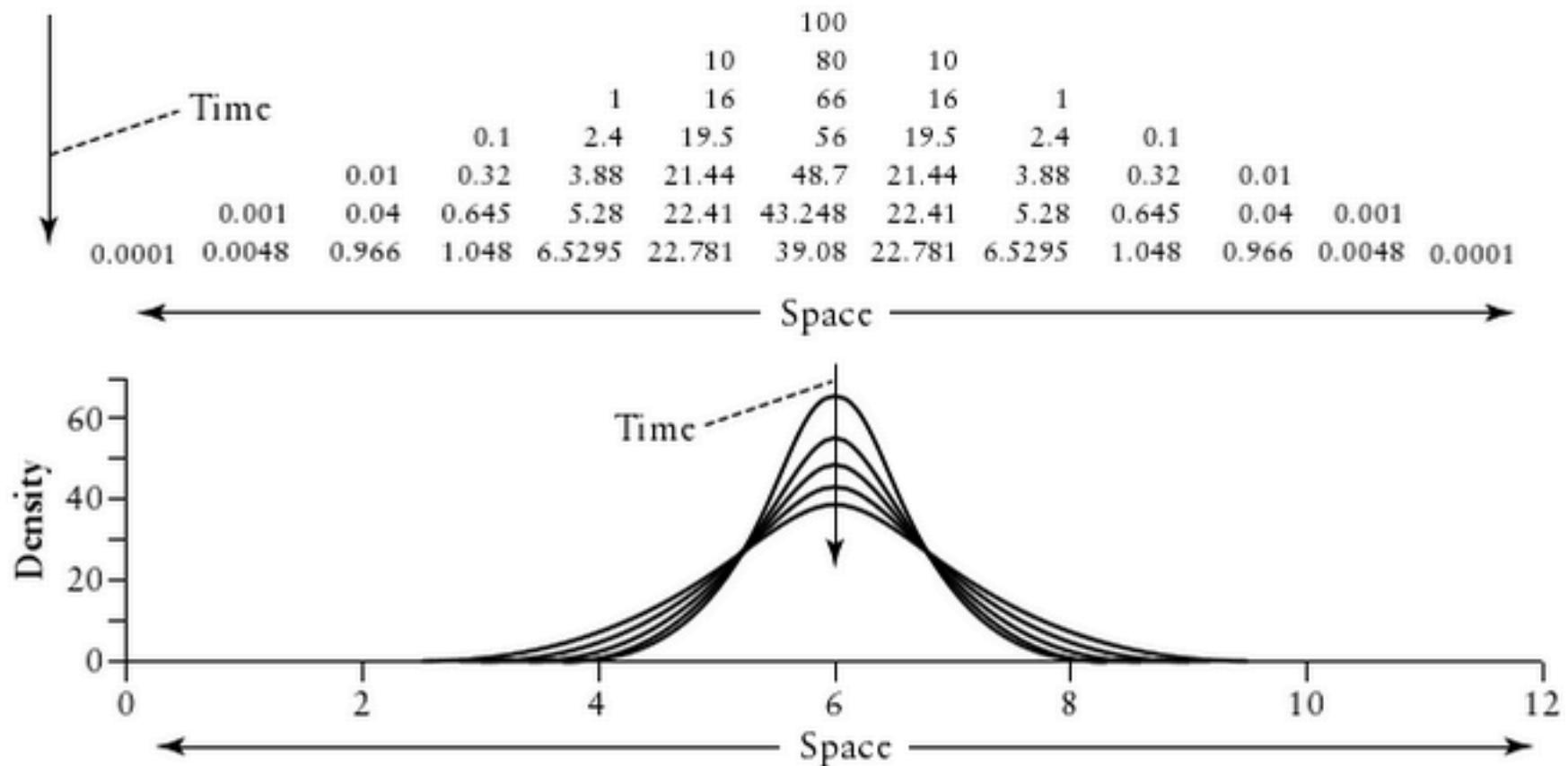


FIG. 1.—Expansion of the range of the California sea otter along the central California coast. Only representative locations of the position of the range boundaries are shown. Point Sur is the traditional location of the division of the range into northern and southern halves. Crosshatching, the approximate location of sandy or soft-bottom habitats. Data are taken from table 1. (Map after Wild and Ames 1974.)

Assumptions of diffusive movement



Vandermeer and Goldberg. 2013. Figure 5.11 p139.

Assumptions of reaction-diffusion

- At the population level, the dispersal distances follow a normal distribution
- The assumptions regarding population growth are as those for the non-spatial model
- There is no relationship between movement and reproduction
- Reproduction and dispersal parameters do not depend on spatial location
- There is no defined order for reproduction and dispersal, both processes happen continuously

Estimating parameters

- The parameters for the population growth model, $f(N)$, can be estimates from data describing:
 - Population size over time (i.e. the Tribolium lab)
 - Birth and death rates (i.e., the Protection Island worksheet)

Estimating parameters

- The diffusion coefficient, D , can be estimated if the mean dispersal distance, $M_D(t)$, over a fixed period of time, t , is known:

$$D = \frac{2M_D(t)^2}{\pi t}$$

(i.e. mark recapture, radiotelemetry)

What does reaction diffusion predict?

- If $f(N)$ is exponential or logistic growth then,
 - 1 dimensional space: the range (length of habitat occupied by the species) increases linearly over time
 - 2 dimensional space: divide space into sectors: distance from release point to a point on the boundary of the occupied habitat increases linearly over time

What does reaction diffusion predict?

