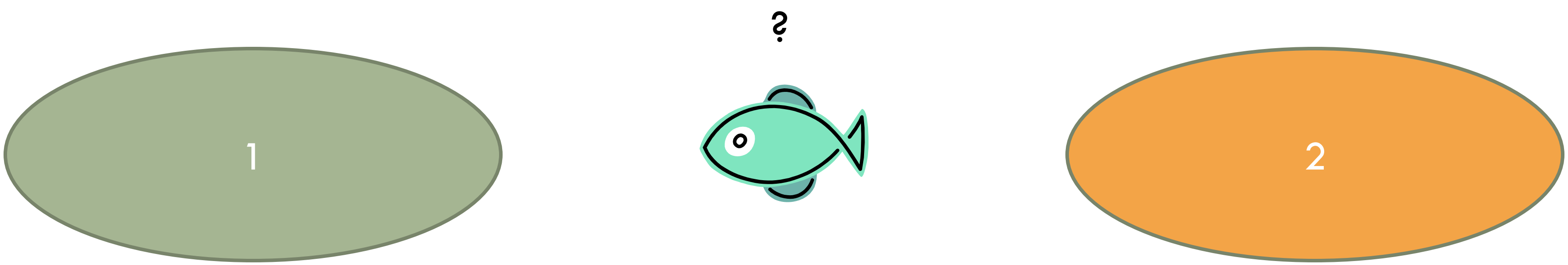
HABITAT SELECTION UNDER THE RISK OF INFECTIOUS DISEASE

Suzanne Robertson
Virginia Commonwealth University
December 14, 2012

Everything Disperses to Miami

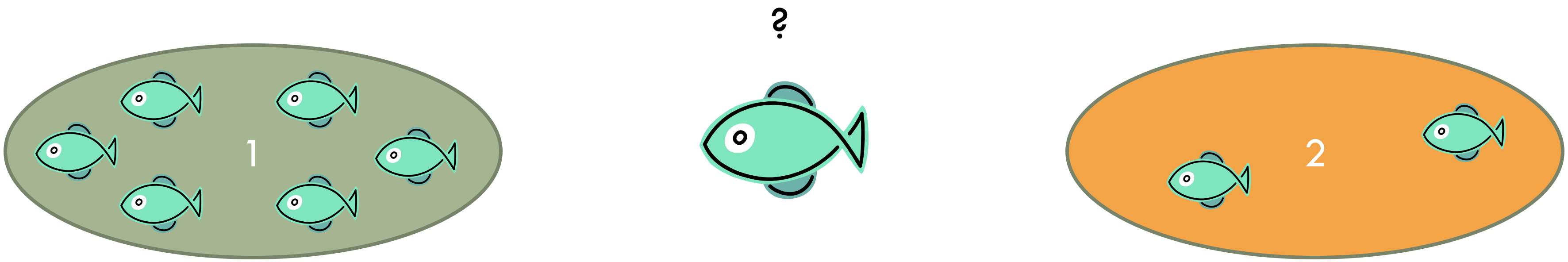
Habitat Selection

- How does an individual decide where to spend its time when faced with a choice between potential habitats?
- Benefits and costs associated with each habitat
  - Availability of resources
  - Safety from predation risk



Habitat Selection

- Costs and benefits may be frequency dependent
  - Competition for resources
- Payoff for using a habitat depends on number of other individuals using that habitat
  - Optimal habitat selection strategy may depend upon strategy of others

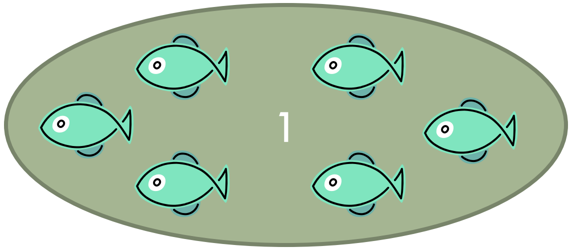


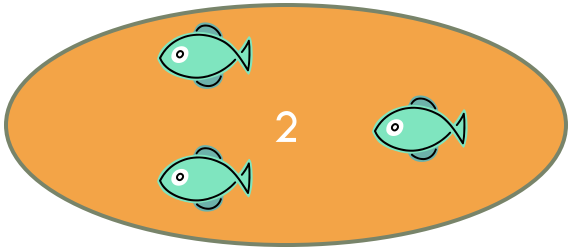
Ideal Free Distribution (IFD)

- IFD theory assumes:
  - Complete knowledge of resource distribution
  - Free to move between habitats at no cost
  - Equal competitors
  - Continuous input of resources
  - Individuals act to maximize their fitness
- If fitness determined by resource intake rate, IFD predicts input matching
  - Distribution of population "matches" distribution of resources across habitats

Input Matching

- Habitat selection "game against field"
  - Input matching is Nash equilibrium
  - Stable – No individual can improve its fitness by changing strategy
  - Equilibrium can refer to fraction of population using each patch exclusively or fraction of time individuals spend in each patch





