Behavior & Ecology

- Chapters 22, 25

I. Communication

II. Home Range & Territoriality

III. Dispersal & Migration

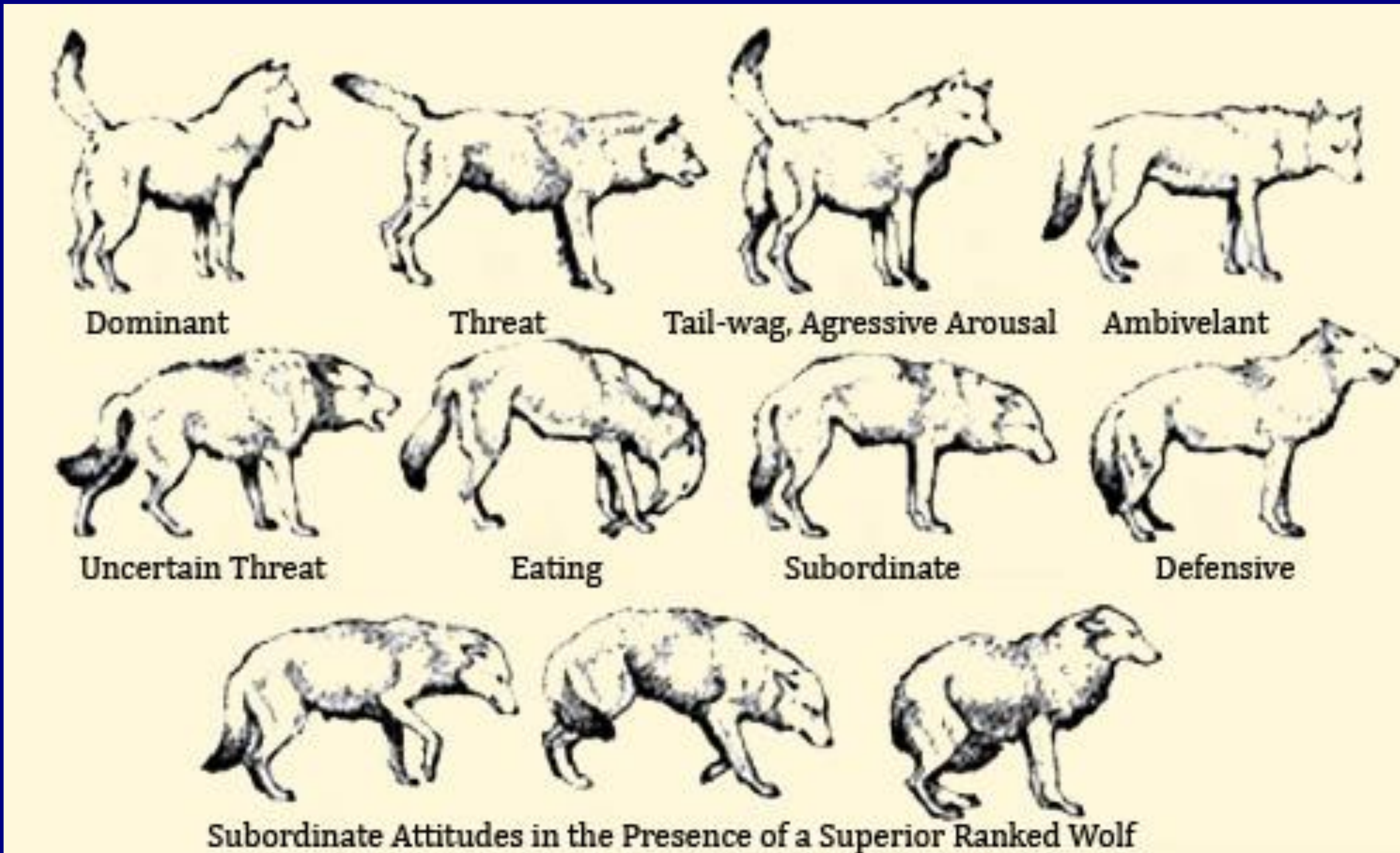
IV. Habitat Selection: theory & practice

I. Communication

- Behavioral, physiological, or morphological characteristics that convey information to other organisms
   - ➢Arose & maintained by natural selection
- Players: sender, receiver, signal
- Cui bono?
- Signals are some type of code that can easily be detected or decoded

A. Modes of Communication

1. Vision
2. Olfaction
   - **Pheromones** – chemical signals between conspecifics
   - Can elicit *behavioral* or *physiological* response
3. Hearing
4. Tactile


Dominant
Threat
Tail-wag, Agressive Arousal
Ambivelant
Uncertain Threat
Eating
Subordinate
Defensive
Subordinate Attitudes in the Presence of a Superior Ranked Wolf


alamy

B. Functions of Communication

- Ultimate function is to increase fitness, proximate functions are variable

1. Group spacing & coordination
2. Recognition
    a. Species
    b. Kin (**nepotism)**
    c. Genetic mechanisms (**MHC**)
3. Reproduction
4. Aggression & social dominance
5. Alarm
    a. Semantic communication
6. Hunting & foraging
    a. ex. **Rally**

Reading for next time

- Hebblewhite & Merrill (2009) ***Ecology*** 90:3445-3454

Animal Behavior
Space Use & Movements

- Intrinsic factors – who YOU are
- Extrinsic factors – what is around you
- So why do animals do what they do?
- Intrinsic qualities
- Extrinsic qualities
  - Food
  - Other animals – conspecifics & heterospecifics
  - Humans
  - Non-animal habitat features

II. Home Range & Territoriality

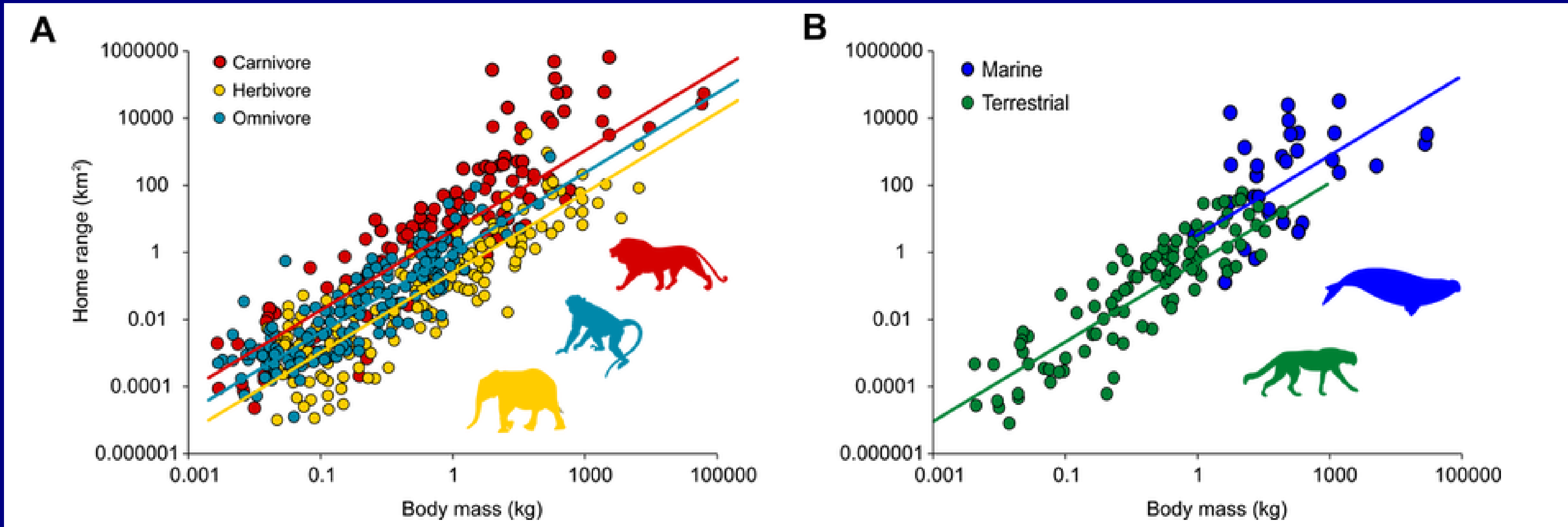
- Burt 1943: Area traversed by individual in its normal activities of food gathering, mating, and caring for its young
- Limits/complications?
- “normal”
- Time period?
- Migratory species
- Forays
  - Burt (1943): “Occasional sallies”

A. Benefits of Home Ranges

1. Energy efficiency – obtain resources in smallest area possible
2. Familiarity with environment
3. Familiarity with local conspecifics

