

Parasite infection can favor seasonal migration by hosts

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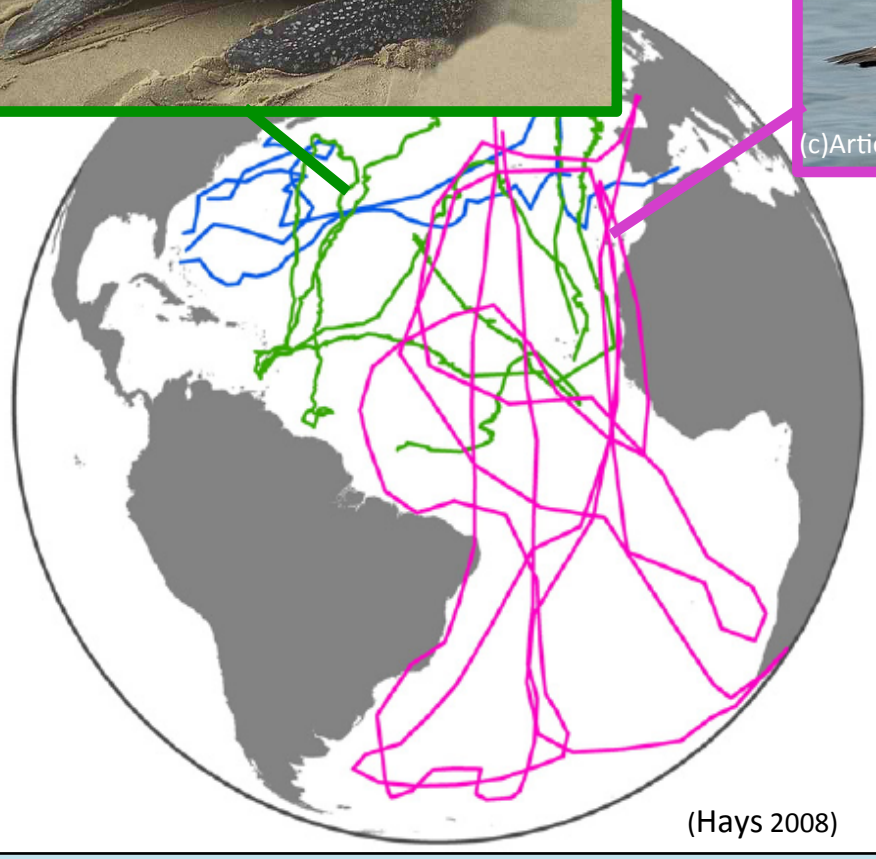
April 2016



(c)Artie Kopelman, CC BY-NC 2.0



http://seattletimes.nwsources.com/news/local/links/salmon_reprint.html



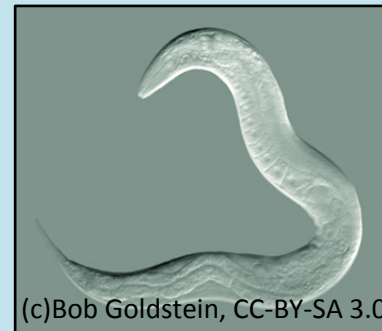
(Hays 2008)



(c)Entomology, CSIRO, CC-BY-3.0



(c)Andrew Snyder, flickr.com



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1 cm

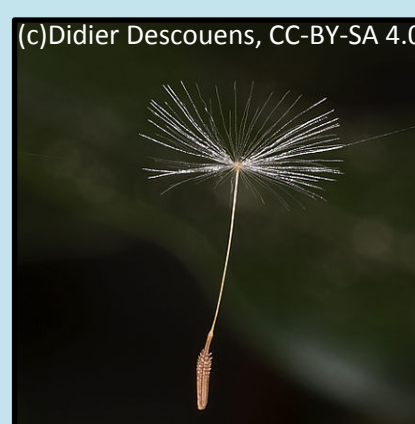
(Pierce-Shimomura et al. 1999)



(c)Peter Parks, pbs.org



(c)Johma Luhta, naturepl.com



(c)Didier Descouens, CC-BY-SA 4.0

Why move?

Find Food



Avoid predators

(c)Pauk, CC-BY-2.0

Find Mates



(c)Animalparty, CC-BY-2.0

*Avoid
climate*



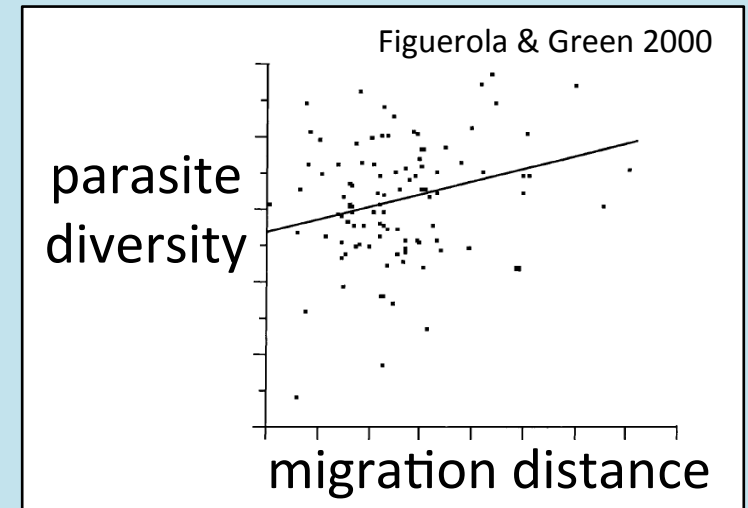
Avoid parasites



(c)Coprid, Shutterstock

Infection & movement

Moving helps avoid infection ...or increases parasite exposure



Different movement once infected:
can be driven by hosts

...or by parasite manipulation

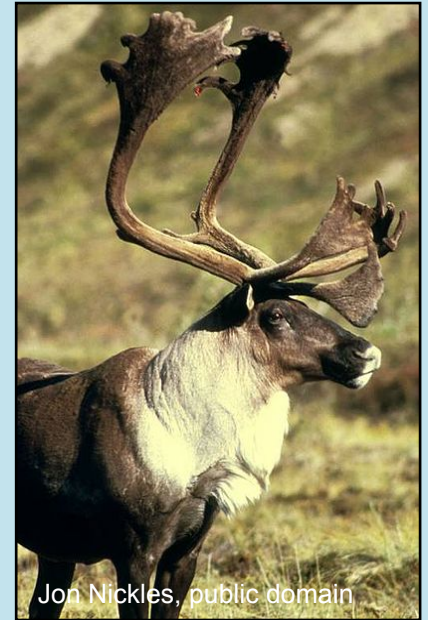


Migration and parasites

Migration (round-trip) can reduce parasite infection via:

1. *Migratory escape*: temporarily migrating away from infected areas or individuals

(Loehle 1995)



2. *Migratory culling*: increased mortality of infected individuals during migration

(Bradley & Altizer 2005)



Third infection-related benefit of migration

Some migratory species experience different rates of infection recovery in different environmental conditions:



Flounders (*Platichthys flesus*) migrate between fresh and salt water; their parasites (*Lepeophtheirus pectoralis*) die and detach faster at lower salinities

(Möller 1978)