Undermatching

- Under use of higher quality patch relative to input matching prediction (undermatching) observed in field/experimental data
  - Violation of ideal free assumptions
  - More factors affecting fitness
    - Predation, Kleptoparasitism
- Payoff now dependent upon the strategy of predators and kleptoparasites

Indirect Cost of Predation

- Increased risk in higher quality habitats (associated with higher population sizes)
- Predators will congregate in patches with higher host densities
- Change in behavior to avoid risk can result in undermatching
  - Individuals forced to settle for lower quality or less food to avoid risk
  - Behavioral effects of predation risk can be costly and comparable to direct consumptive effects

Risk of Infection

- Infection by pathogens or parasites can also affect an individual's fitness
- Infection can affect behavior (reducing fitness)
  - Reduced movement → decreased intake rate
  - Increased vulnerability to predation → increased mortality
- Transmission may vary among habitats
  - Higher host density → higher risk

http://en.wikipedia.org/wiki/Decline_in_amphibian_populations

Behavioral Defenses

http://saveoursymphony.info

- Immune defenses costly
- Evidence of change in behavior in response to threat of disease
  - Grey treefrog: Fewer eggs in pools with parasites
  - Bullfrog tadpoles: Avoid diseased conspecifics
  - Eastern grey kangaroo: Avoids foraging from contaminated sites
  - Bats and Great tit: Selective nesting in uninfected sites
  - White-tailed deer: Giving-up densities (perceived risk) increase with density of ticks

Disease and Habitat Selection

- How are theoretical habitat selection predictions altered by incorporating the risk of infectious disease?
- Can a change in behavior in response to this risk result in undermatching as observed in field studies and experiments?
- Implications of results?

The Model

- We consider habitat selection by a single population with a choice of two habitats differing only in resource inputs
- Habitat 1 of greater quality: $Q_1 > Q_2$
- Birth rates proportional to intake rates
- Natal dispersal: Offspring choose patch at birth, remain for life
  - p - probability of choosing patch 1 (heritable)
- Density dependent disease transmission
  - Disease reduces fecundity and/or increases mortality

The Model

$$\dot{S}_1 = p\left(\frac{b_S Q_1}{S_1 + I_1} S_1 + \frac{b_S Q_2}{S_2 + I_2} S_2 + \frac{b_I Q_1}{S_1 + I_1} I_1 + \frac{b_I Q_2}{S_2 + I_2} I_2\right) - \beta I_1 S_1 - \mu_S S_1$$

$$\dot{I}_1 = \beta I_1 S_1 - \mu_I I_1$$

$$\dot{S}_2 = (1 - p)\left(\frac{b_S Q_1}{S_1 + I_1} S_1 + \frac{b_S Q_2}{S_2 + I_2} S_2 + \frac{b_I Q_1}{S_1 + I_1} I_1 + \frac{b_I Q_2}{S_2 + I_2} I_2\right) - \beta I_2 S_2 - \mu_S S_2$$

$$\dot{I}_2 = \beta I_2 S_2 - \mu_I I_2$$

Parameter	Description
b_S	Susceptible birthrate constant
b_I	Infected birthrate constant
μ_I	Infected mortality
μ_S	Susceptible mortality rate
β	Transmission rate of disease
Q_1	Resource Input Rate in Patch 1
Q_2	Resource Input Rate in Patch 2

Model Equilibria

- 4 Equilibria:
  - Disease free equilibrium
  - Disease in patch 2 only
  - Disease in patch 1 only
  - Disease in both patches

$$R_0 = \frac{\beta p b_S (Q_1 + Q_2)}{\mu_I \mu_S}$$

Fitness

- Fitness: expected lifetime reproductive success of an individual

$$F_i = \frac{b_S Q_i}{N_i^*} \frac{1}{\mu_S + \beta I_i^*} + \frac{b_I Q_i}{N_i^*} \frac{1}{\mu_I} \frac{\beta I_i^*}{\mu_S + \beta I_i^*}$$

Susceptible birthrate in patch i

Expected amount of time spent susceptible

Infected birthrate in patch i

Expected amount of time spent infected

Probability of becoming infected

Fitness

- Fitness: expected lifetime reproductive success of an individual

$$F_i = \frac{b_S Q_i}{N_i^*}\frac{1}{\mu_S + \beta I_i^*} + \frac{b_I Q_i}{N_i^*}\frac{1}{\mu_I}\frac{\beta I_i^*}{\mu_S + \beta I_i^*}$$

- $F_1 = F_2$ for $p = p^*$ (ESS and CSS)
- At p^*, fraction of the population in patch 1:

$$n^* = \frac{N_1^*}{N_1^* + N_2^*}$$

Disease Free

- Input matching predicted in the absence of disease
- Disease Free Equilibrium:

$$(S_1^*, I_1^*, S_2^*, I_2^*) = \left(p\,\frac{b_S(Q_1 + Q_2)}{\mu_S},\, 0,\, (1-p)\,\frac{b_S(Q_1 + Q_2)}{\mu_S},\, 0 \right)$$

$$p^* = n^* = \frac{Q_1}{Q_1 + Q_2}$$

Disease affects mortality

- If $b_I = b_S = b$:

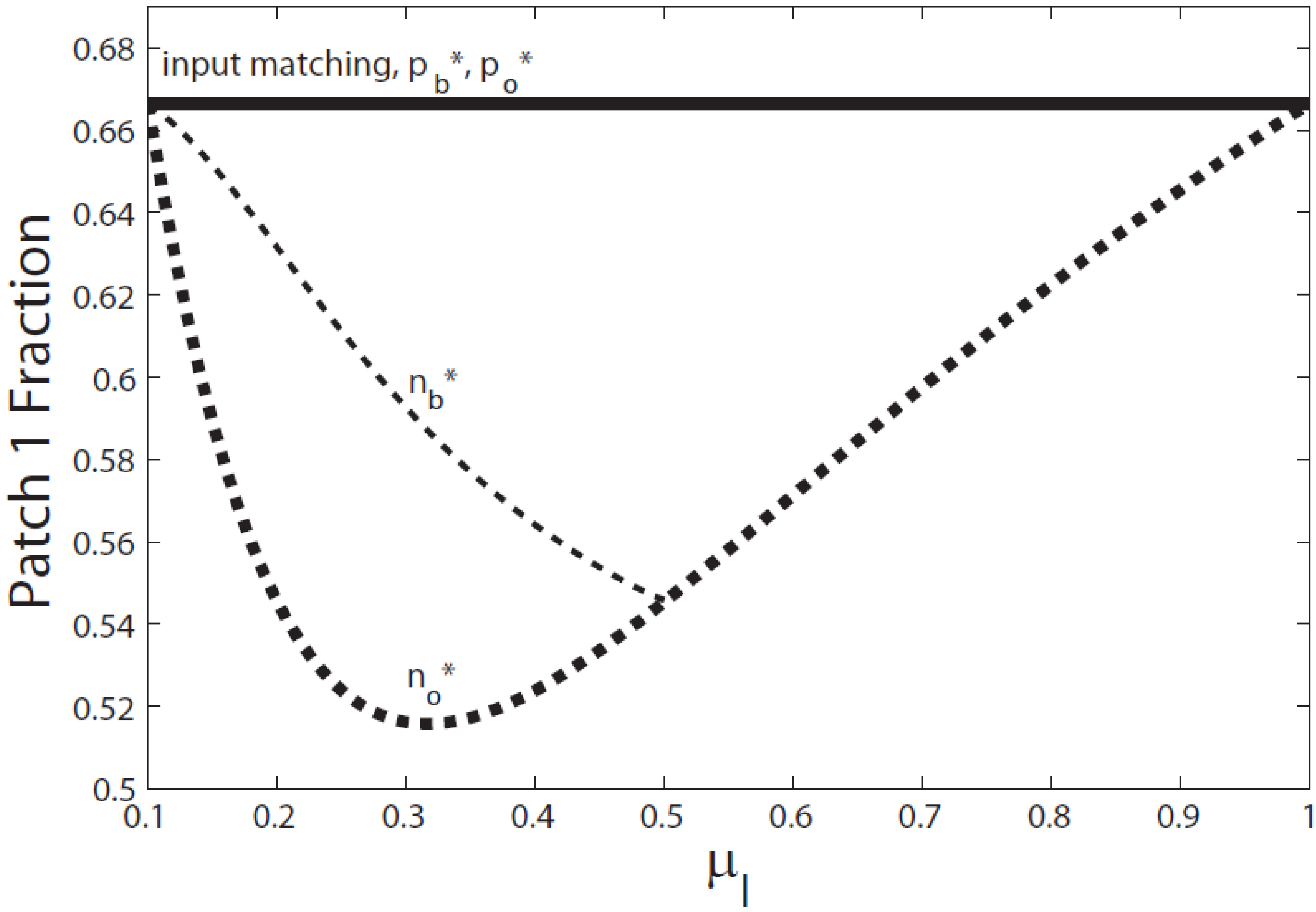
$$(S_1^*, I_1^*, S_2^*, I_2^*) = \left(\frac{\mu_I}{\beta}, \frac{pb(Q_1+Q_2)}{\mu_I} - \frac{\mu_S}{\beta}, \frac{\mu_I}{\beta}, \frac{(1-p)b(Q_1+Q_2)}{\mu_I} - \frac{\mu_S}{\beta} \right)$$