B. Home Range Size

1. Body size (across species)
2. Available resources (within species)
3. Others
    1. Population density (across & within populations)
    2. Fragmentation
        – Can have variable effects

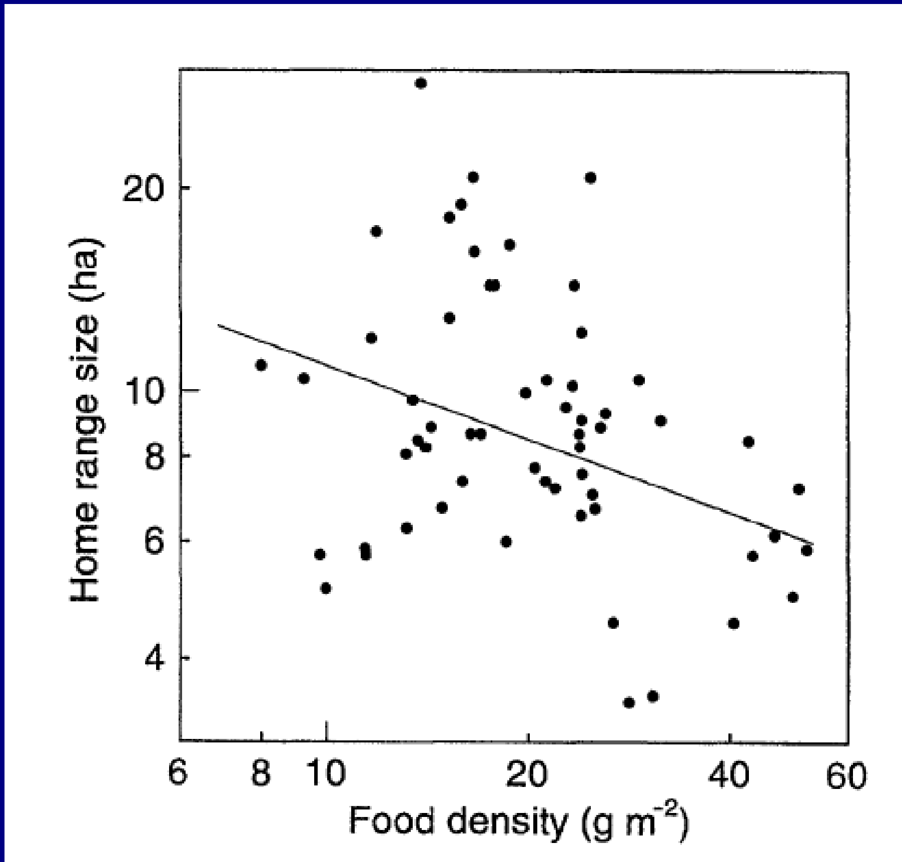


1. **Body size = 53-85 % of variation**

2. **Diet = 15% of variation**

3. **Environment (marine vs. terrestrial) = 1-2 % of variation**

Tucker et al. 2014, Global Ecology & Biogeography 23



Roe Deer

Food Availability

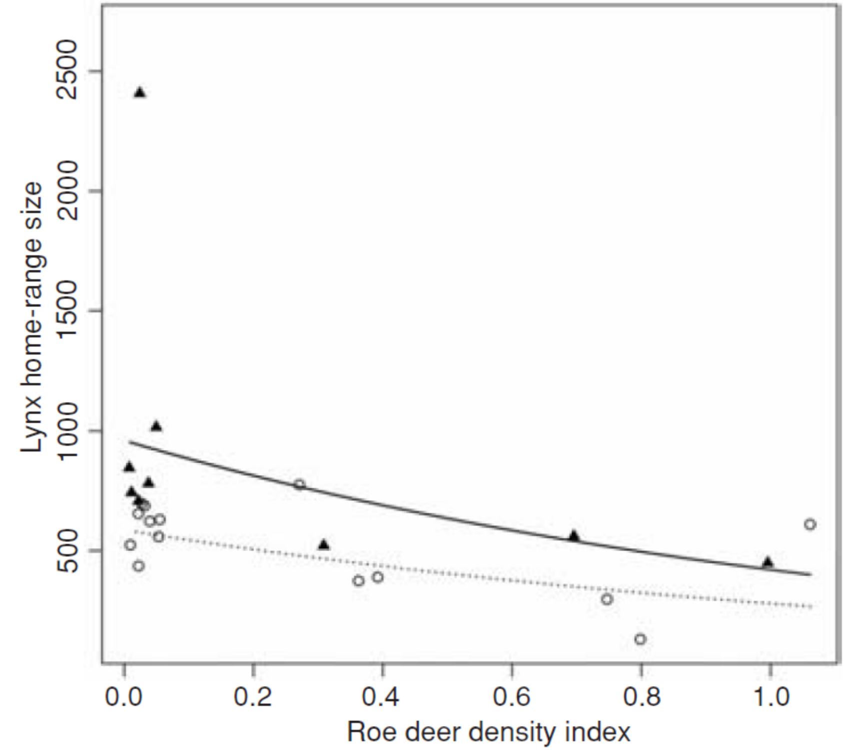


Fig. 2. Observed home-range size and roe deer *Capreolus capreolus* density for males (filled triangles) and females (open circles), and predicted relationship from the multivariate linear mixed model (filled line, males; dashed line, females). The models are calculated from all 52 annual home ranges, whereas the symbols are illustrative and reflect an average value for each of the 23 individual lynx *Lynx lynx*.

European Lynx

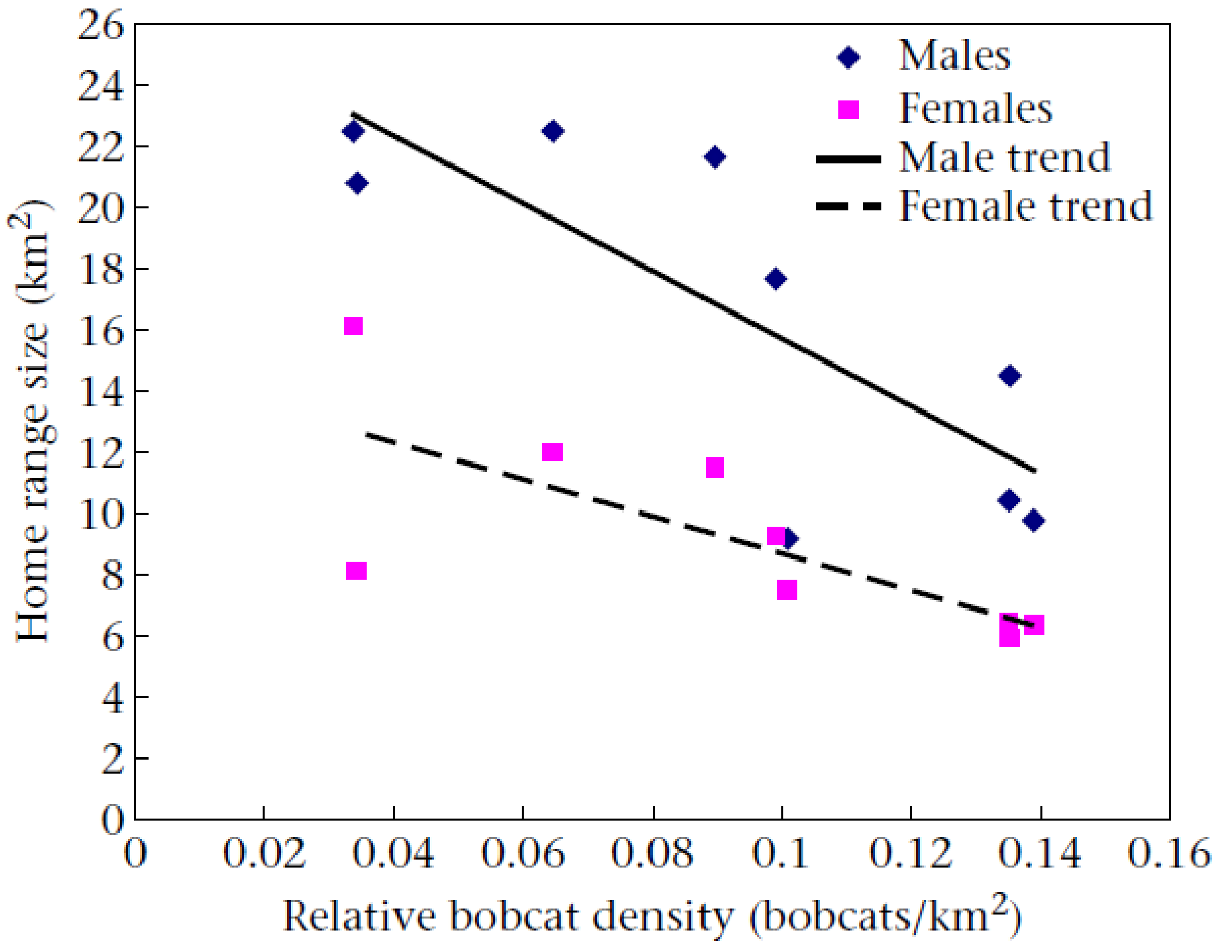


Figure 1. Relationships between bobcat density during 1989–1997 and mean annual male ($R^2 = 0.64$, $N = 9$, $P = 0.0096$) and female ($R^2 = 0.56$, $N = 9$, $P = 0.020$) home range size estimates.