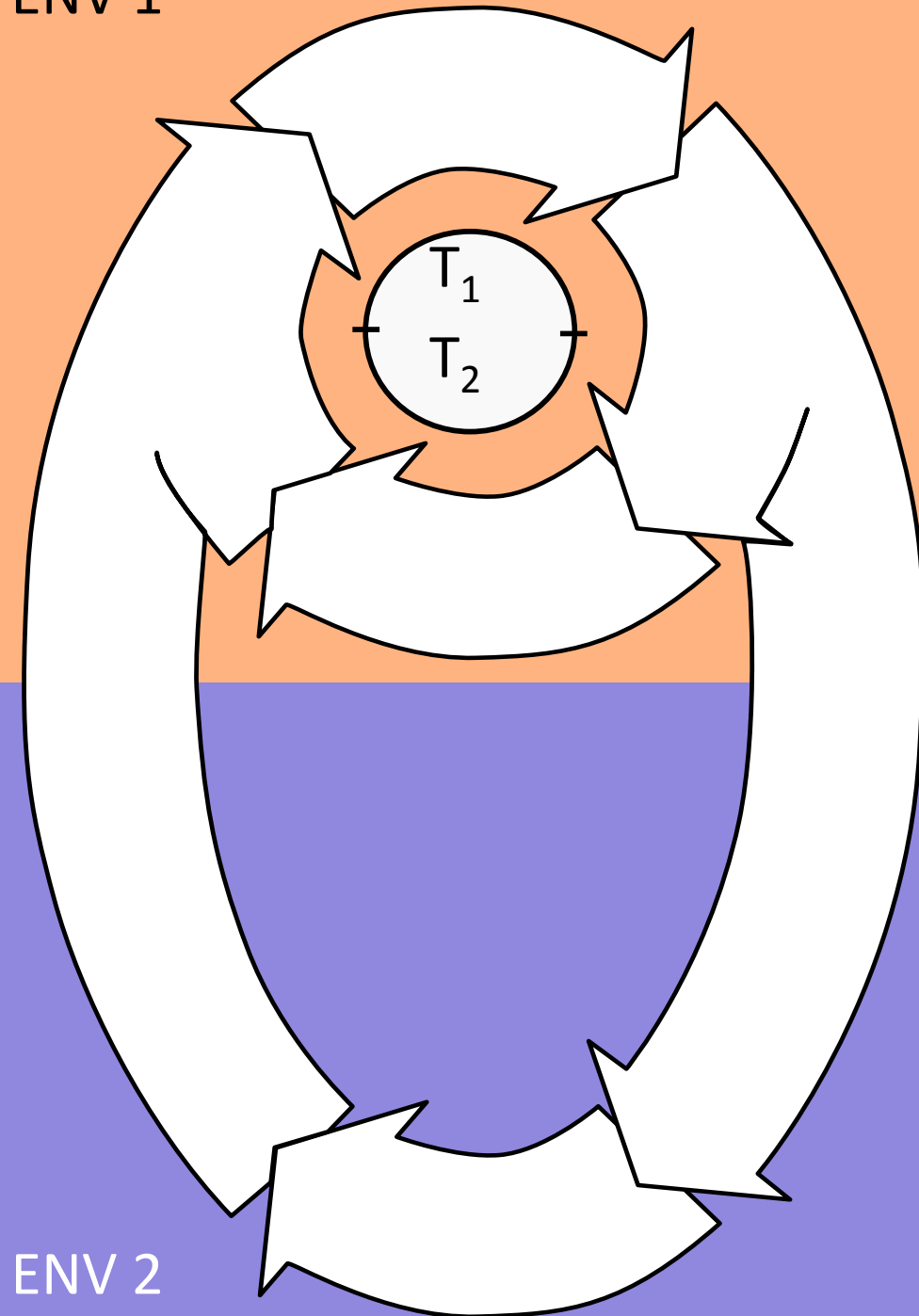
Alpine newts (*Mesotriton alpestris*) migrate overland between ponds. Newts infected with *Batrachochytrium dendrobatidis* recovered faster on land than in water

(Daversa et al. in review)

When can recovery from infection be a sufficient selective pressure to favor migration by the host species?

Model framework

ENV 1



ENV 2

Model dynamics (T_1)

Infection

$$\frac{dS}{dt} = -\beta S \quad \frac{dI}{dt} = \beta S$$

S = susceptible individuals

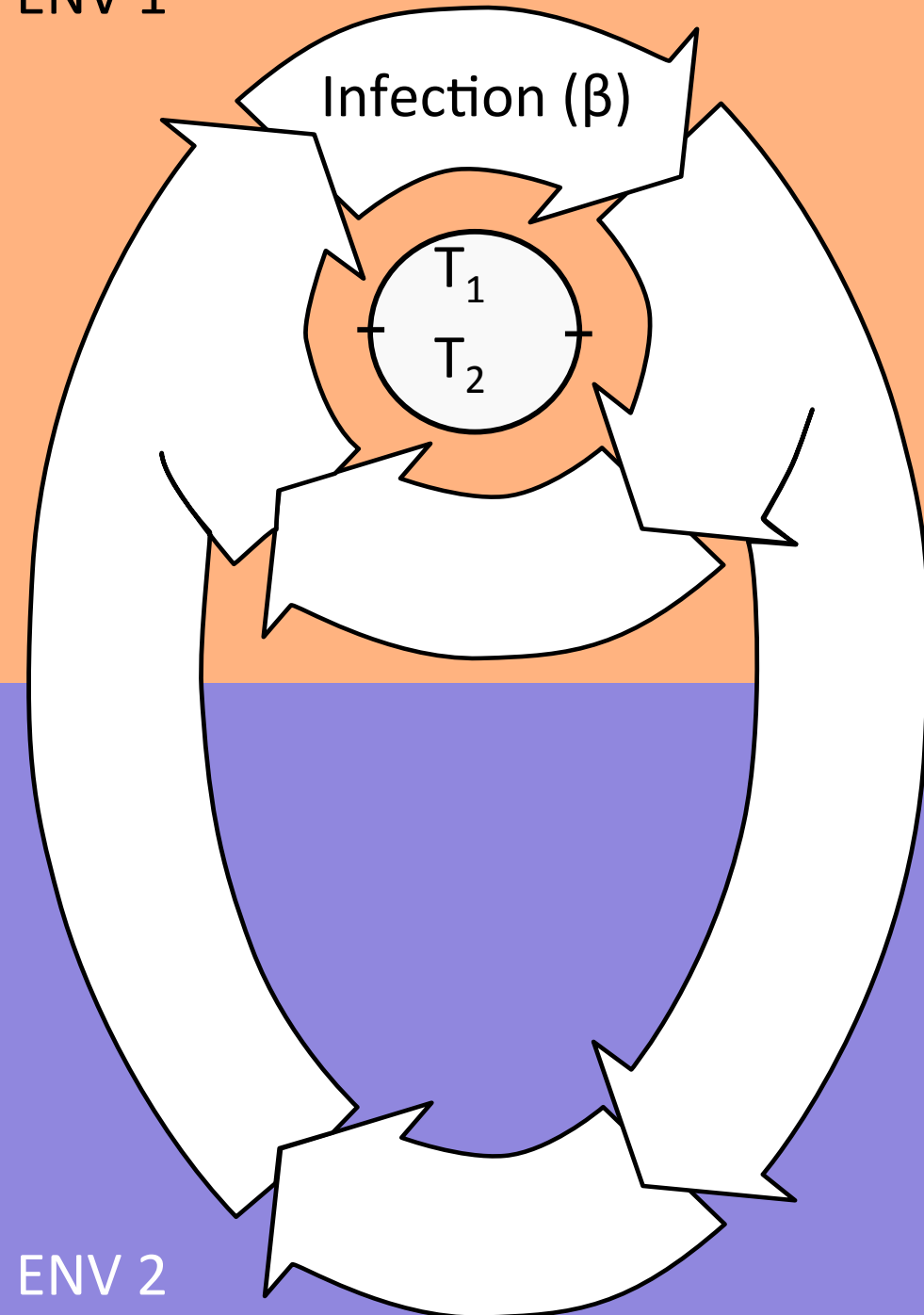
I = infected individuals

β = rate of infection

$$S(T_1) = S_0 e^{-\beta T_1}$$

$$I(T_1) = I_0 + S_0 (1 - e^{-\beta T_1})$$

ENV 1



ENV 2

Model dynamics (T_2 – residents)