- If $f(N)$ is exponential or logistic growth then,
 - The asymptotic rate of change in habitat occupied is

$$V_F = \sqrt{4\alpha D}$$

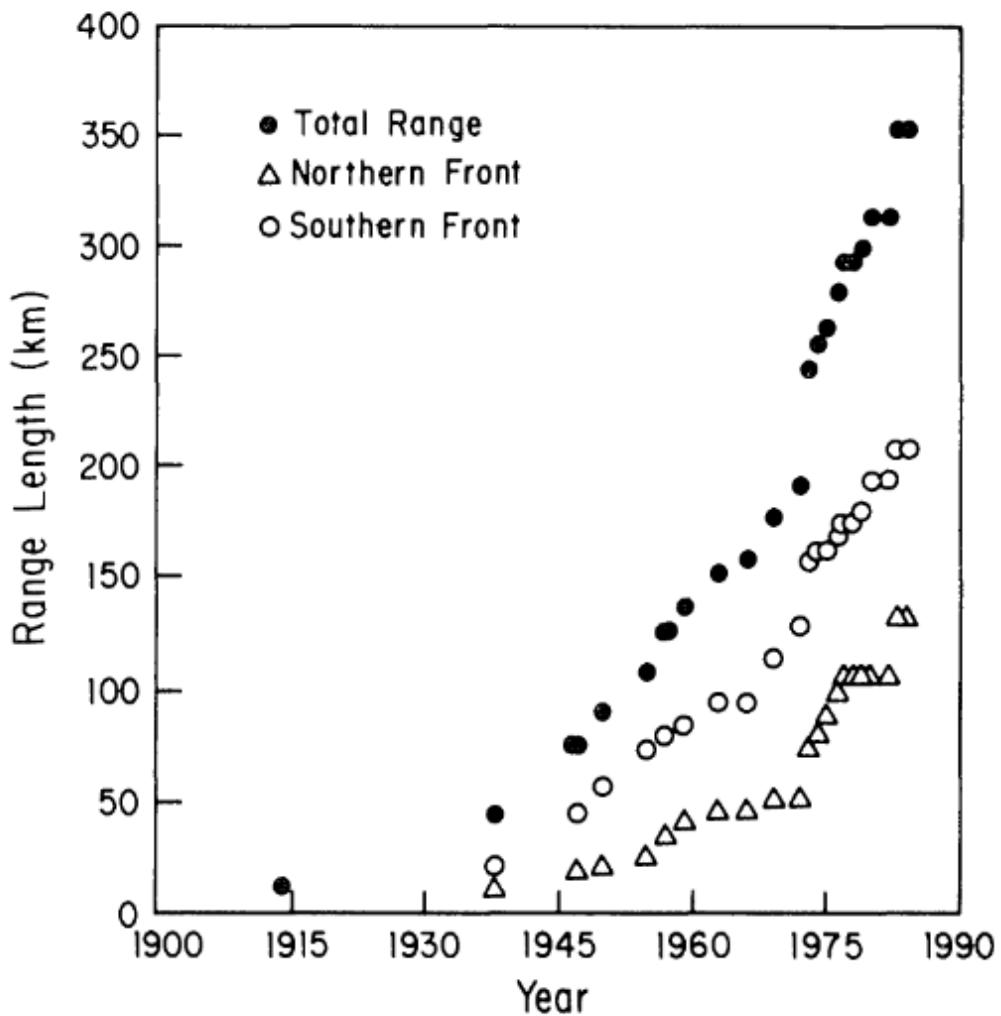


FIG. 2.—Range increase versus time for the California sea otter population. The overall range increase, together with the movement of the northern and southern fronts, is shown. The overall rate of range increase was 5.6 km/yr. However, as discussed in the text, habitat dependence appears to affect the movement rates. The habitat discontinuities encountered in 1972–1973 are evident, as is the pattern of piecewise linear expansion of the range. See the text for further discussion.

Habitat heterogeneity

In the north, along Monterey Bay, the otters remained close to shore, traversing over 35 km of coastline (fig. 1). The data for the northern front show an overall rate of range increase of 4.6 km/yr between 1973 and 1984. These data, however, are complicated by the occurrence of a major habitat discontinuity. Monterey Bay may have inhibited recruitment to the northern front, resulting in the apparent stalling of the front at Soquel Point between 1977 and 1982. Along the soft-bottom habitat of Monterey Bay, a more rapid movement of 8.2 km/yr occurred. A deep-water trench off Moss Landing (fig. 1) may have forced the northern otters to stay close to the shore. Deep water is thought to influence movements in Alaskan otter populations (Kenyon 1969), and it may be similarly avoided by California otters.

Estimation of r

mates suggest a recent decline in otter numbers (table 1). We assume, however, that nonlinear effects contributing to the slowing of population growth were minimal during the initial spread of the population, and we use the slope of the regression of the log-transformed early population data (reliable population size estimates from 1938 to 1959) to estimate an intrinsic growth rate of 5.6% per year ($r_{xy} = 0.9961$, $P < 0.001$).

We use $r = 0.056$ as our initial estimate of the intrinsic growth rate of the California sea otter population. This estimate is consistent with an evaluation of

Estimation of D

The best way to estimate D would be by tracking individual movements. Where this is possible, A , an estimate of the diffusivity, could be related to the individual step length per time unit of observation (Pielou 1977; Okubo 1980). The step length could be estimated by using the mean free path, or net displacement, computed from observational data. Although data on the movements of otters exist (e.g., Loughlin 1979; Ribic 1982), they are not sufficient for the task at hand.

As discussed earlier, even when D is not directly measurable, it still can be estimated sometimes from distributional data. Were the diffusion and advection

Based on the above, our estimate of D , within rocky subtidal habitat, is 104.0 km²/yr. However, since these data are from late in the period of range expansion,

D is 13.5 km²/yr for the north and D is 54.7 km²/yr for the south.

	α (yr ⁻¹)	D (km ² /yr)	V_F (km/yr)
Empirical data (combined N+S)	-	-	5.6 9.4 (1973-84) 4.5 (1938-72)
Model predictions (combined N + S)	0.056	104	4.8 $2V_F = 9.6$
Empirical data N	-	-	1.4
Model predictions N	0.056	13.5	1.74
Empirical data S	-	-	3.1 (1938-72) 3.8 (1973-1980)
Model predictions S	0.056	54.7	3.5



Photo by jumpingmaniac

Why the sectors?