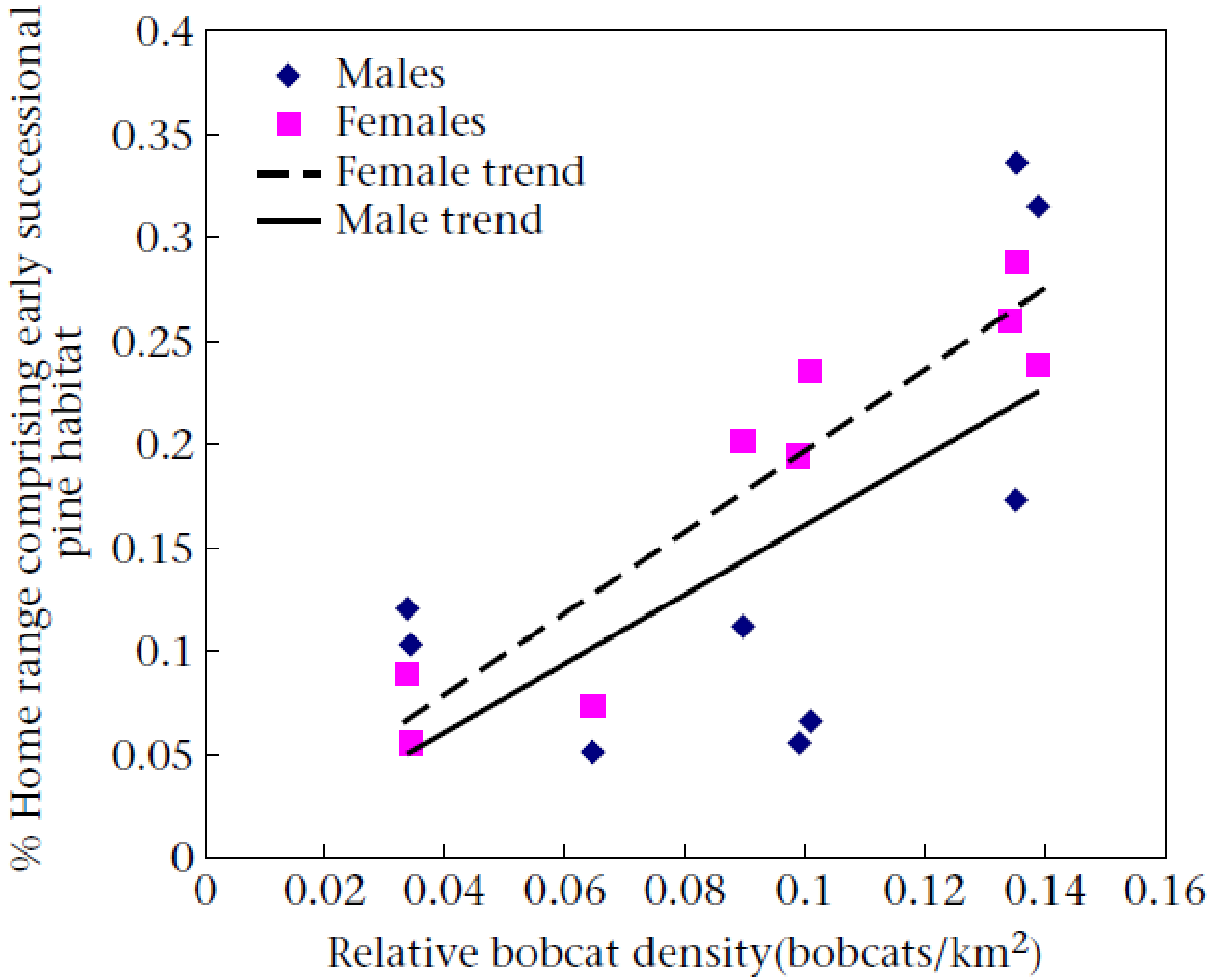


Figure 2. Relationships between bobcat density during 1989–1997 and male ($r_7 = 0.64$, $P = 0.065$) and female ($r_7 = 0.94$, $P = 0.002$) annual use of early successional pine habitat.

Mountain Lions

- Sex ratio: 2 or 3 females per male (adults)
- Adult males breed with multiple females
- Solitary except females with offspring
- Kittens stay with mother ~14 months
  - All males disperse, ~50% females disperse
- Males kill other pumas
- Large home ranges:
  - 200-800 km^2 (males)
  - 90 – 300 km^2 (females)

Smallest Puma HR EVER!

P22 (Hollywood Lion)

Home Range Size Review

- Body size?
  - Across species & populations
- Food availability/quality?
  - Within and across populations
- Density?
  - Across & sometimes within populations
  - Often confounded with food availability
- Fragmentation?
  - Can lead to larger or smaller home ranges

C. Core Area

- Area within the home range of greatest use
- Often arbitrary (50% or 60%)
- Can be useful though!

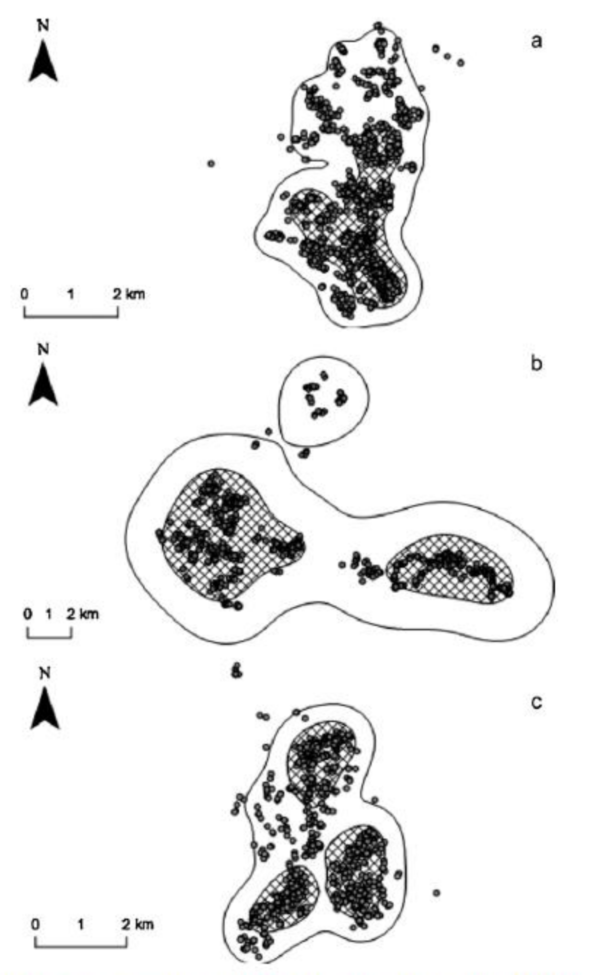


Fig. 2. Examples of core areas (hatched) nested within home ranges (95% utilization distribution) of GPS-collared adult female moose. Points are relocations from which the home range was derived. Number of spatially discrete cores and the relative intensity of use values (*I*) vary among the 3 individuals: one core, 2.0 (a); two cores, 1.9 (b); and three cores, 2.9 (c), respectively.