Infection

$$\frac{dS}{dt} = -\beta S \quad \frac{dI}{dt} = \beta S$$

S = susceptible individuals

I = infected individuals

β = rate of infection

θ = migration probability

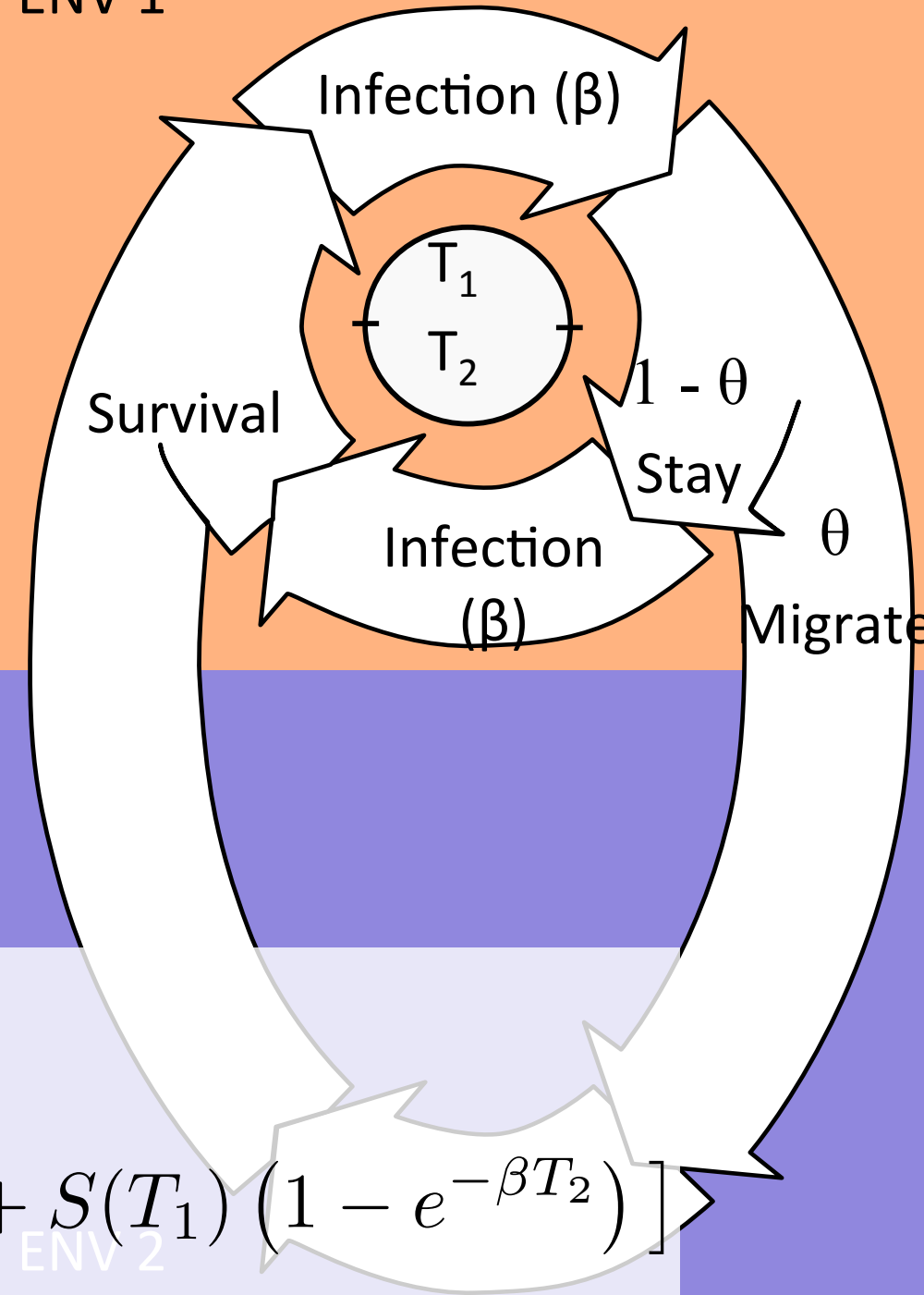
σ = suscep. resident survival

c_I = infection survival cost

$$S_R = (1 - \theta)\sigma \left[S(T_1) e^{-\beta T_2} \right]$$

$$I_R = (1 - \theta)(1 - c_I)\sigma \left[I(T_1) + S(T_1) (1 - e^{-\beta T_2}) \right]$$

ENV 1



Model dynamics (T_2 – migrants)

Recovery

$$\frac{dS}{dt} = \gamma S \quad \frac{dI}{dt} = -\gamma S$$

θ = migration probability

γ = rate of recovery

σ = suscep. resident survival

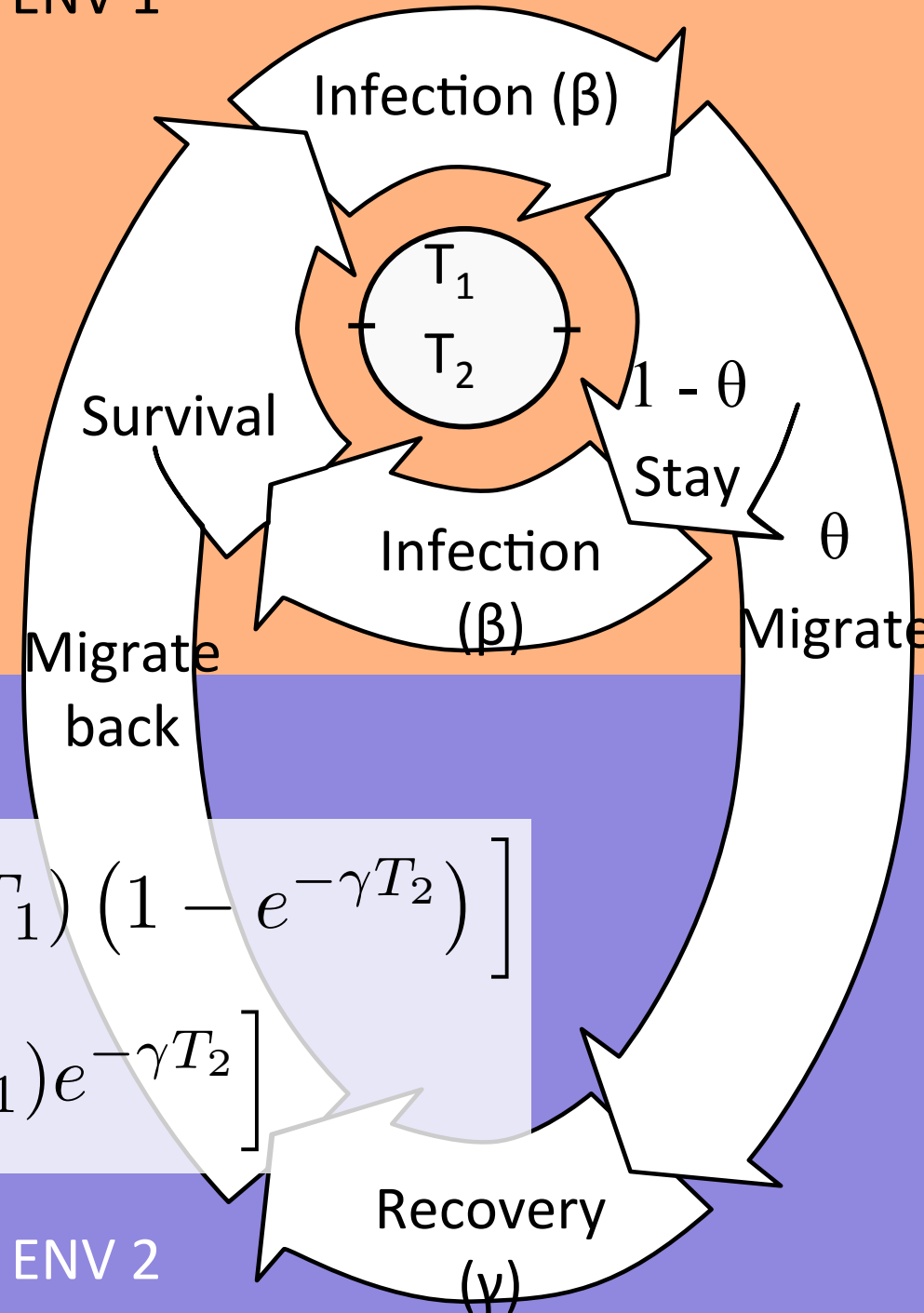
c_I = infection survival cost

c_M = migration survival cost

$$S_M = \theta(1 - c_M)\sigma \left[S(T_1) + I(T_1) (1 - e^{-\gamma T_2}) \right]$$

$$I_M = \theta(1 - c_M)(1 - c_I)\sigma \left[I(T_1) e^{-\gamma T_2} \right]$$

ENV 1



ENV 2

Model dynamics (reproduction)