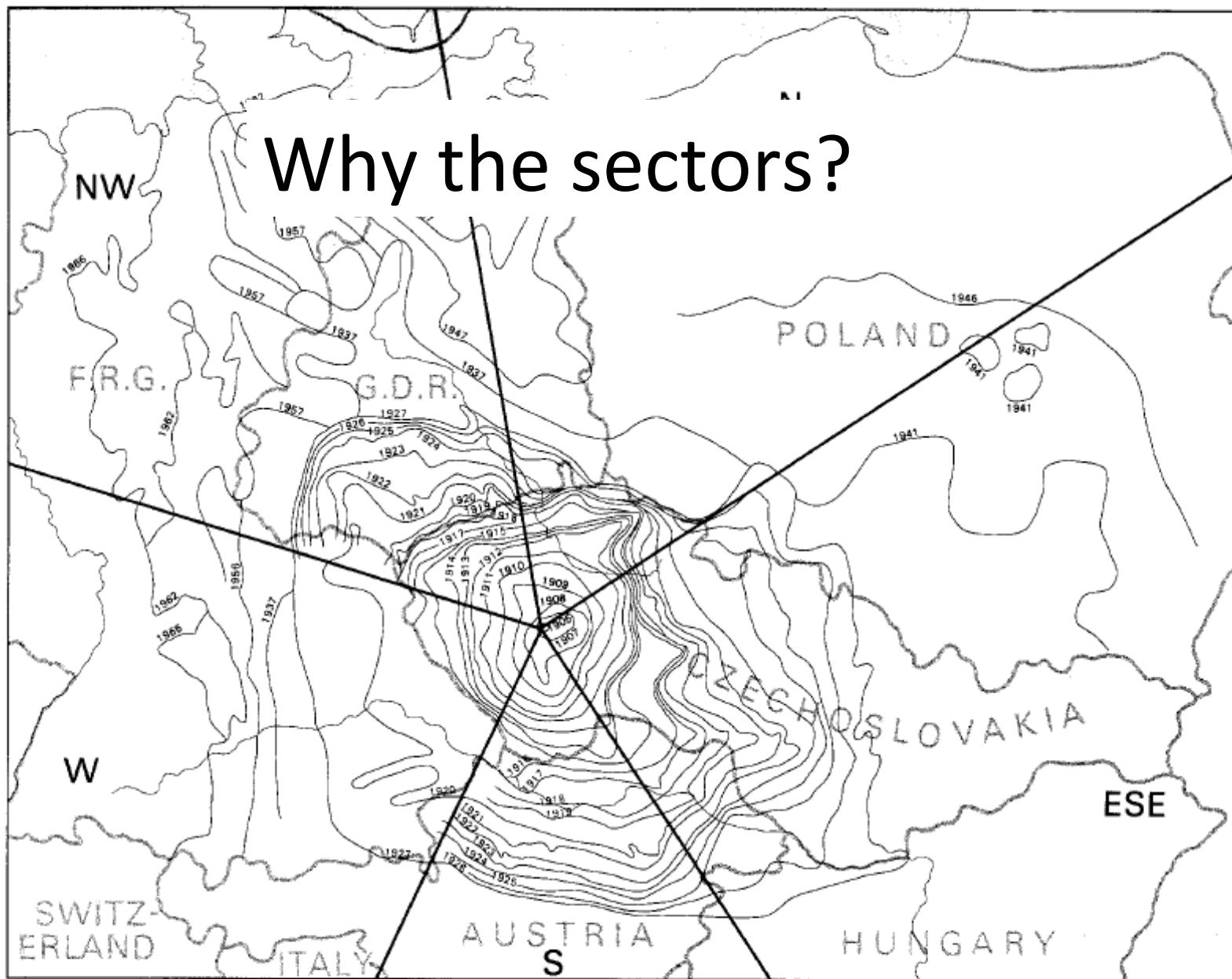


Fig. 1. Spread of muskrat from Prague in five sectors. The S/ESE and ESE/N boundaries roughly separate the eastern European plain; the N/NW boundary distinguishes spread down the Oder River from spread down the Elbe River; the NW/W and W/S boundaries isolate the poorly known W sector.