- Fitness equal in both patches when:

$$p_b^* = \frac{Q_1}{Q_1+Q_2}$$

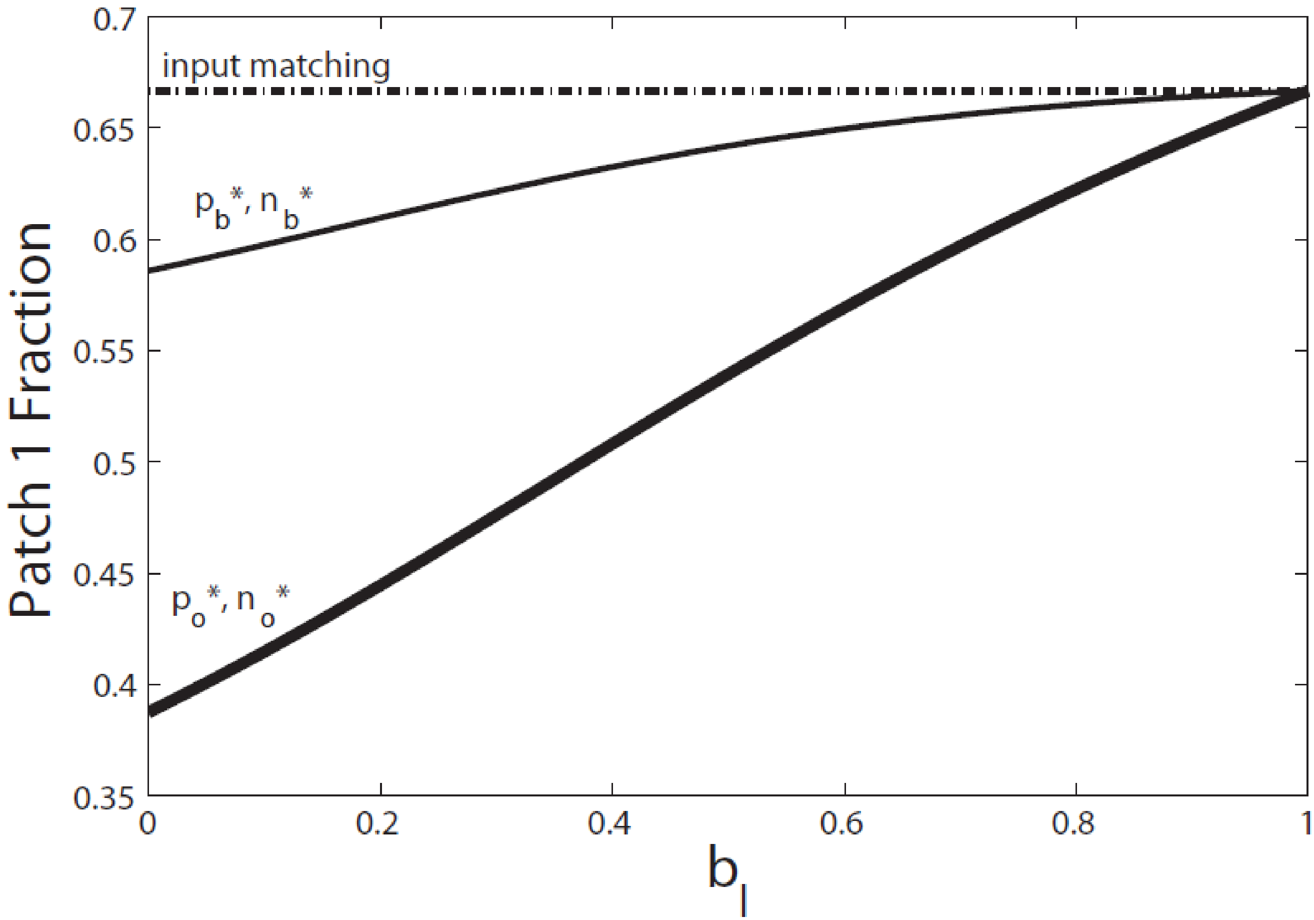
$$\frac{N_1^*}{N_2^*} = \frac{b\beta Q_1 + \mu_I(\mu_I - \mu_S)}{b\beta Q_2 + \mu_I(\mu_I - \mu_S)} \quad \Longrightarrow \quad n_b^* < \frac{Q_1}{Q_1+Q_2}$$