Reproduction

ϕ = susceptible fecundity

c_F = infection fecundity cost

$$b_{max} = \phi(S_R + S_M) + \phi(1 - c_F)(I_R + I_M)$$

$$b = b_{max}DD$$

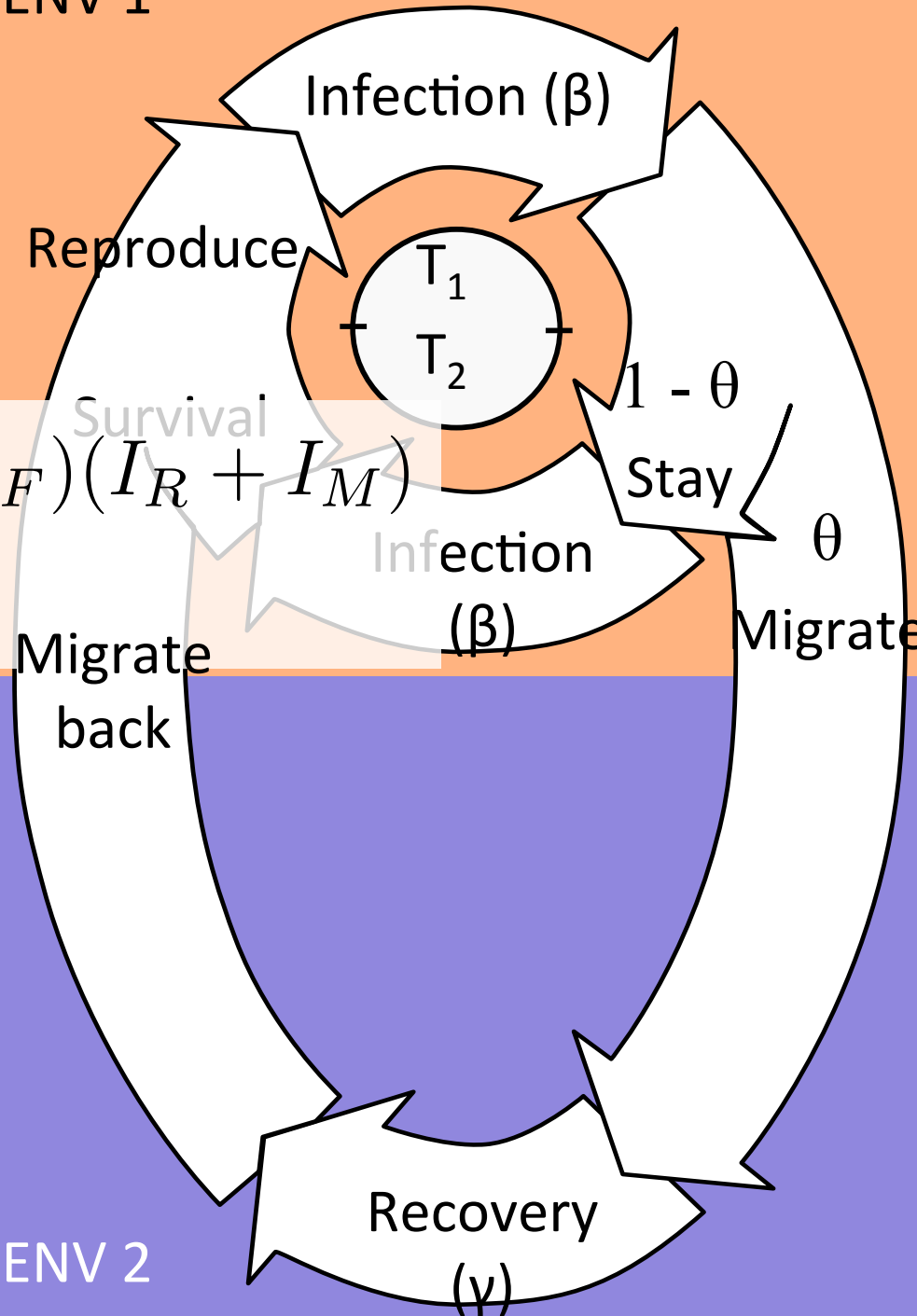
$$DD(S = 0, I = 0) = 1$$

$$\frac{\partial DD}{\partial S} < 0$$

$$\frac{\partial DD}{\partial I} < 0$$

$$DD \geq 0$$

ENV 1



Full model

$$\begin{bmatrix} S \\ I \end{bmatrix}_{\tau+1} = \begin{bmatrix} A\theta + B(1-\theta) & C\theta \\ +DD[J\theta + K(1-\theta)] & +DD[L\theta + M(1-\theta)] \\ E\theta + F(1-\theta) & G\theta + H(1-\theta) \end{bmatrix} \begin{bmatrix} S \\ I \end{bmatrix}_{\tau}$$

$\theta = \text{migration probability}$

with coefficients:

$$\begin{aligned} A &= \sigma_{SM} \left[e^{-\beta T_1} + (1 - e^{-\beta T_1}) (1 - e^{-\gamma T_2}) \right] & G &= \sigma_{IM} e^{-\gamma T_2} \\ B &= \sigma_{SR} e^{-\beta(T_1+T_2)} & H &= \sigma_{IR} \\ C &= \sigma_{SM} (1 - e^{-\gamma T_2}) & J &= \phi_S A + \phi_I E \\ E &= \sigma_{IM} e^{-\gamma T_2} (1 - e^{-\beta T_1}) & K &= \phi_S B + \phi_I F \\ F &= \sigma_{IR} \left[(1 - e^{-\beta T_1}) + (1 - e^{-\beta T_2}) e^{-\beta T_1} \right] & L &= \phi_S C + \phi_I G \\ & & M &= \phi_I H \end{aligned}$$

Methods 1: Ecological equilibrium

Step 1: find ecological equilibrium

Given our model, what population size do we expect to see?

- I.e. the stable population size: $S(\tau + 1) = S(\tau) = S^*$
 $I(\tau + 1) = I(\tau) = I^*$

$$DD^* = \frac{\left[1 - A\theta - B(1 - \theta)\right] \left[1 - G\theta - H(1 - \theta)\right] - C\theta \left[E\theta + F(1 - \theta)\right]}{\left[J\theta + K(1 - \theta)\right] \left[1 - G\theta - H(1 - \theta)\right] + \left[L\theta + M(1 - \theta)\right] \left[E\theta + F(1 - \theta)\right]}$$

$$I^* = S^* \left[\frac{E\theta + F(1 - \theta)}{1 - G\theta - H(1 - \theta)} \right]$$

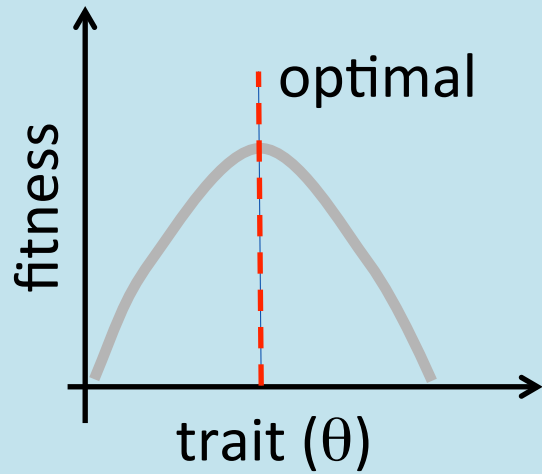
Methods 2: Evolutionary equilibrium

Step 2: find evolutionary equilibrium (ESS)

Given our model, what migration strategy (θ) do we expect?

- I.e. the migration probability that if adopted by a population cannot be invaded by a mutant with a different migration probability

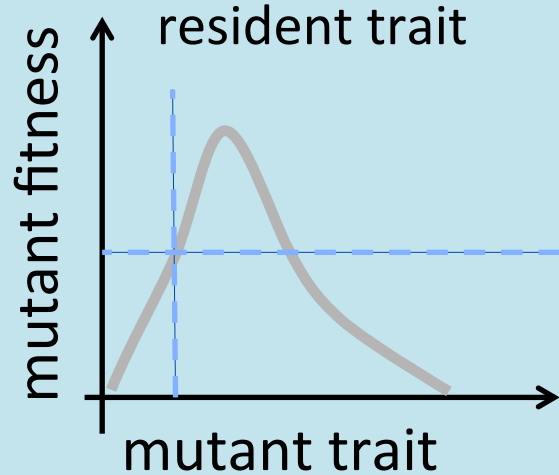
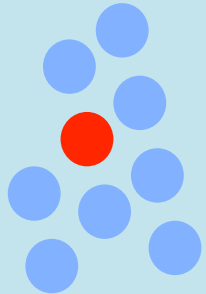
ASIDE: Optimal vs Evolutionarily Stable



Evolutionarily Stable Strategy (ESS):

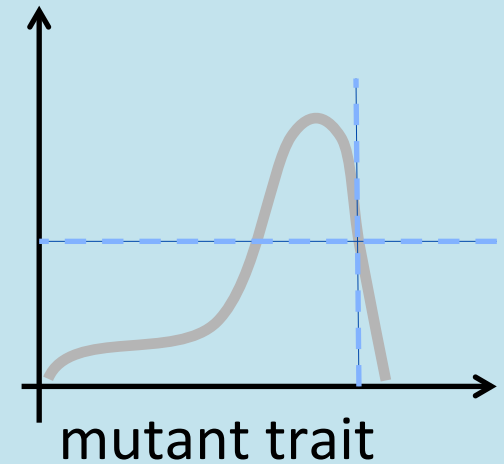
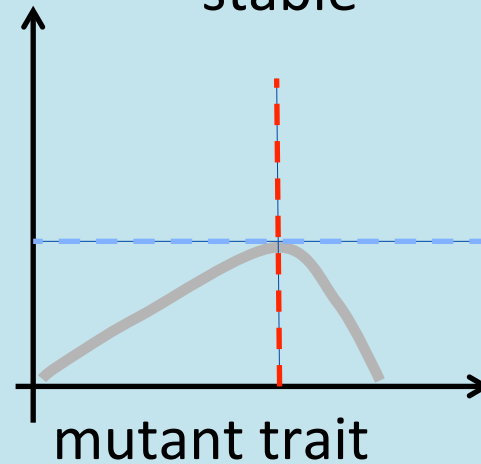
$$G(\theta_R, \theta_R) > G(\theta_M, \theta_R)$$

$$G(\theta_R, \theta_R) = G(\theta_M, \theta_R) \text{ and } G(\theta_R, \theta_M) > G(\theta_M, \theta_M)$$



resident fitness

evolutionarily stable



Methods 2: Evolutionary equilibrium

Step 2: find evolutionary equilibrium (ESS)

Given our model, what migration strategy (θ) do we expect?