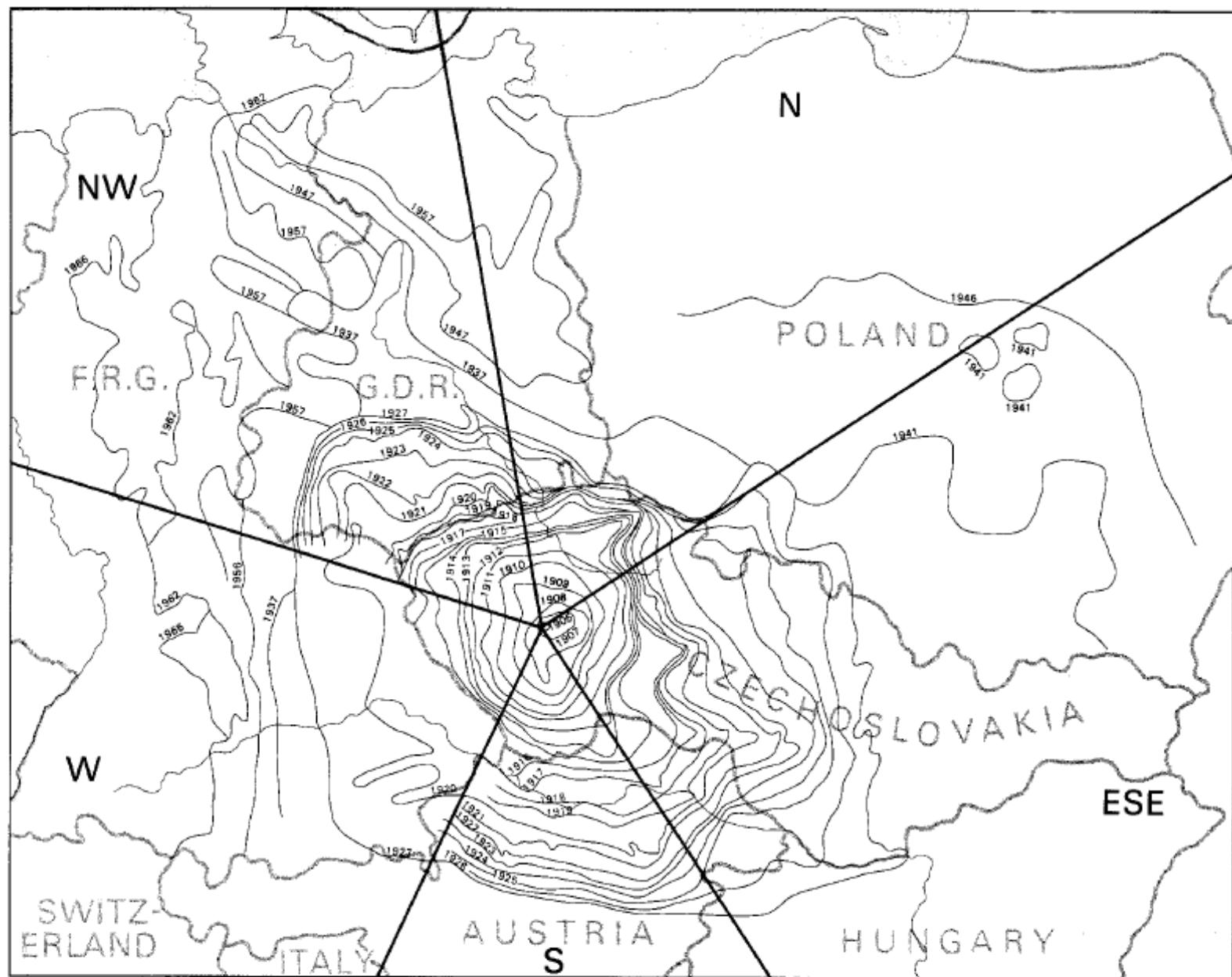


Fig. 1. Spread of muskrat from Prague in five sectors. The S/ESE and ESE/N boundaries roughly separate the eastern European plain; the N/NW boundary distinguishes spread down the Oder River from spread down the Elbe River; the NW/W and W/S boundaries isolate the poorly known W sector.

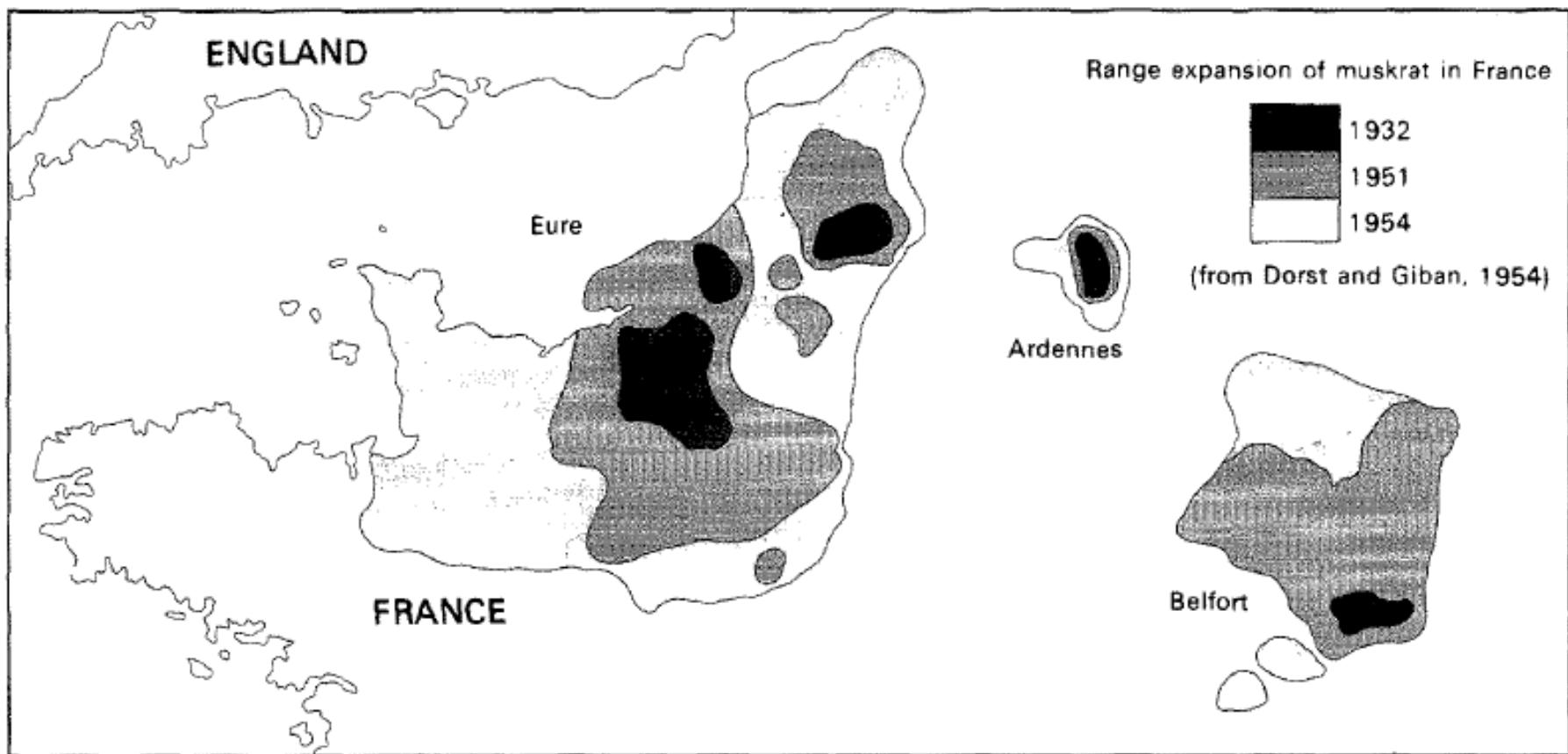


Fig. 2. Spread of muskrat in France at three localities.