Disease affects mortality

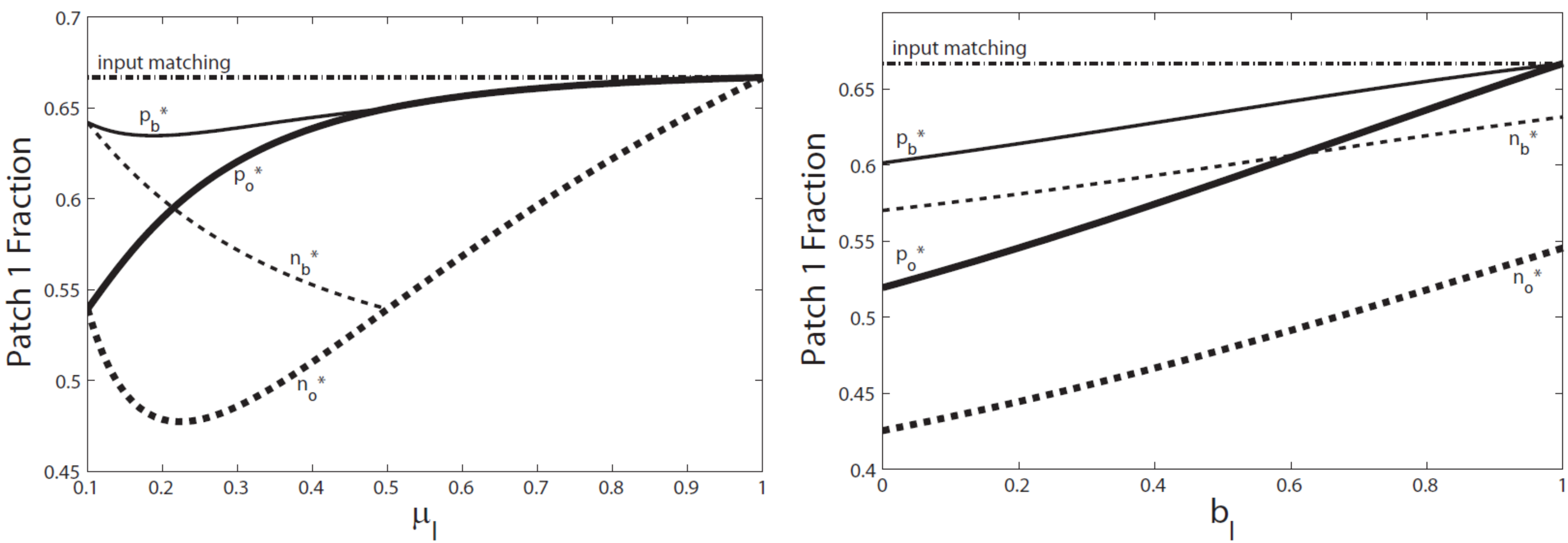


Disease affects fecundity

$$p^* = n^* < \frac{Q_1}{Q_1 + Q_2}$$

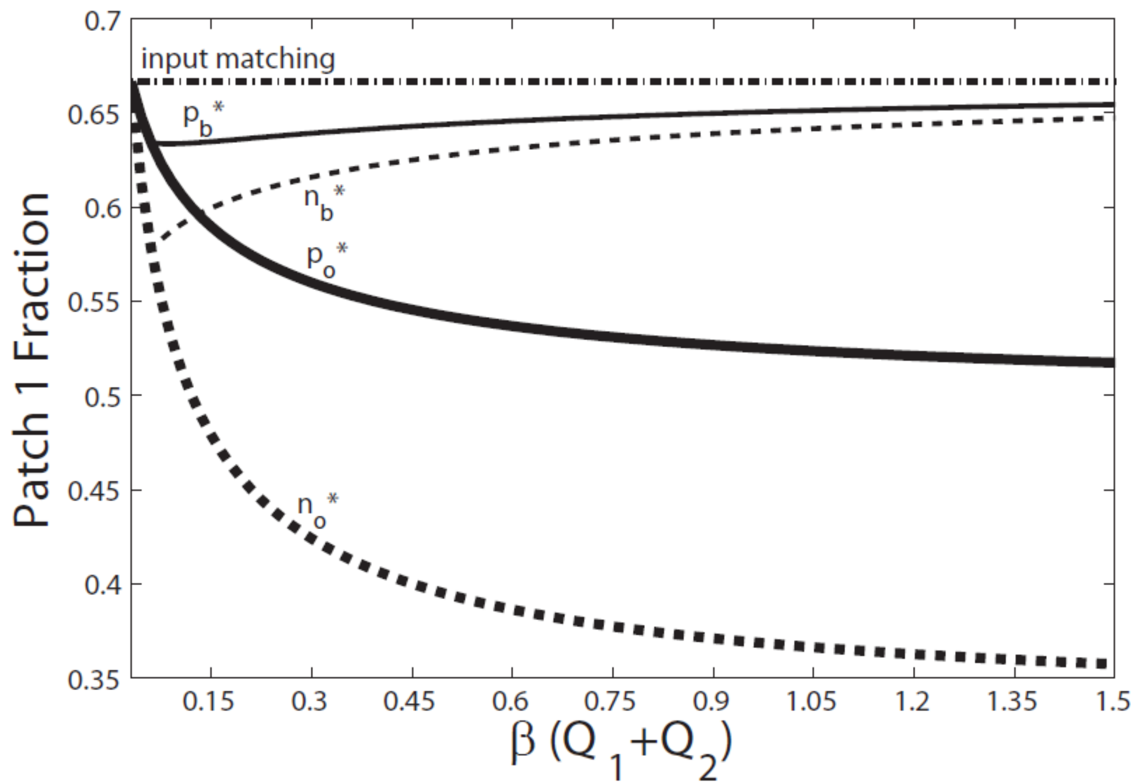


Disease affects fecundity and mortality



Transmission Rate/Total Resource Input

- Increases the overall prevalence of the disease and probability of infection
- Both habitats infected:
  - Overall risk increased, lesser relative cost of using habitat 1 → decreases undermatching
- One habitat infected:
  - Increases difference in risk between habitats → increases undermatching