D. Territory

- Burt 1943: Defended portion of the home range
- Exclusion: portion of home range used exclusively by individual or group
- Benefits: access to resources
- Costs: energy expenditure and/or risk of injury

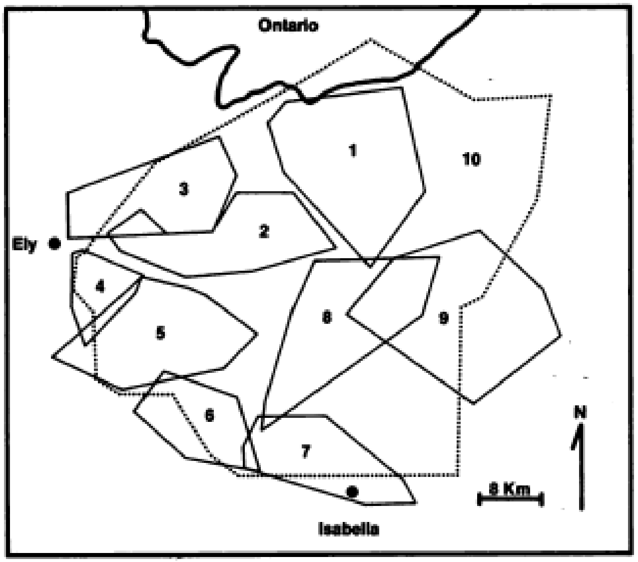


Figure 1.—*Wolf census area (2060 km² in the central Superior National Forest of northeastern Minnesota. Outlined, numbered areas represent minimum wolf pack territory boundaries for winter 1984-1985 as follow: 1, Ensign L. Pack; 2, Pagami Pack No. 2; 3, Wood L. Pack; 4, Birch L. Pack; 5, Little Gabbro Pack; 6, Jackpine Pack No. 4; 7, Sawbill Pack; 8, Quadga L. Pack No. 2; 9. Maniwaki L. Pack No. 2; 10, Malberg L. Pack (approximate territory because pack was not radioed in 1984-85).*

III. Dispersal & Migration

- **Dispersal**: movement from natal to breeding range
- **Philopatry**: breeding at or near natal area
  - Philopatric mammals do not disperse
- **Successful dispersal**: animal that survives dispersal, establishes breeding range, breeds

Proximate vs. Ultimate

- Proximate: immediate physiological or environmental factor/cue that causes event or trait
  - "How something works"
- Ultimate: underlying evolutionary process leading to the event or trait
  - "Why something exists"
- Ex.: Female elk breed w/ males that bugle deepest
- Proximate: deeper bugle elevates female hormones
- Ultimate: deeper bugle indicates size & strength of male

➢ Thus females that breed with better buglers have offspring that are stronger and more likely to survive

A. Reasons for Dispersal

1. Proximate:
   - Aggression from parents
   - Physiological (e.g., testosterone)
   - Food availability
2. Ultimate
   a. **Inbreeding avoidance**
      i. Inbreeding
      ii. Inbreeding depression
   b. **Competition** (intraspecific; subordinates disperse)
      I. Food
      II. Mating opportunities

➢ 3 explanations: *Inbreeding, Food Comp, Mate Comp*

Example: Mountain Lions

- Females: some disperse, some do not
  - Philopatry & matrilines
  - Shorter distances than males
- Males: all disperse
- Females:
  - Competition for food
- Males
  - Competition for mates?
  - Competition for food?
  - Inbreeding avoidance?

B. Migration
1. (overview)

a. Migration = movements from one location to another usually on a seasonal basis

b. Usually round-trip but not always

c. Evolved to avoid unfavorable or exploit favorable conditions
   1) Food availability
   2) Weather
   3) Predation risk
   4) Mating opportunities

d. Environmental cues
   a. Photoperiod
   b. Water (equatorial regions)

2. Benefits of Migration

1. Increased resources (food, water, cover)
2. Avoidance of extreme climatic conditions
3. Better conditions for parturition
4. Increased mating opportunities

3. Migratory Mammals

1. Bats
2. Cetaceans & pinnipeds
3. Ungulates

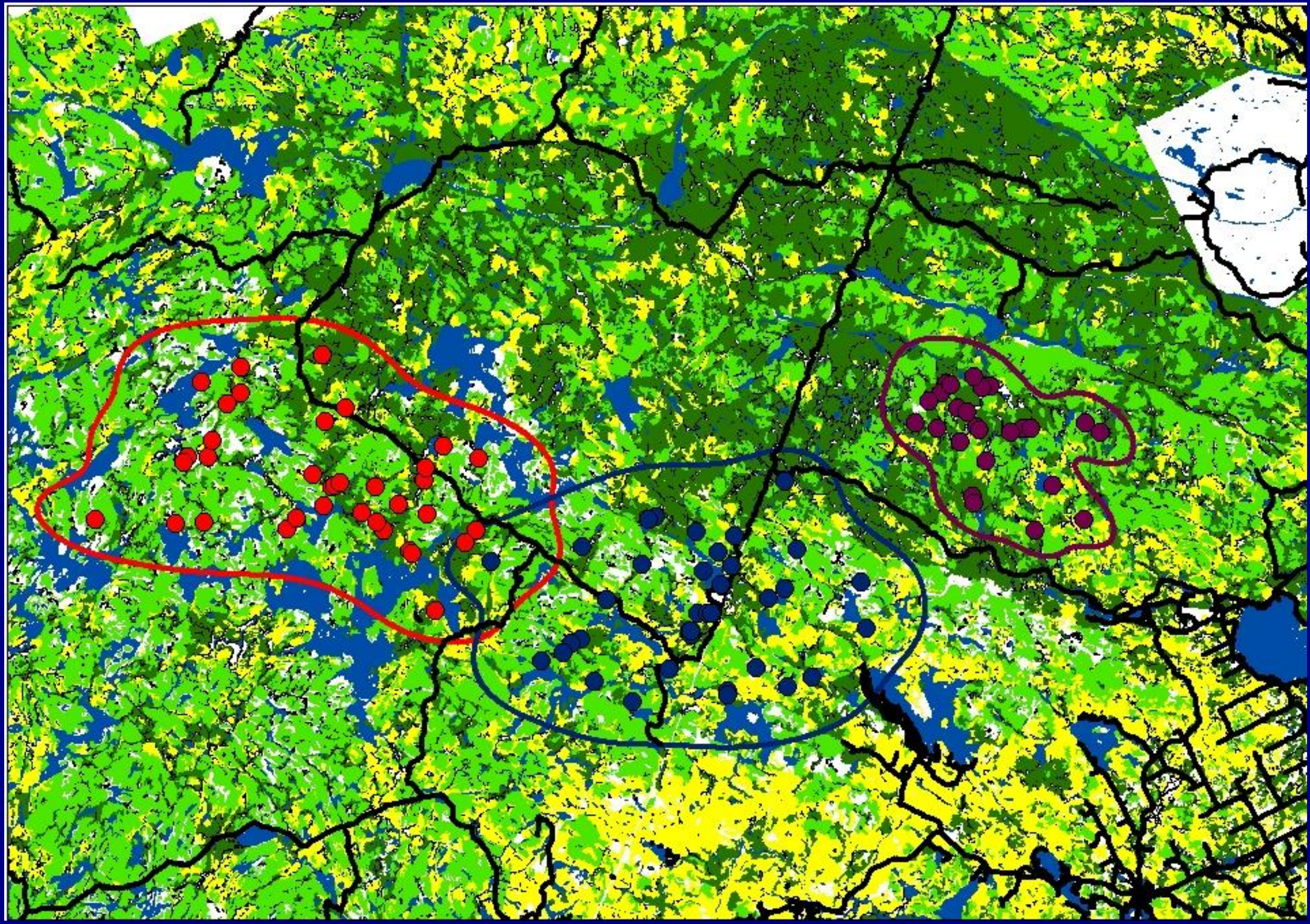
Johnson 1980 *Ecology* 61:65-71

- Read abstract
- Read part of discussion P. 69 ONLY
- Don’t have to read the rest

IV. Habitat Selection

- What is habitat selection?
- What is habitat use?
- Selection = use relative to availability
- Defining use & availability requires consideration of scale (more later…)
- Use tells us little about ‘decisions’ made by animals or what they seek out
- Selection provides inference on these decisions

Use vs. Availability



Wildlife Habitat Relationships

- Fundamental pursuit in ecology & Con Bio
- Selection of habitat & resources should reflect strategies to maximize fitness
  - *Rarely tested explicitly*
- Can be used to detect trade-offs
- Selection of habitat may indicate quality
  - Density/social pressure can be confounding
- Many ways to evaluate habitat selection
- Selection = used > available