- I.e. the migration probability that if adopted by a population cannot be invaded by a mutant with a different migration probability
- Growth of mutant (θ') in a resident ($\bar{\theta}$) population:

$$\begin{bmatrix} S' \\ I' \end{bmatrix}_{\tau+1} = \begin{bmatrix} A\theta' + B(1 - \theta') & C\theta' \\ +\overline{DD} [J\theta' + K(1 - \theta')] & +\overline{DD} [L\theta' + M(1 - \theta')] \\ E\theta' + F(1 - \theta') & G\theta' + H(1 - \theta') \end{bmatrix} \begin{bmatrix} S' \\ I' \end{bmatrix}_{\tau}$$

Methods 2: Evolutionary equilibrium

Step 2: find evolutionary equilibrium (ESS)

$$\theta_{ESS} = \begin{cases} -y/(2x) & \text{if } 0 < y < -2x \\ \text{either 0 or 1} & \text{if } -2x < y < 0 \\ 1 & \text{if } 0 < y, -2x < y \\ 0 & \text{if } y < 0, y < -2x \end{cases}$$

where

$$x = \left[C(E - F) - (A - B)(G - H) \right] \left[1 + \overline{DD}\phi_S \right]$$

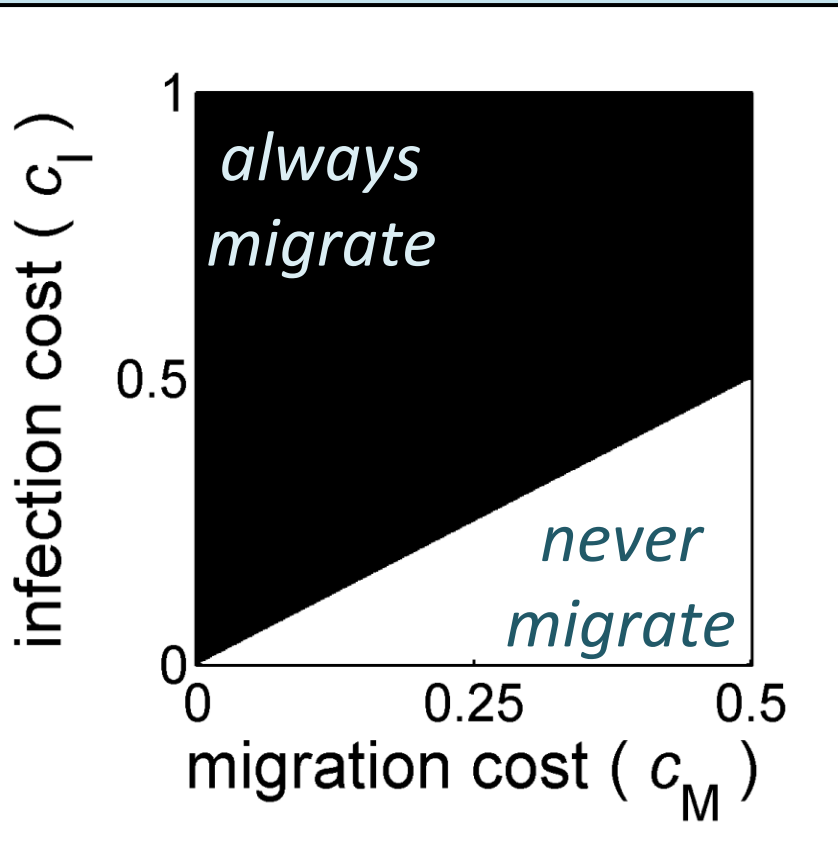
$$y = \left[(A - B)(1 - H) - B(G - H) + CF \right] \left[1 + \overline{DD}\phi_S \right] \\ + (G - H) + \overline{DD}\phi_I(E - F)$$

$\theta = \text{migration probability}$

Result 1: choose the less costly/risky option

Fast infection in env. 1
& Fast recovery in env. 2

$$e^{-\beta T}, e^{-\gamma T} \rightarrow 0$$

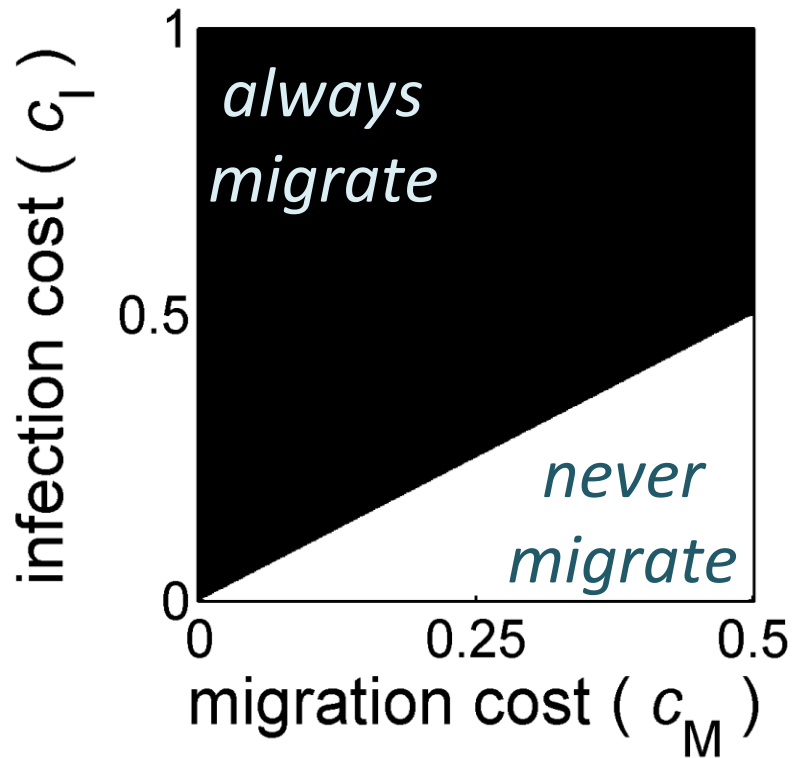


$$\theta_{ESS} = \begin{cases} 0 & \frac{\sigma(1-c_M)\phi}{1-\sigma(1-c_M)} < \frac{\sigma(1-c_I)\phi(1-c_F)}{1-\sigma(1-c_I)} \\ 1 & \frac{\sigma(1-c_M)\phi}{1-\sigma(1-c_M)} > \frac{\sigma(1-c_I)\phi(1-c_F)}{1-\sigma(1-c_I)} \end{cases}$$

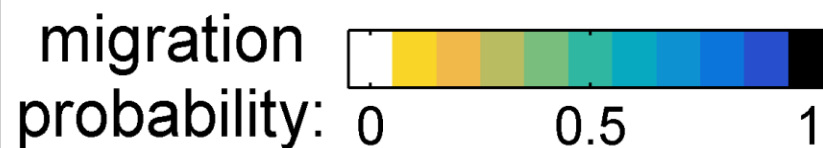
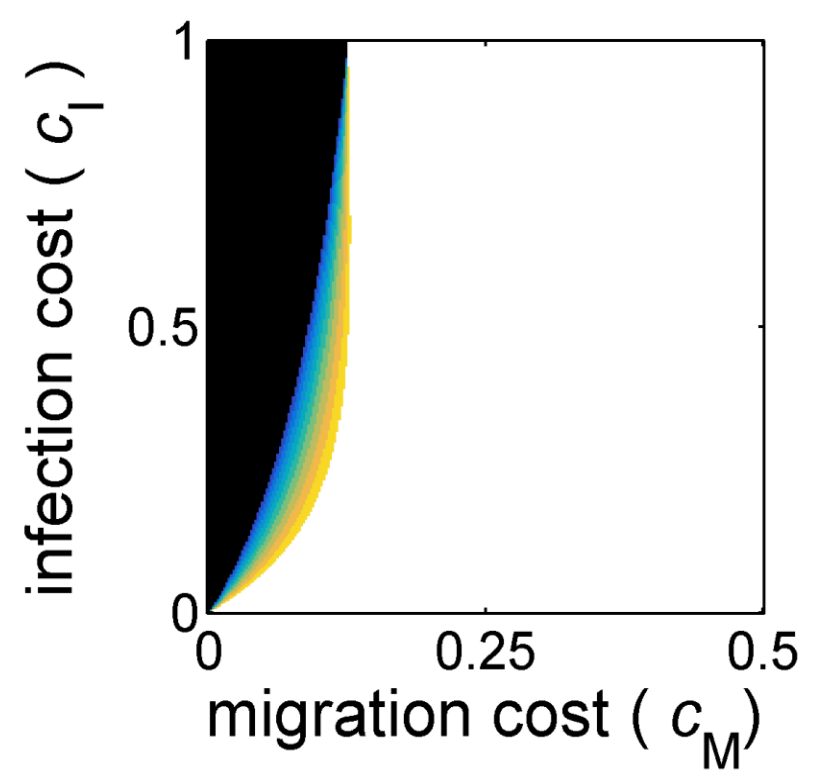