Extended Model

$$\dot{S}_1 = p\left(\frac{b_S Q_1}{N_1} S_1 + \frac{b_S Q_2}{N_2} S_2 + (1-\delta)\left(\frac{b_R Q_1}{N_1} R_1 + \frac{b_R Q_2}{N_2} R_2\right) + (1-\tau)\left(\frac{b_I Q_1}{N_1} I_1 + \frac{b_I Q_2}{N_2} I_2\right)\right) - \beta I_1 S_1 - \mu_S S_1$$

$$\dot{I}_1 = \tau p\left(\frac{b_I Q_1}{N_1} I_1 + \frac{b_I Q_2}{N_2} I_2\right) + \beta I_1 S_1 - \gamma I_1 - \mu_I I_1$$

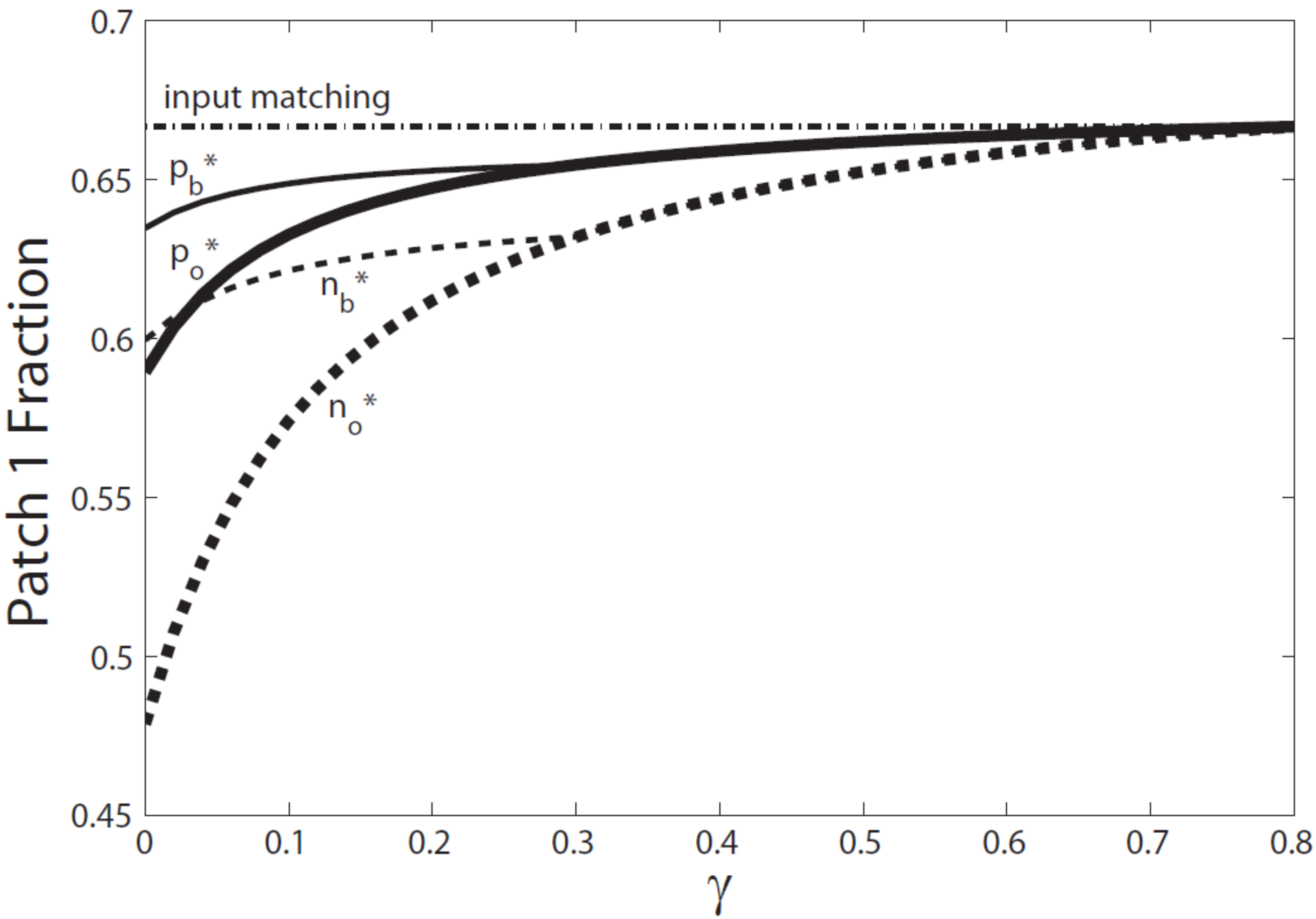
$$\dot{R}_1 = p\delta\left(\frac{b_R Q_1}{N_1} R_1 + \frac{b_R Q_2}{N_2} R_2\right) + \gamma I_1 - \mu_R R_1$$

$$\dot{S}_2 = (1-p)\left(\frac{b_S Q_1}{N_1} S_1 + \frac{b_S Q_2}{N_2} S_2 + (1-\delta)\left(\frac{b_R Q_1}{N_1} R_1 + \frac{b_R Q_2}{N_2} R_2\right) + (1-\tau)\left(\frac{b_I Q_1}{N_1} I_1 + \frac{b_I Q_2}{N_2} I_2\right)\right) - \beta I_2 S_2 - \mu_S S_2$$