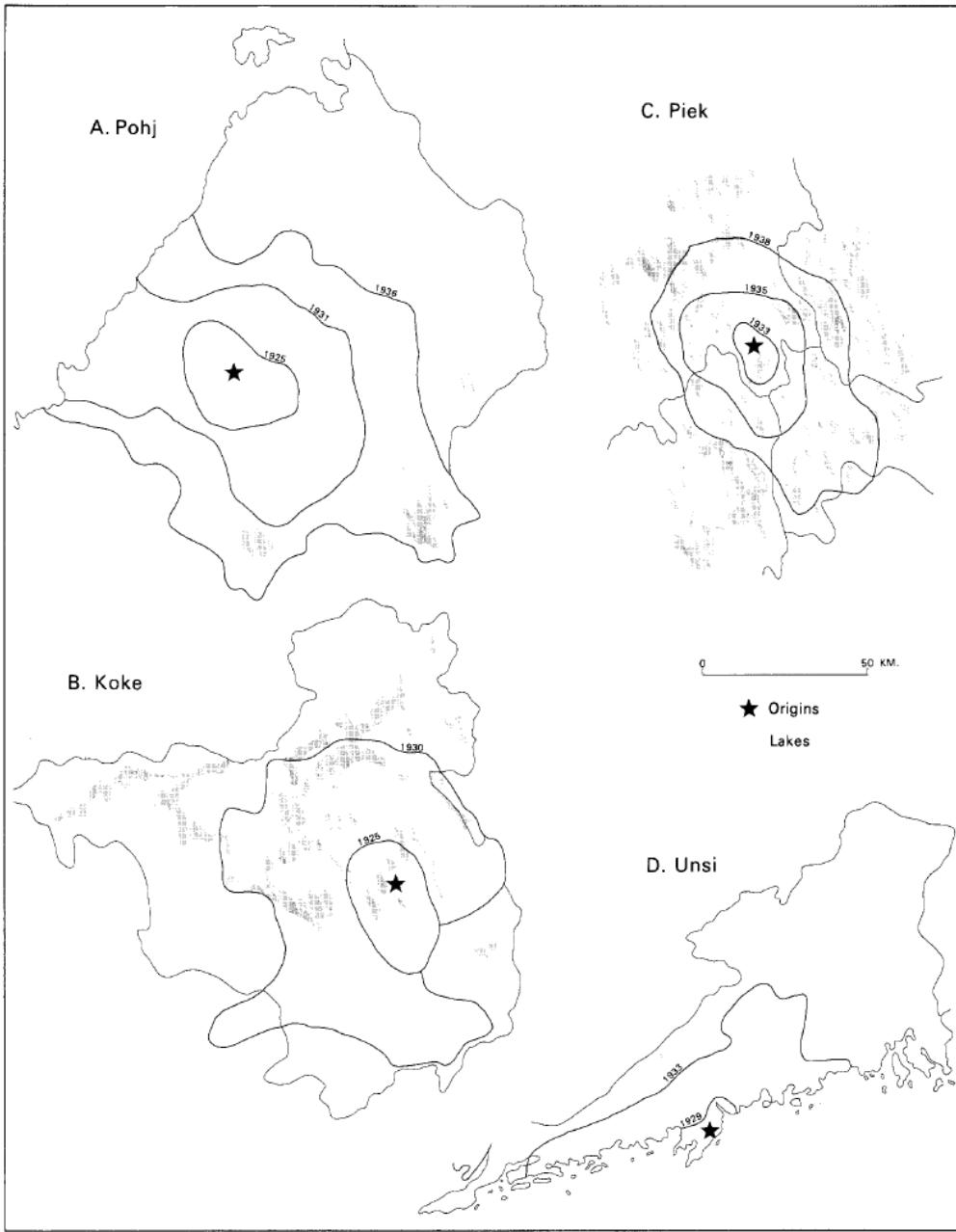


Fig. 3. Spread of muskrat in Finland at four localities. A. Northern Pohjanmaa (Pohj) release in 1923. B. Southern Kokemäenjoki (Koke) release in 1923. C. Pieksämäki (Piek) release in 1932. D. Coastal Unsimaa (Unsi) release in 1924. Muskrats were released at ².

Table 1. Test of the linear spread hypothesis for range expansion by muskrat, cereal leaf beetle, and small cabbage white butterfly. The linear spread hypothesis predicts that average acceleration of spread is zero. Means with standard errors given.

	df	Average spread rate (km/yr)	Average acceleration of spread (km/yr ²)
Muskrat			
Prague, Czechoslovakia			
S	20	21.3 ± 0.3****	0.27 ± 0.36 ^{NS}
ESE	22	25.4 ± 0.8****	0.51 ± 0.39 ^{NS}
NW	23	18.7 ± 0.5****	-0.05 ± 0.23 ^{NS}
N	19	11.5 ± 0.5****	-0.25 ± 0.25 ^{NS}
W	14	10.3 ± 0.4****	0.04 ± 0.09 ^{NS}
France			
Eure	2	4.6 ± 0.8*	0.23 ± 0.53 ^{NS}
Ardennes	2	0.9 ± 0.3 ^{NS}	0.03 ± 0.16 ^{NS}
Belfort	2	3.0 ± 0.2**	0.10 ± 0.09 ^{NS}
Finland			
Pohj	2	4.0 ± 0.6*	-0.58 ± 0.09 ^{NS}
Piek	2	5.7 ± 0.4**	-0.50 ± 0.04*
Koke	1	6.7 ± 0.1**	-
Unsi	1	3.5 ± 1.4 ^{NS}	-