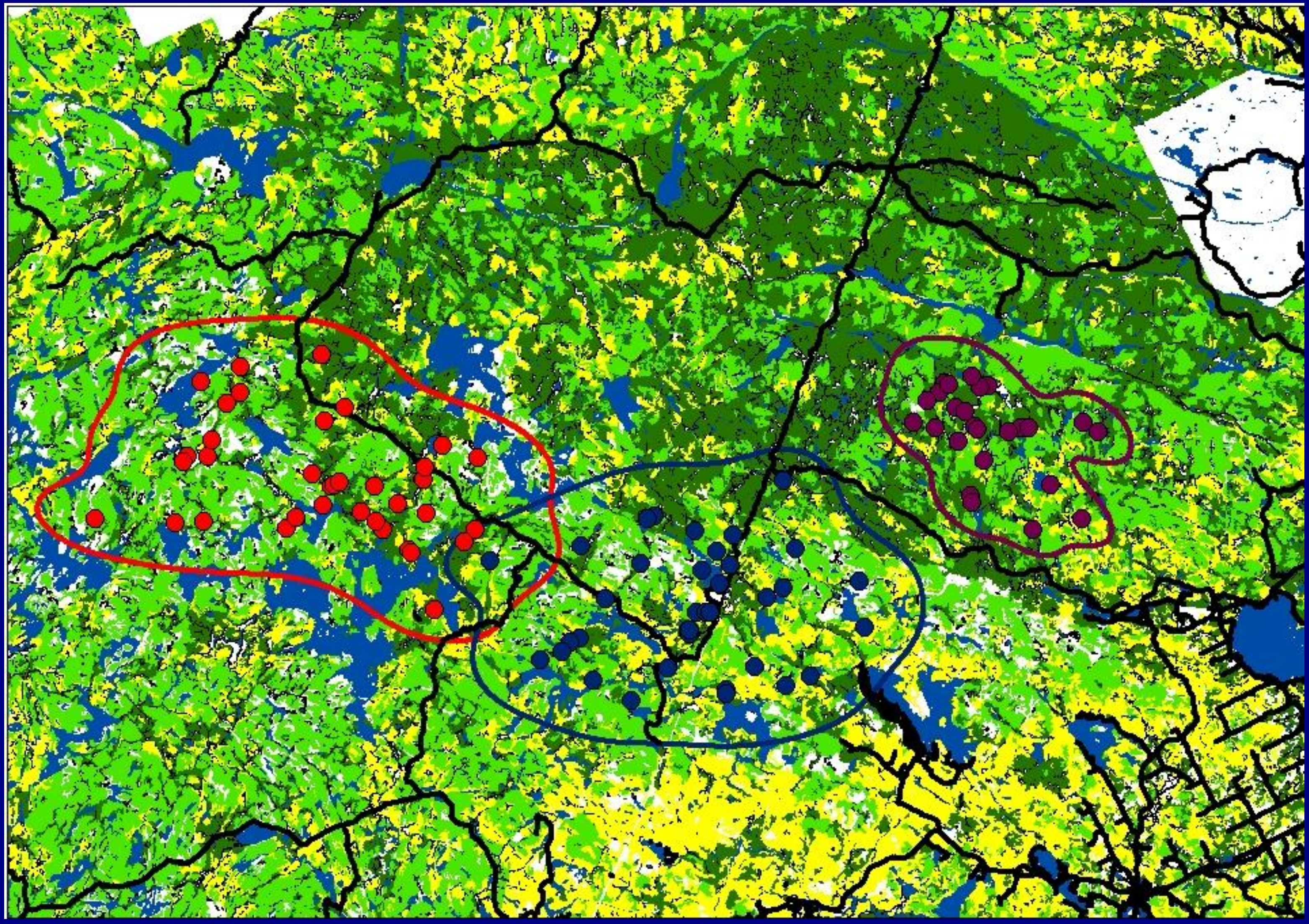
A. Habitat Selection Theory

1. Hierarchical habitat selection
2. Ideal free and other distributions

1. Hierarchical Habitat Selection

- Johnson (1980) “order of selection”

Use vs. Availability



Habitat Selection is Hierarchical
Johnson 1980 (cited by >3400)

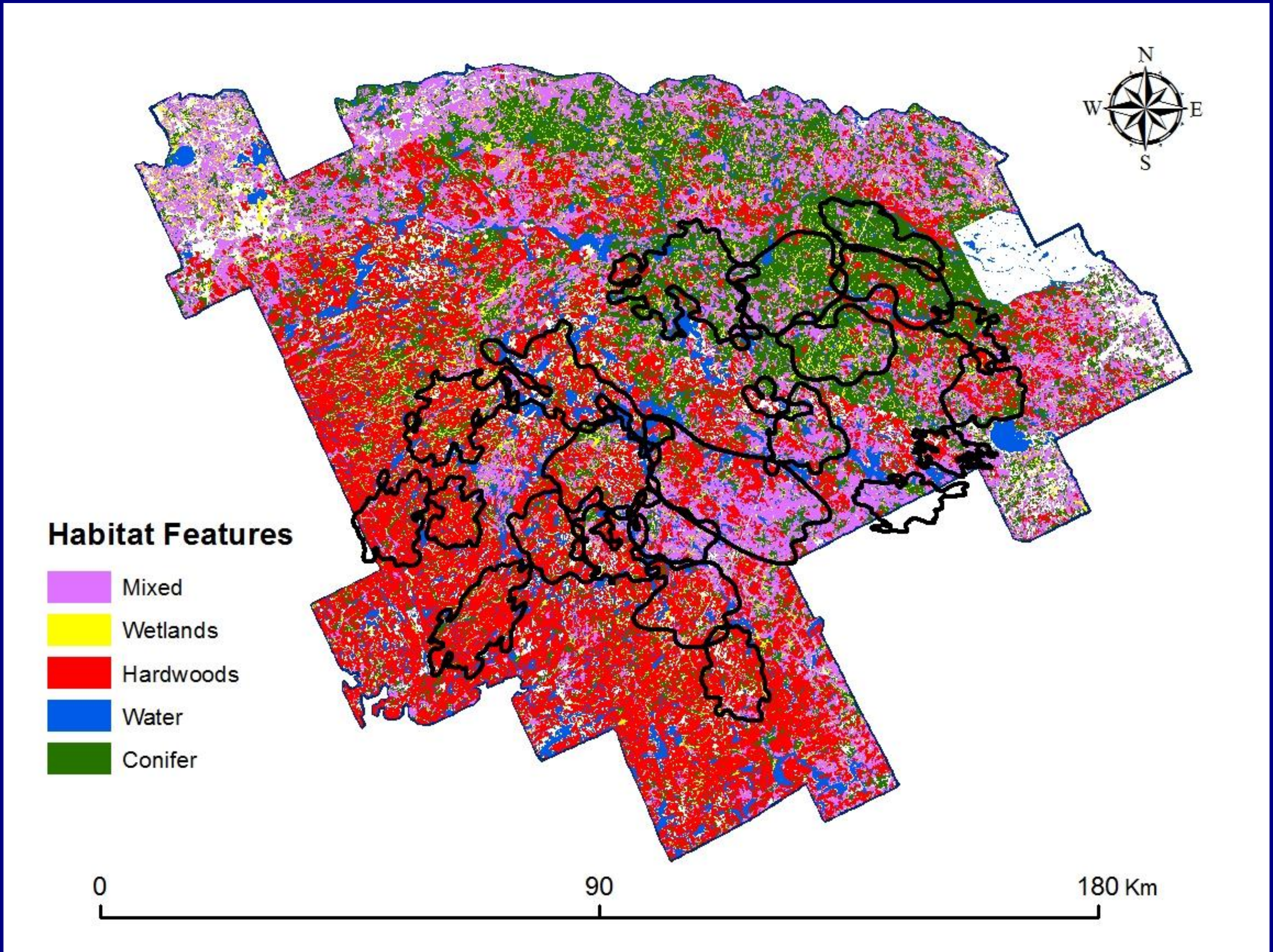
- 1st order: geographical range of species
  - *Geographical range (use), entire earth (available)*
  - Species distribution modeling
- 2nd order: landscape level
  - *home range (use), larger landscape (available)*
  - Defining landscape problematic & arbitrary
- 3rd order: within home range
  - *animal locations (use), home range (available)*
  - Popular and effective
- 4th order: procurement of resources at a site
  - Food items (use), feeding site (available)
  - 4th order a little open-ended

Habitat Selection is Hierarchical

Johnson 1980 (cited by >3794)