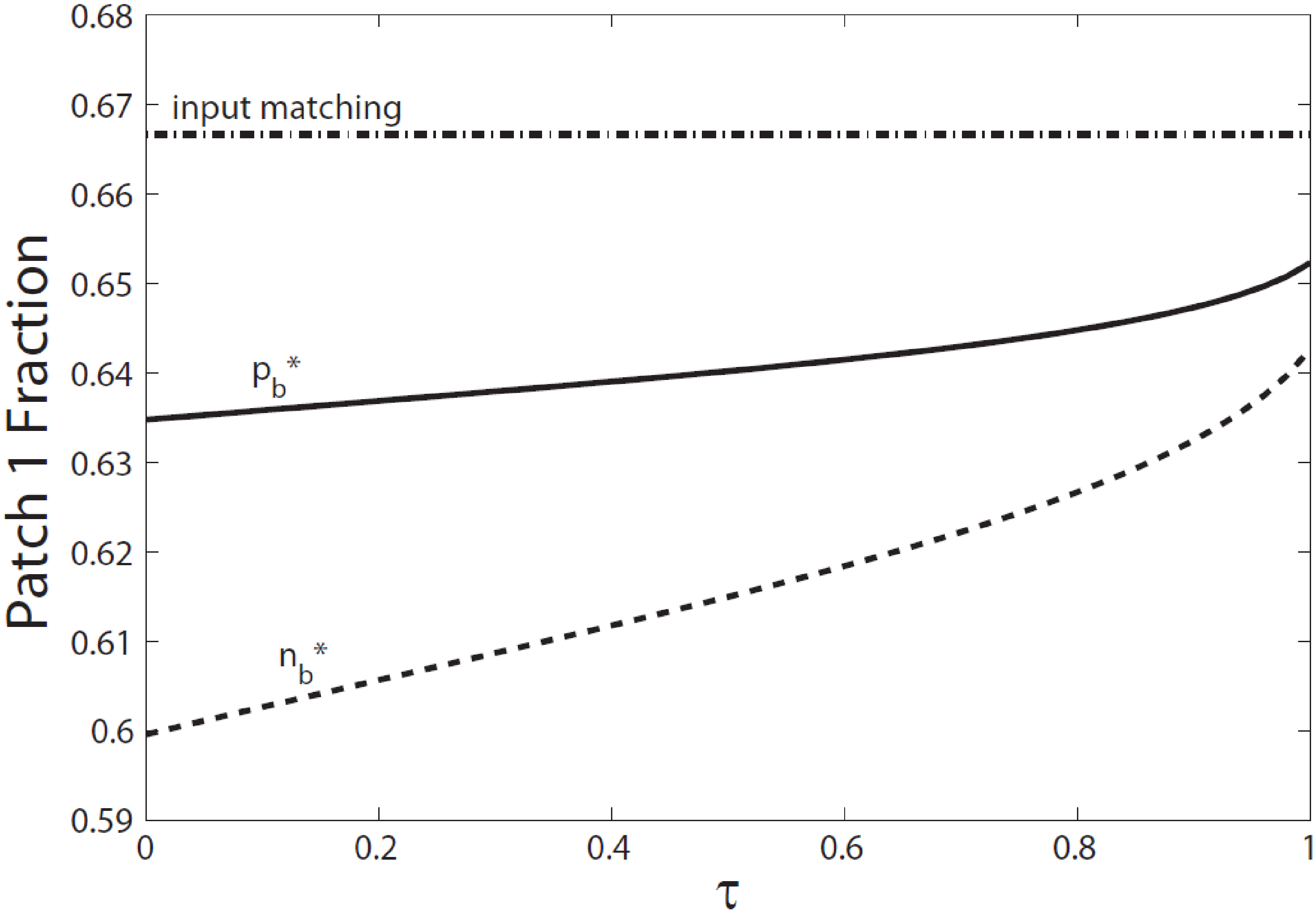
$$\dot{I}_2 = \tau(1-p)\left(\frac{b_I Q_1}{N_1} I_1 + \frac{b_I Q_2}{N_2} I_2\right) + \beta I_2 S_2 - \gamma I_2 - \mu_I I_2$$

$$\dot{R}_2 = (1-p)\delta\left(\frac{b_R Q_1}{N_1} R_1 + \frac{b_R Q_2}{N_2} R_2\right) + \gamma I_2 - \mu_R R_2$$