Result 1: choose the less costly/risky option

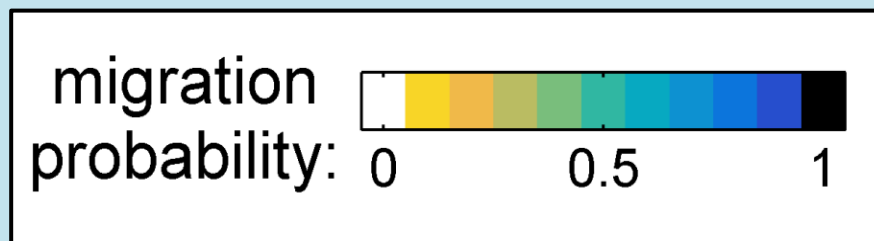
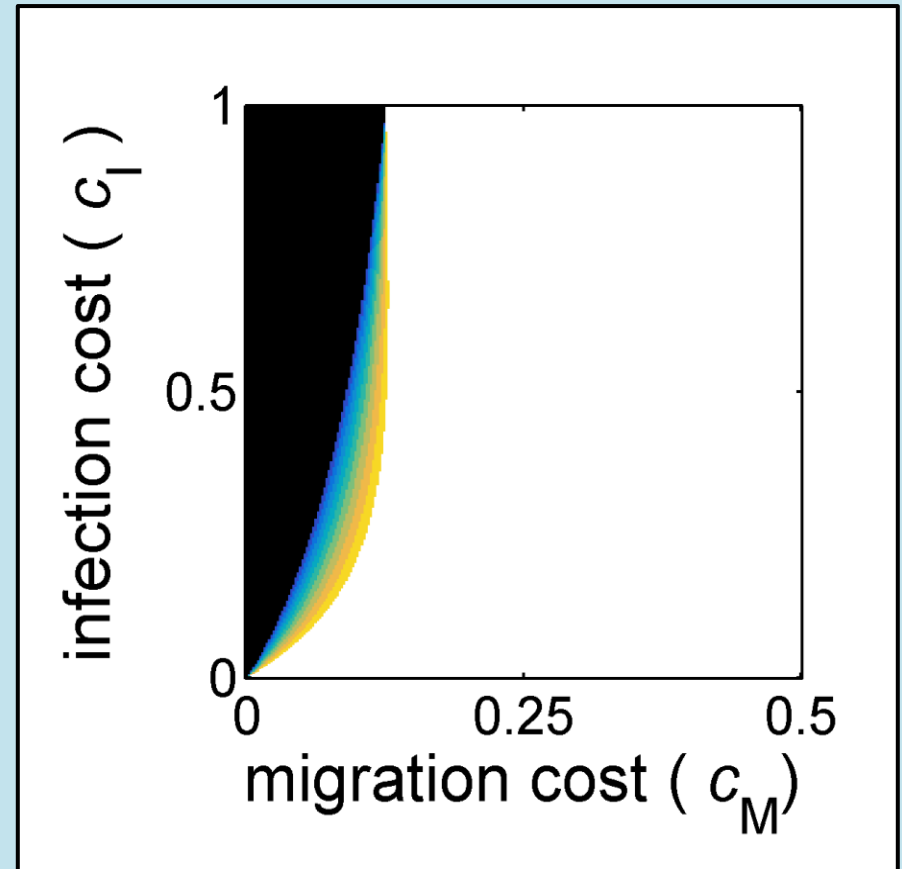
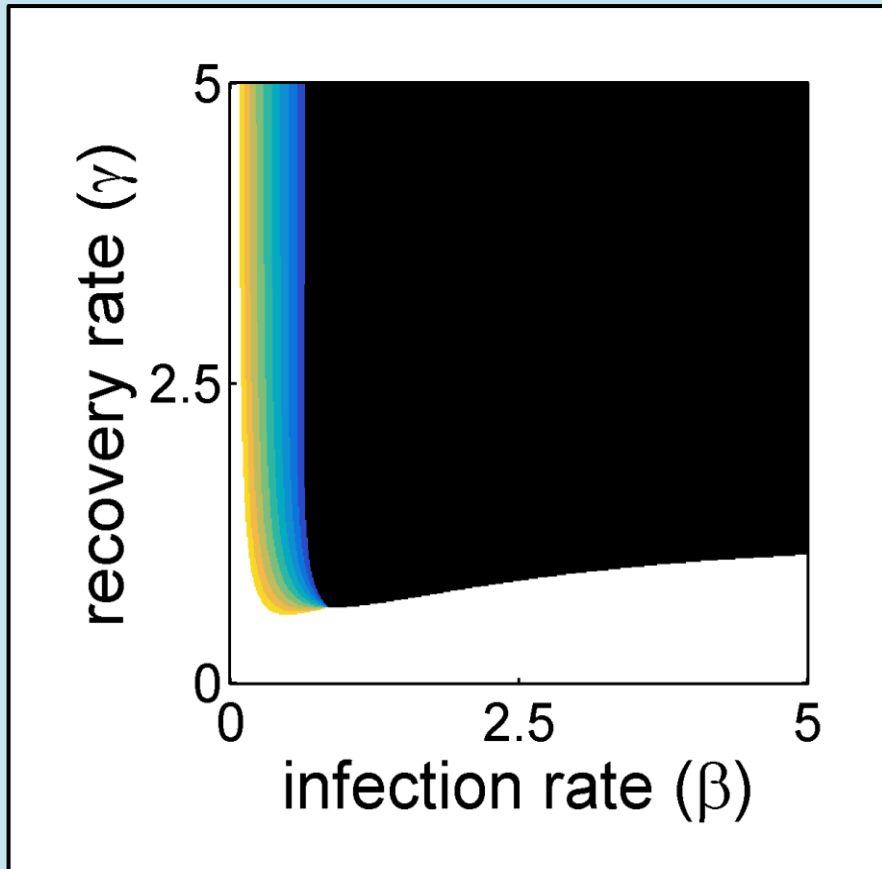
Fast infection in env. 1
& Fast recovery in env. 2