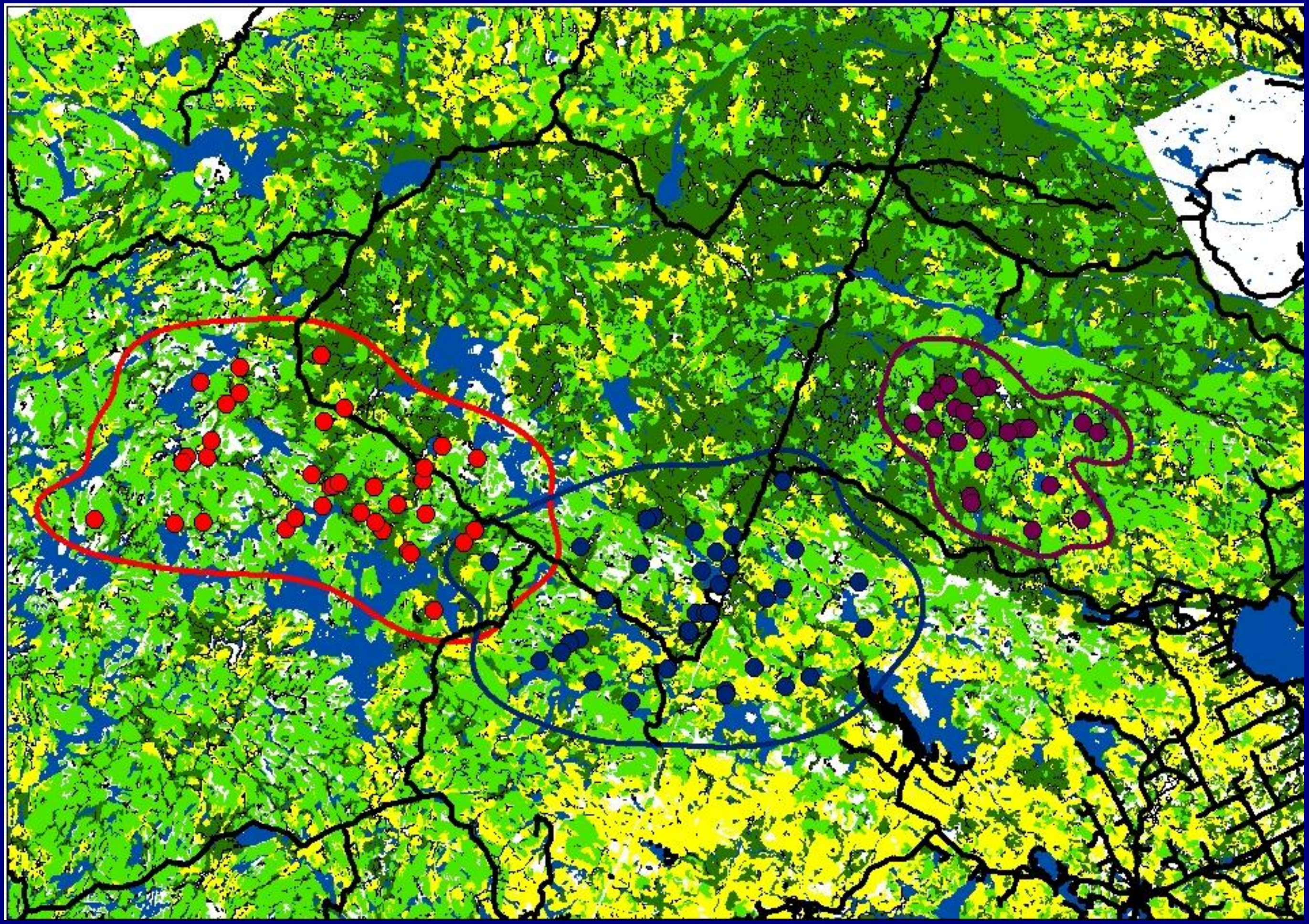
- 1st order: geographical range of species
  - *Geographical range (use), entire earth (available)*
  - Species distribution modeling
- **2nd order: landscape level**
  - ***home range (use), larger landscape (available)***
  - **Defining landscape problematic & arbitrary**
- **3rd order: within home range**
  - ***animal locations (use), home range (available)***
  - **Popular and effective**
- 4th order: procurement of resources at a site
  - Food items (use), feeding site (available)
  - 4th order a little open-ended

2^{nd} Order Selection
Use: Home Range
Available: Landscape (study area)