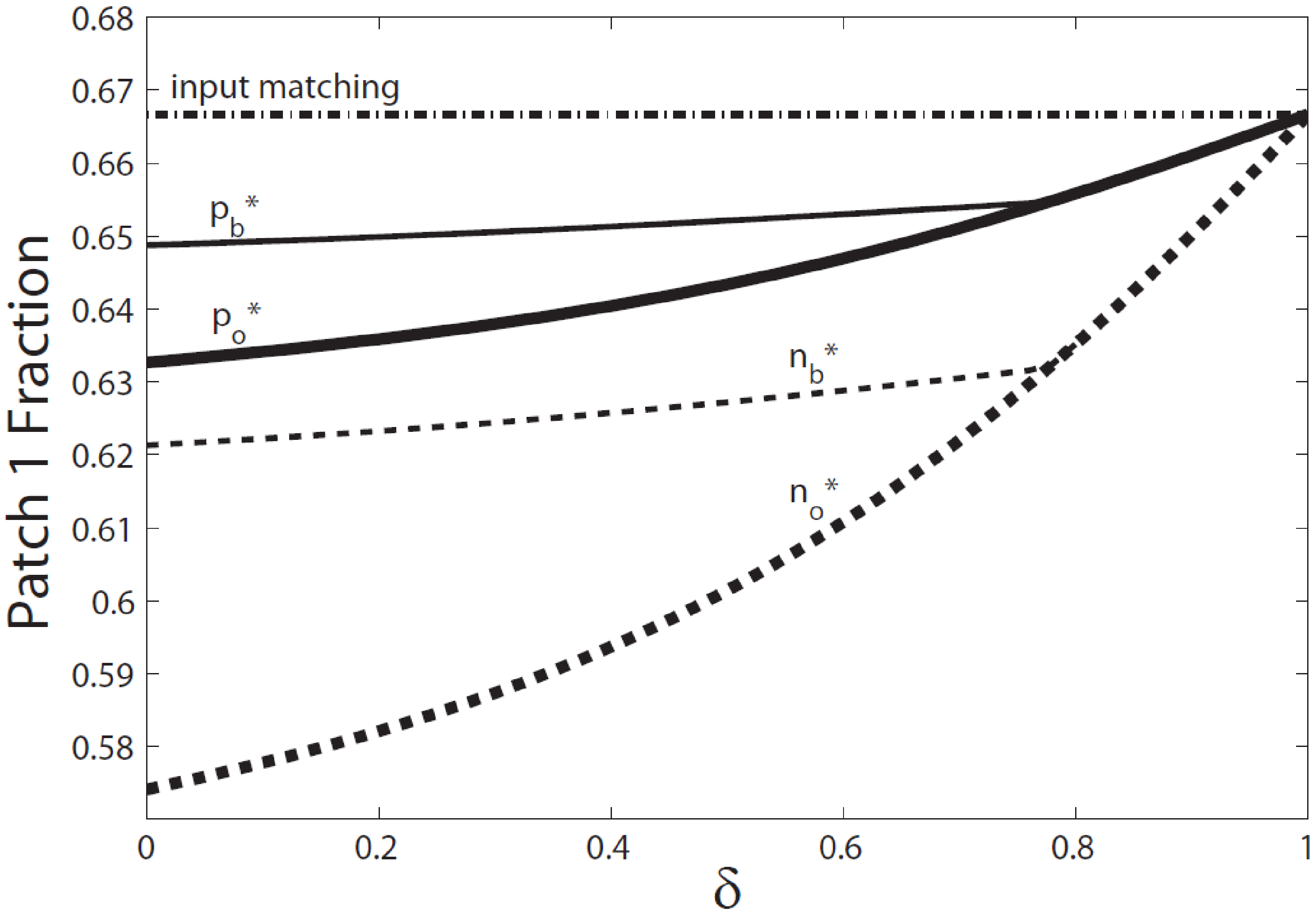
Recovery Rate



Vertical Transmission



Inherited Immunity



Summary

- The risk of infectious disease can have a significant impact on habitat selection and the resulting spatial distribution of populations across patches differing only in resource quality
- Undermatching predicted when disease has negative impact on fitness
  - May be due to a change in habitat selection behavior or direct density effects of infection
  - Degree of undermatching varies with fitness consequences of becoming infected as well as the risk of infection associated with each habitat

Summary

- Degree of undermatching increases with difference in risk between habitats
  - Increase in disease prevalence in both habitats can reduce undermatching by reducing the relative cost of choosing the higher quality habitat
  - Increase in disease prevalence in single habitat increases risk difference between habitat and increases undermatching
  - Implies risk of disease may play lesser role in habitat selection as population densities increase

Future Work

- Implications for pathogen evolution
- Behavioral changes in response to both predators and parasites can result in undermatching
  - Avoidance of predators can influence risk of infection
  - Infection can directly influence vulnerability to predators, and avoidance of infection risk may increase exposure to predation
  - Parasites may be passed from prey to predator
  - How does predation risk interact with the risk of infectious disease to affect habitat selection?

Acknowledgments

- Ian Hamilton, OSU
- Mathematical Biosciences Institute
- NSF

Thank you!

mbi
Mathematical Biosciences Institute
at The Ohio State University