Slow infection in env. 1
& Slow recovery in env. 2

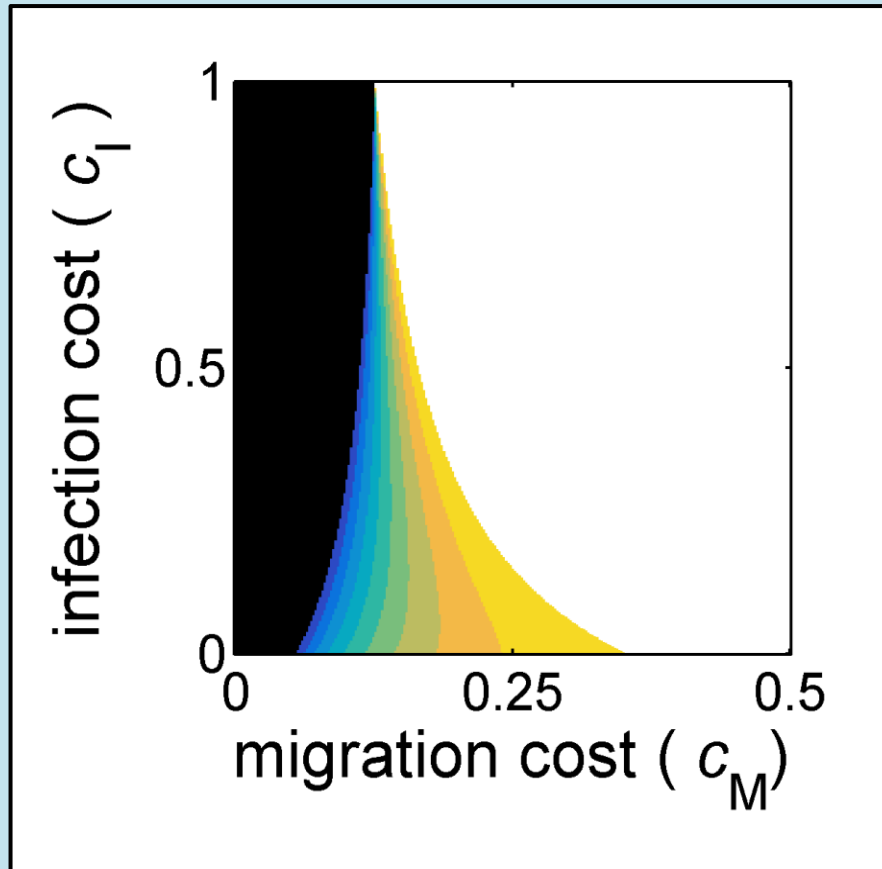


Result 2: play a mixed strategy

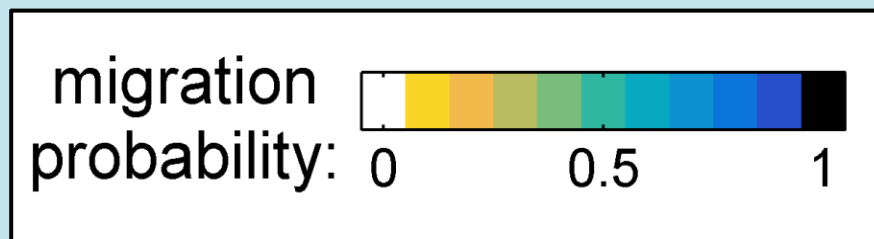
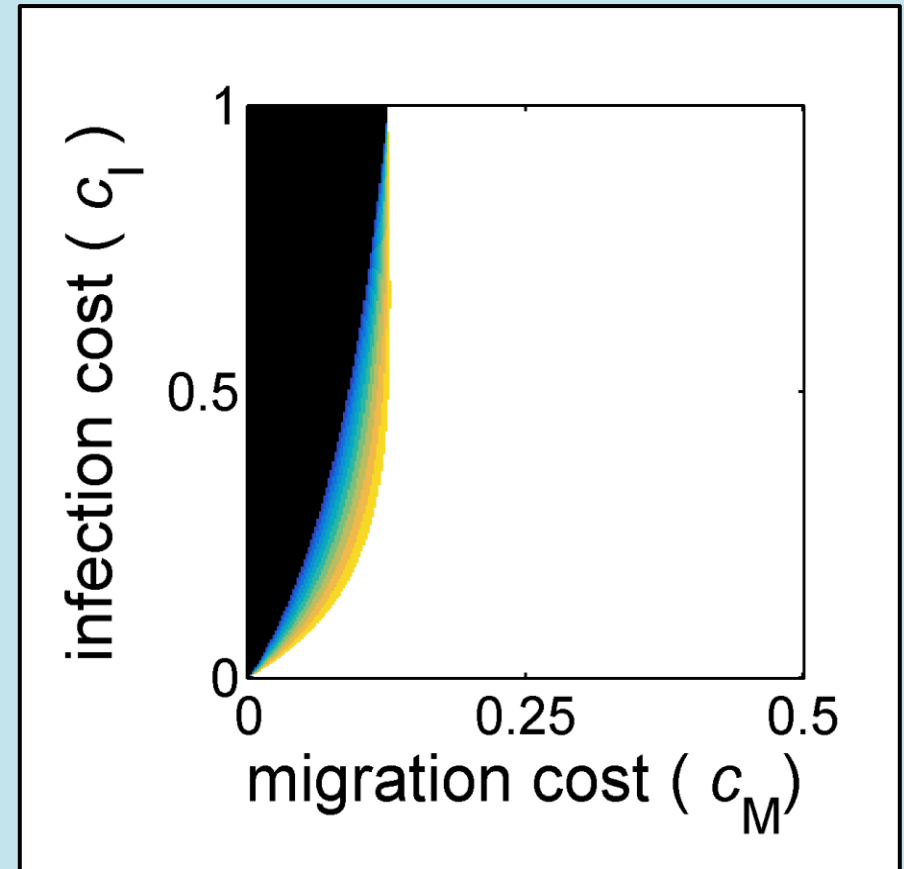


Result 3: multiple costs generate surprising results

Infection has both survival and fecundity costs



Infection has only survival cost



Empirical comparisons

In Threespine sticklebacks, *S. solidus* causes:

- 47% mortality (vs. 20%) under food stress
- 15% reduction in body condition

(Pascoe and Matthey 1977; Tierney et al. 1996)



Batrachochytrium dendrobatidis can cause 100% mortality in some amphibians

(Skerratt et al. 2007)



In Mourning doves, *Ischnocera* lice can cause:

- 2.4% body and 19% feather weight loss
- reduced survival in high infestations

(Clayton et al. 1999)



Where to from here?

Different transmission dynamics

Indirect

$$\frac{dS}{dt} = -\beta S$$

Density-dependent

$$\frac{dS}{dt} = -\beta SI$$

Frequency-dependent

$$\frac{dS}{dt} = -\frac{\beta SI}{S + I}$$

- No longer get closed-form ESS, need to simulate

S = susceptible individuals

I = infected individuals

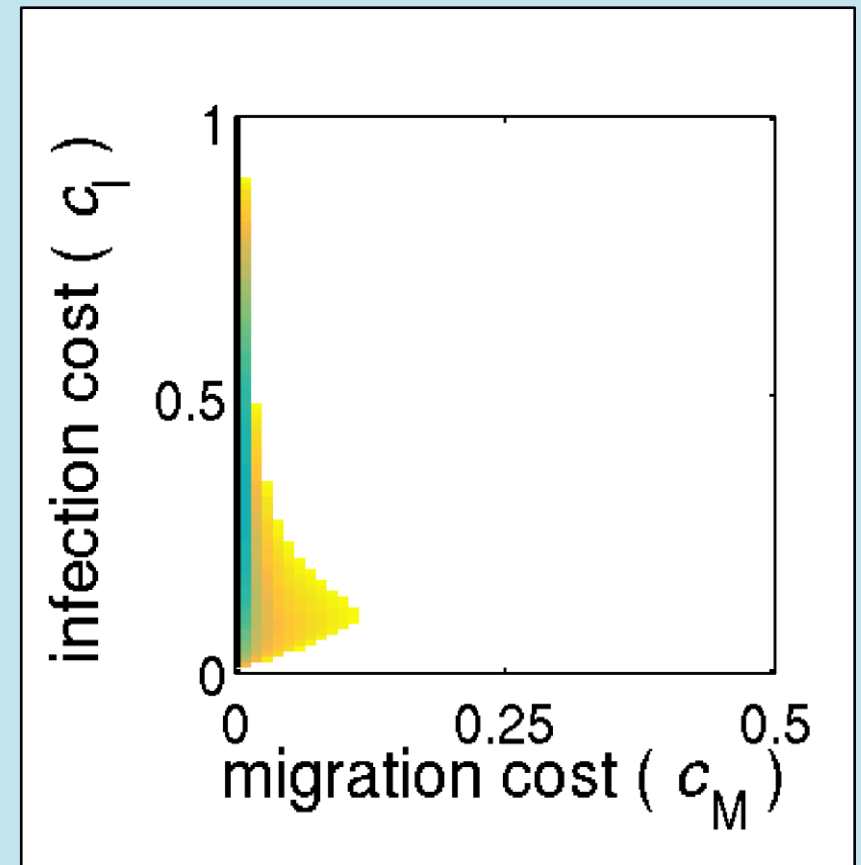
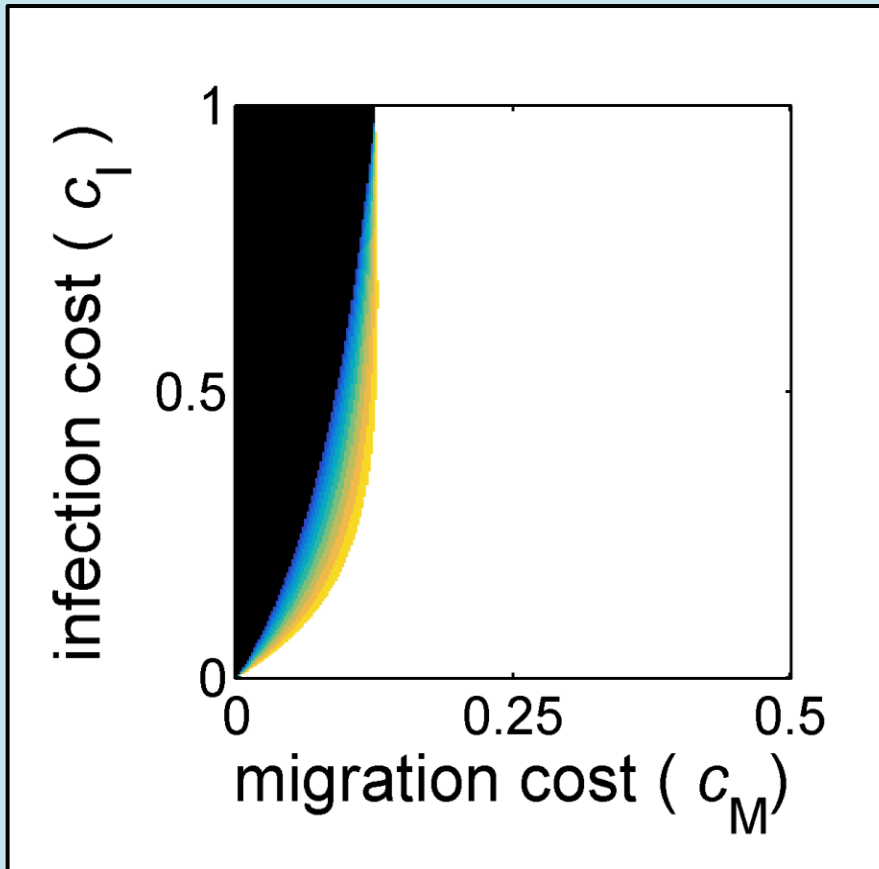
β = rate of infection

Where to from here?