	α (yr ⁻¹)	D (km ² /yr)	V _F (km/yr)
Predictions	0.2-1.1	51 230.1	6-32



Source : <http://home.tiscali.be/entomart.ins>

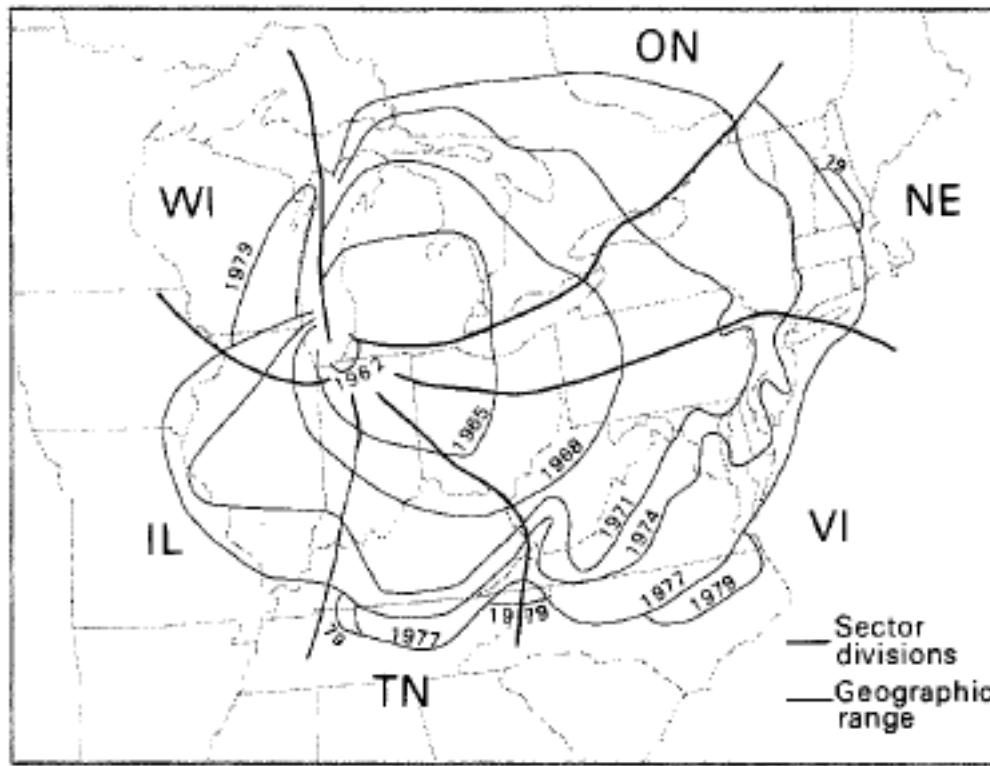


Fig. 4. Spread of cereal leaf beetle from southwest Michigan in six sectors: WI – along the eastern border of Wisconsin; IL – west into the plains of Illinois; TN – south into Tennessee, west of the Appalachians; VI – southeast toward Virginia and east of the Appalachians; NE – east into New England south of the Great Lakes; ON – east into Ontario and northeast.

	df	Average spread rate (km/yr)	Average acceleration of spread (km/yr ²)
Cereal Leaf Beetle			
Michigan, USA			
NE	5	89.5 ± 2.7****	-0.67 ± 1.82 ^{NS}
ON	4	89.2 ± 3.8****	45.52 ± 24.15 ^{NS}
VI	5	75.8 ± 4.8****	-1.08 ± 3.08 ^{NS}
TN	5	44.8 ± 2.9****	-1.92 ± 1.33 ^{NS}
IL	4	48.6 ± 2.0***	45.03 ± 26.25 ^{NS}
WI	5	26.5 ± 2.3***	-2.51 ± 0.94 ^{NS}

	α (yr ⁻¹)	D (km ² /yr)	V _F (km/yr)
Predictions	1.6-1.9	0.4	1.6-1.7

Failure to account for:

- long range movement on air currents
- hitchhiking on human transport



photo: JJ Harrison (jjharrison89@facebook.com)

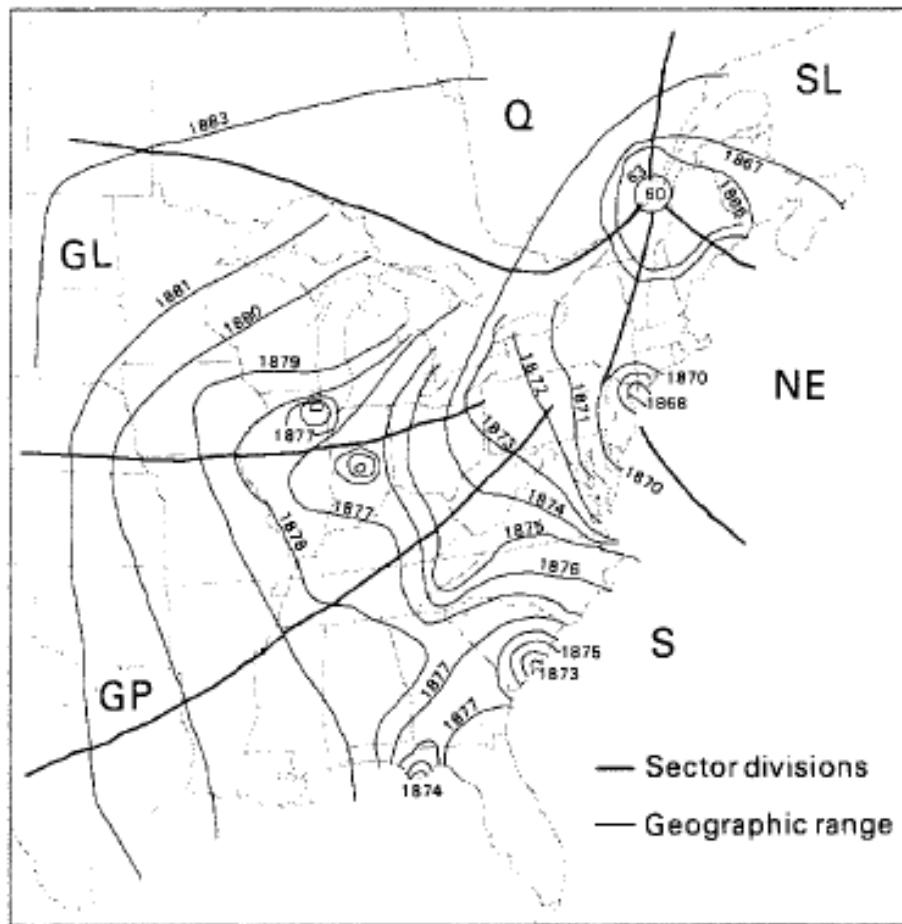


Fig. 5. Spread of small cabbage white butterfly from Quebec City in six sectors: NE – south to New England; SL – northeast down the St. Lawrence River; Q – west through Quebec and Ontario, north of the Great Lakes; GL – south of St. Lawrence River and Great Lakes; GP – southwest to Ohio and west across the Great Plains; S – southwest through the Appalachian Mountains and Louisiana. Secondary invasions occurred at New York, South Carolina and Florida. Disjunct colonies were established at Indiana and Chicago.