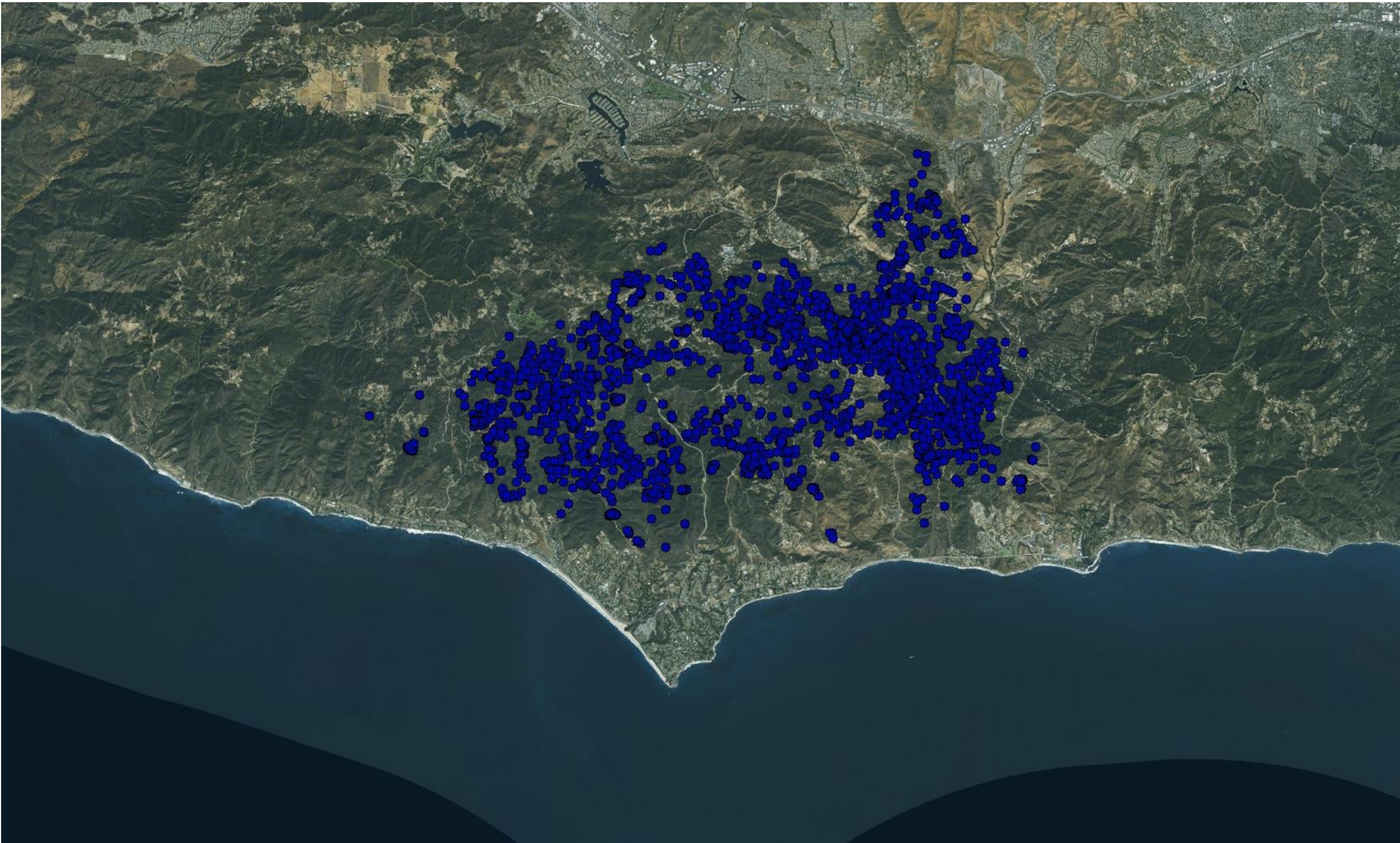


3rd Order Selection

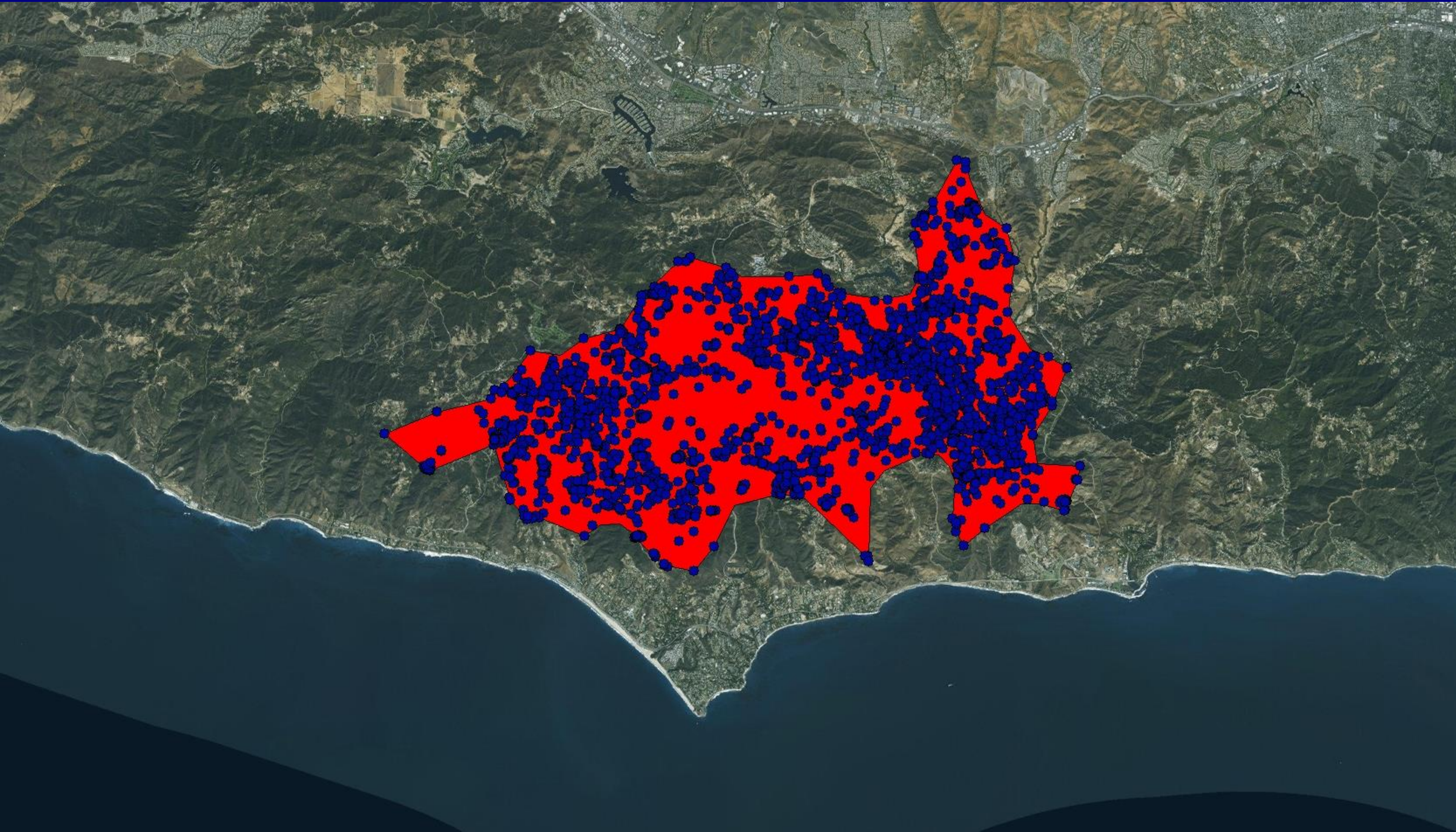
Use: Animal Locations
Available: Across home range



Use: Telemetry Data



Estimate Home Range



Estimate Availability (3rd Order)

Readings

- Crooks & Soule. 1999. Nature 400: 563-566.
- Gehrt & Clark. 2003. Wildlife Society Bulletin 31: 836-842.

Resource Selection Functions

- Broad class of models and analyses
- Most commonly refers to logistic regression based RSF models
- See also: resource utilization functions
  - e.g, Marzluff et al. 2004; Millspaugh et al. 2006
- Logistic regression-based RSFs currently the most popular habitat selection analysis

RSF Basics

- Response variable: used and available locations (OR used and unused locations)

  0 = available, 1 = used

- Predictor variables are
  - Most common are habitat/landscape features
  - Measures of food resources
  - Probability of encountering prey/predator/etc.
  - Intrinsic characteristics of animals (e.g., sex, age, ancestry), temporal metrics (e.g., night vs. day) can be fit as interactions

- **$w(x) = \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots \beta_n X_n)$**

Advantages of RSFs

- Truly multivariate: response variable = locations on landscape (pixels)
- Handles continuous & discrete independent variables (resources/habitats)
- Interactions can be incorporated
- Can examine marginal (population-level) and conditional (individual or group level) habitat selection
- ***RSFs allow us to ask questions beyond what habitats are selected and avoided!***

Basic RSF Model

y = resource1 + resource 2… + resource k

y = r1 + r2 + r3 + random intercept (animal)

y: 0= available to animal, 1 = used by animal

Let’s Do It

- Field study, GIS work, data organization
- What are questions?
- What are predictor variables?
- *Y* = slope + elevation + roads (dist) + conifer (dist) + hardwood (dist) + water (dist)
- Random intercept of individual (1|animalID)
- Logistic model with binary response variable

Compare Use - Availability

AnimalID	Use	Sex	Age	chap	css	pm	rw	up	roads	trails	elev	urban	LMTDate	Latitude	Longitude
P01	1	M	A	0	150.0	0.0	90.0	300.0	276.6	241.9	212.2	1714.2	7/19/2002	34.08946	-118.913
P01	1	M	A	0	150.0	0.0	90.0	330.0	276.6	241.9	222.4	1714.2	7/19/2002	34.08952	-118.913
P01	1	M	A	0	150.0	0.0	90.0	330.0	276.6	241.9	229.2	1714.2	7/19/2002	34.0896	-118.913
P01	1	M	A	0	189.7	30.0	90.0	335.4	342.1	276.6	262.5	1747.5	7/19/2002	34.08995	-118.913
P01	1	M	A	0	123.7	94.9	30.0	421.1	390.0	360.0	427.8	1710.3	7/20/2002	34.09059	-118.912
P01	0	M	A	0	123.7	94.9	30.0	421.1	390.0	360.0	176.3	1710.3	7/20/2002	34.09059	-118.912
P01	0	M	A	0	123.7	123.7	30.0	451.0	390.0	360.0	176.6	1710.3	7/20/2002	34.09066	-118.912
P01	0	M	A	0	30.0	108.2	0.0	408.0	365.0	313.2	242.9	1644.5	7/20/2002	34.09024	-118.911
P01	0	M	A	0	30.0	108.2	0.0	408.0	365.0	313.2	128.8	1644.5	7/20/2002	34.09024	-118.911
P01	0	M	A	0	134.2	0.0	90.0	330.0	276.6	247.4	132.0	1714.2	7/20/2002	34.0896	-118.913
P02	1	F	A	0	153.0	30.0	60.0	360.0	331.4	270.0	88.0	1722.9	7/20/2002	34.08995	-118.913
P02	1	F	A	0	153.0	30.0	60.0	360.0	331.4	270.0	96.2	1722.9	7/20/2002	34.08995	-118.913
P02	1	F	A	0	182.5	30.0	60.0	360.0	331.4	271.7	108.1	1722.9	7/20/2002	34.08995	-118.913
P02	1	F	A	0	182.5	591.7	30.0	920.3	660.7	787.5	126.0	1824.1	7/21/2002	34.09443	-118.909
P02	1	F	A	0	0.0	247.4	450.0	494.8	960.0	30.0	106.9	1055.1	7/22/2002	34.14556	-118.947
P02	0	F	A	0	0.0	276.6	212.1	381.8	1290.0	318.9	126.5	1320.3	7/23/2002	34.14471	-118.98
P02	0	F	A	182.483	94.9	0.0	722.5	212.1	1474.9	603.0	112.3	2346.9	7/23/2002	34.14479	-119.005
P02	0	F	A	90	42.4	30.0	660.0	30.0	2882.5	0.0	131.5	3649.7	7/23/2002	34.13084	-119.014
P02	0	F	A	30	30.0	436.8	456.9	0.0	4052.8	67.1	105.3	2571.1	7/23/2002	34.12025	-119.022
P02	0	F	A	0	42.4	558.0	256.3	0.0	4139.8	30.0	72.8	2634.7	7/23/2002	34.11875	-119.021
P03	1	M	SA	84.8528	0.0	543.3	134.2	150.0	3622.4	189.7	37.0	2800.3	7/24/2002	34.11314	-119.019
P03	1	M	SA	30	30.0	531.6	150.0	120.0	3568.9	150.0	23.9	2839.2	7/24/2002	34.11236	-119.018
P03	1	M	SA	212.132	30.0	362.5	67.1	0.0	3552.9	30.0	90.3	3394.8	7/24/2002	34.10944	-119.013
P03	1	M	SA	90	42.4	768.4	0.0	123.7	2038.7	30.0	172.4	3558.0	7/24/2002	34.09622	-119.018
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P03	0	M	SA	30	94.9	630.7	295.5	67.1	918.3	0.0	312.1	331.4	7/26/2002	34.06258	-118.961
P03	0	M	SA	0	94.9	607.5	742.8	597.7	1110.0	216.3	260.7	840.5	7/26/2002	34.06144	-118.956
P03	0	M	SA	0	108.2	268.3	646.2	67.1	1464.8	212.1	324.3	1288.6	7/26/2002	34.064	-118.95
P03	0	M	SA	0	67.1	108.2	1008.0	488.4	1008.0	180.0	318.2	2351.7	7/27/2002	34.07104	-118.942