Different transmission dynamics

$$\frac{dS}{dt} = -\beta S$$

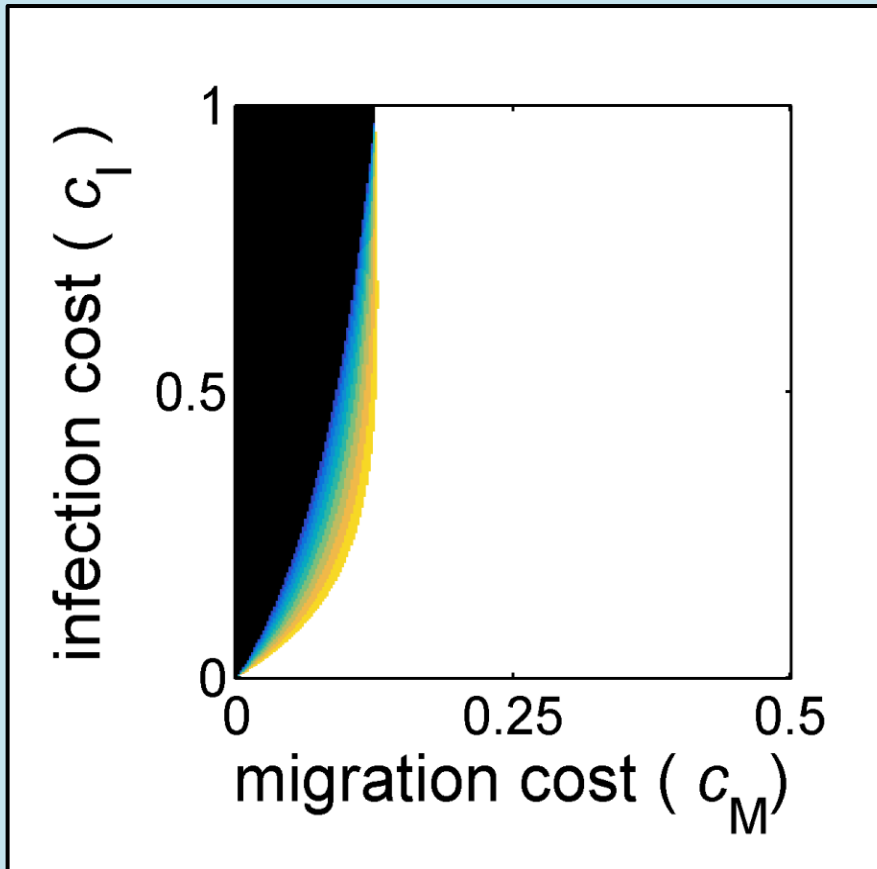
$$\frac{dS}{dt} = -\frac{\beta SI}{S + I}$$



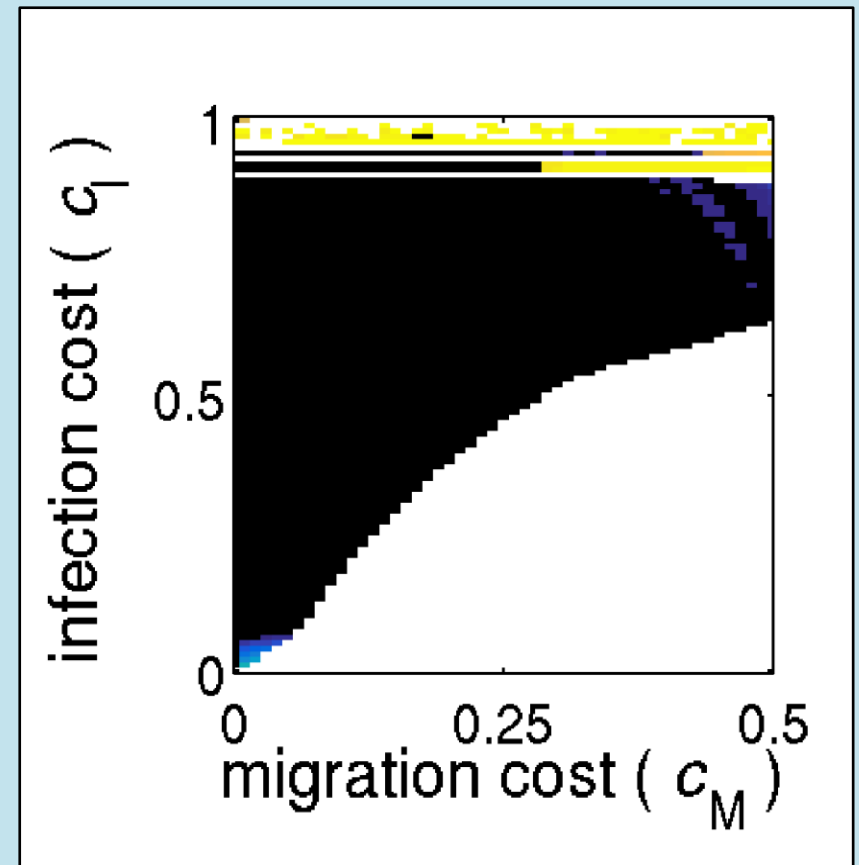
Where to from here?

Different transmission dynamics

$$\frac{dS}{dt} = -\beta S$$



$$\frac{dS}{dt} = -\beta SI$$



Where to from here?



Natural Systems in Changing Climates

www.sciencemag.org/special/climate2013

REVIEW

Climate Change and Infectious Diseases: From Evidence to a Predictive Framework

Sonia Altizer,^{1*} Richard S. Ostfeld,² Pieter T. J. Johnson,³ Susan Kutz,⁴ C. Drew Harvell⁵

Vol. 7: 87–99, 2009
doi: 10.3354/esr00095

ENDANGERED SPECIES RESEARCH
Endang Species Res

Printed May 2009
Published online June 17, 2008

Contribution to the Theme Section 'Incorporating climate change into endangered species conservation'

REVIEW



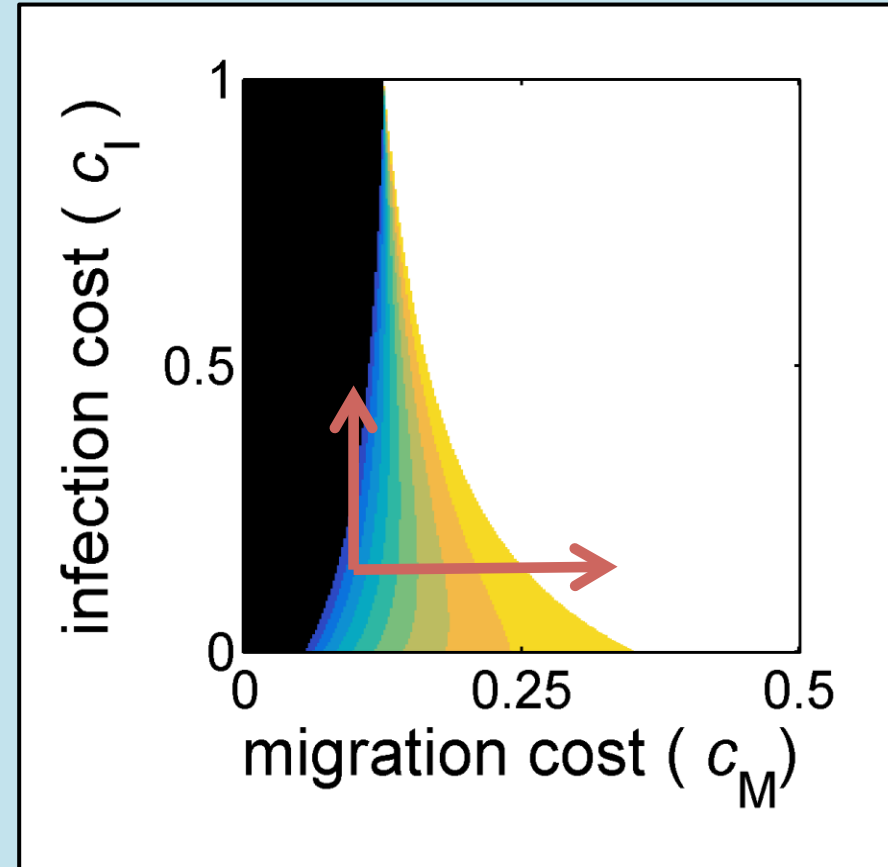
Travelling through a warming world: climate change and migratory species

Robert A. Robinson^{1,*}, Humphrey Q. P. Crick¹, Jennifer A. Learmonth²,

Where to from here?

How does climate change affect migration?

- Move across parameter space (e.g. increased mortality)
- Assumes that evolution keeps up with change
- Ignores tradeoffs



What are alternative approaches?

Acknowledgements

Coauthor:

Sandra Binning

Institute of Biology

University of Neuchâtel

Switzerland



Citation:

Shaw AK, Binning S (2016) "Migratory recovery from infection as a selective pressure for the evolution of migration." *The American Naturalist* 187: 491-501.