	df	Average spread rate (km/yr)	Average acceleration of spread (km/yr ²)
Small Cabbage White Quebec City, Canada			
SL	13	73.7 ± 6.2****	7.31 ± 1.48***
Q	4	42.6 ± 3.0***	1.66 ± 1.07NS
NE	6	65.2 ± 6.1****	10.89 ± 3.30*
S	16	169.6 ± 13.4****	18.53 ± 3.35****
GP	17	137.8 ± 6.6****	6.85 ± 2.10**
GL	17	145.4 ± 8.7****	10.97 ± 1.84****
New York City, USA			
South	2	153.0 ± 25.5*	63.00 ± 31.03NS
South Carolina, USA			
North	3	42.5 ± 2.4***	8.00 ± 1.73*
South	4	27.4 ± 3.9**	-1.30 ± 1.84NS
West	3	74.0 ± 15.9*	34.50 ± 12.82NS
Florida, USA			
North	2	97.0 ± 23.9NS	52.00 ± 14.25NS
East	3	14.7 ± 1.7**	-0.99 ± 0.74NS
Indiana, USA			
West	2	79.0 ± 21.3NS	41.50 ± 17.05NS
Chicago, USA			
West	2	91.5 ± 24.8NS	50.00 ± 17.39NS

	α (yr ⁻¹)	D (km ² /yr)	V _F (km/yr)
Predictions	9 31.5	4.8 129	13-127

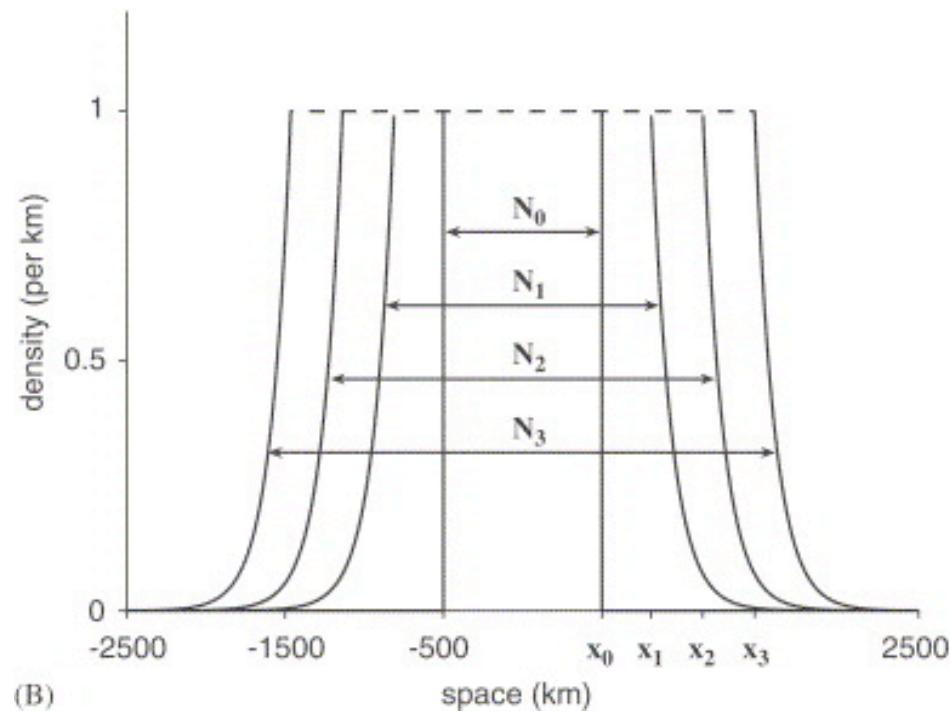
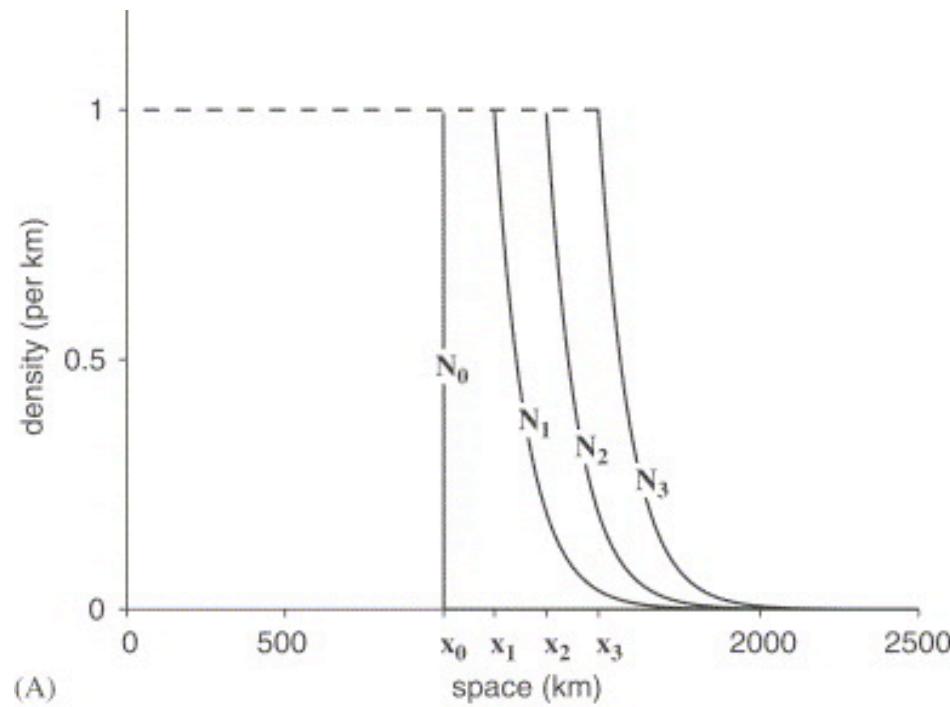
A spatially explicit model for an Allee effect: Why wolves recolonize so slowly in Greater Yellowstone

Amy Hurford ^{a, b}  , Mark Hebblewhite ^{a, 1}, Mark A. Lewis ^{a, b, c}



Table 2. Table of parameters

Parameter	Definition	Estimate	Units
N_c	Critical threshold density that must be exceeded for disperser production	0.25 ^a	Wolves per km
γ	Density of dispersers produced when pack density exceeds N_c	0.09 ^a	Wolves per km
α	Laplace coefficient	0.02	Per km
r	Geometric growth rate for packs > 1 year old	1.33	Unitless
σ	The number of wolves in newly formed breeding units at the end of the first year	5.64	Wolves per pair
φ	The radius at which one disperser can detect another	20.7 ^b , 39.2 ^b	km
ψ	The probability that given two dispersers of the opposite sex meet, they form a pair	1 ^b	Unitless
T_D	Average territory diameter	26.4	km



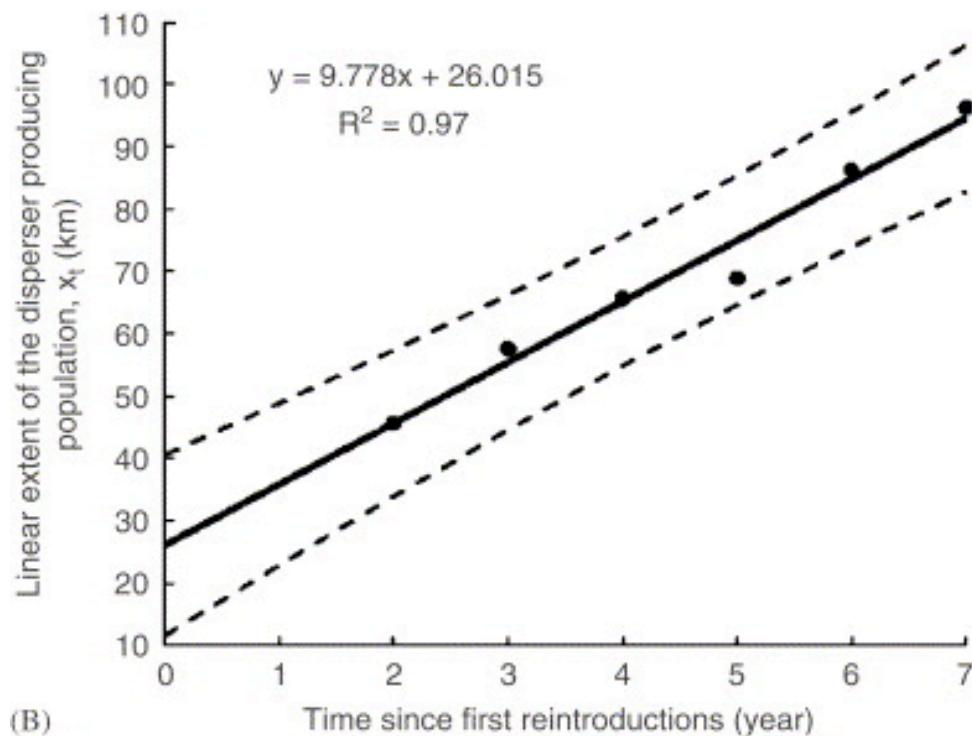
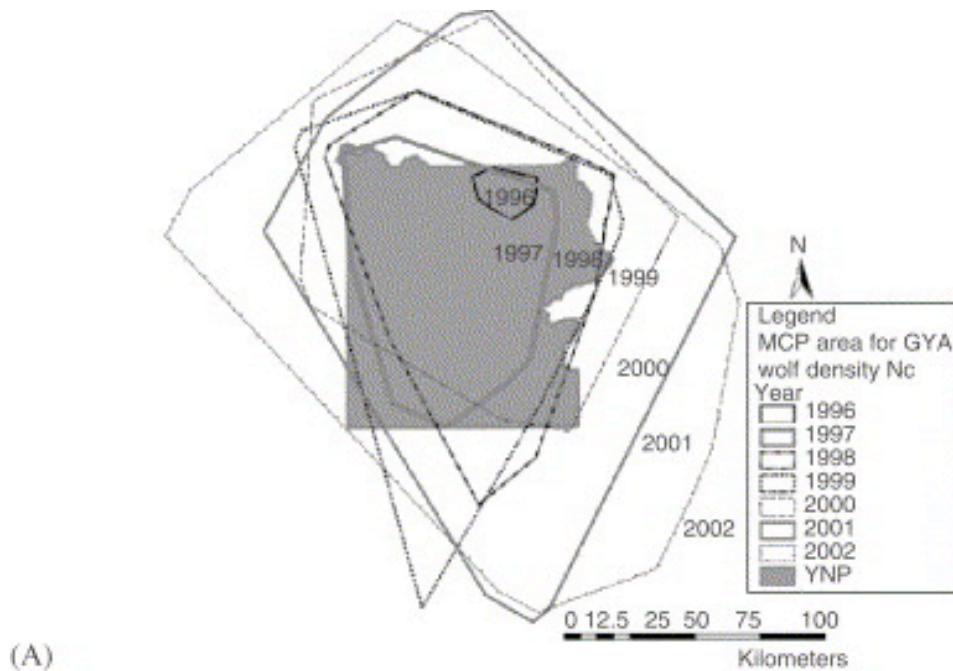


Table 3. The predictions of two models compared to the observed spread rate for wolves recolonizing the GYE

Model	Spread rate (km/year)
Pair formation prior to dispersal	41.11
Pair formation following dispersal	20.00
Observed spread rate (95% CI upper limit)	12.05
Observed spread rate	9.78
Observed spread rate (95% CI lower limit)	7.51

Summary

- Reaction diffusion equations describe populations dynamics in a spatially continuous environment
- Reaction diffusion equations make assumptions
- Reaction diffusion equations predict that range increases linearly over time
- Parameterized model predictions can be tested against empirical data