Compare Use - Availability

AnimalID	Use	Sex	Age	chap	css	pm	rw	up	roads	trails	elev	urban	LMTDate	Latitude	Longitude
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P01	0	M	A	0	30.0	108.2	0.0	408.0	365.0	313.2	242.9	1644.5	7/20/2002	34.09024	-118.911
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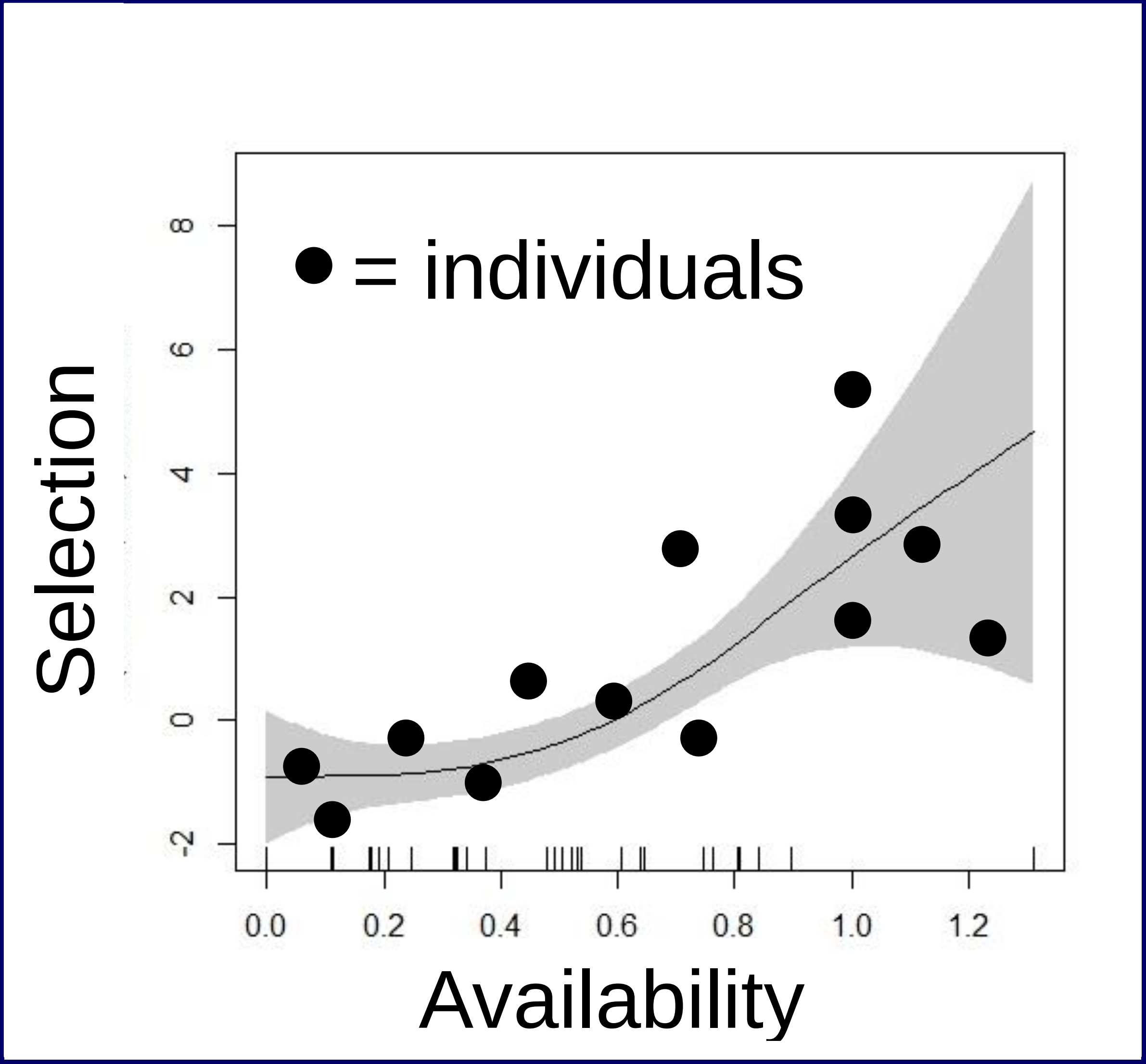
P03	1	M	SA	84.8528	0.0	543.3	134.2	150.0	3622.4	189.7	37.0	2800.3	7/24/2002	34.11314	-119.019
P03	1	M	SA	30	30.0	531.6	150.0	120.0	3568.9	150.0	23.9	2839.2	7/24/2002	34.11236	-119.018
P03	1	M	SA	212.132	30.0	362.5	67.1	0.0	3552.9	30.0	90.3	3394.8	7/24/2002	34.10944	-119.013
P03	1	M	SA	90	42.4	768.4	0.0	123.7	2038.7	30.0	172.4	3558.0	7/24/2002	34.09622	-119.018
P03	1	M	SA	228.473	30.0	510.9	0.0	420.0	1612.2	30.0	152.8	4607.2	7/24/2002	34.08733	-119.012
P03	1	M	SA	0	0.0	256.3	201.2	807.8	1622.5	436.8	137.8	4502.5	7/25/2002	34.08476	-119.007
P03	0	M	SA	134.164	0.0	84.9	300.0	330.0	268.3	134.2	195.4	335.4	7/26/2002	34.05917	-118.969
P03	0	M	SA	30	94.9	630.7	295.5	67.1	918.3	0.0	312.1	331.4	7/26/2002	34.06258	-118.961
P03	0	M	SA	0	94.9	607.5	742.8	597.7	1110.0	216.3	260.7	840.5	7/26/2002	34.06144	-118.956
P03	0	M	SA	0	108.2	268.3	646.2	67.1	1464.8	212.1	324.3	1288.6	7/26/2002	34.064	-118.95
P03	0	M	SA	0	67.1	108.2	1008.0	488.4	1008.0	180.0	318.2	2351.7	7/27/2002	34.07104	-118.942

Ecological Dynamics

- Functional responses in resource selection
  - Selection of a given resource varies as a function of resource availability
  - Mysterud & Ims 1998, *Ecology*
  - Hebblewhite & Merrill 2008, *J. Applied Ecol.*
- Examining fitness-resource selection link
  - Does behavior influence survival, reproduction, lifetime reproductive success?
  - McLoughlin et al. 2005, 2006; Dussault et al. 2012

Functional Response



Mixed Effects RSFs in Action

ex. Benson et al. 2015, Oikos 124:1664-173

- Roads negatively influenced canid survival
  - Shown previously
- Wolves, coyotes, hybrids in same study area
- Questions:

1. Do canids avoid roads more during day?
2. Do these *differences* b/t night & day vary as a function of road availability/density
3. Do these individual level responses influence survival?

➢ Linking resource selection to fitness and demography is important for evolutionary and practical questions!!

Overall Approach

- 3rd order selection (within home range)
- Assessed population-level and individual level response to 2 roads
- *Population level*: secondary roads avoided more during day than at night
- *Individual level*: derived coefficients for each canid with random slope model
- Regressed coefficients against ancestry (% coyote) and availability (dist. to roads)

2 Step Approach to Functional Responses

- 3rd order RSF for night & day
- **Q1: Do canids avoid roads more at day?**
  - Population level response
  - Avoiding roads during day when encounters with humans likely
  - Selecting/avoiding less at night to exploit benefits of roads – ease of travel, human food

Do canids avoid roads more during day?

Population-Level Response

	Winter		Summer	
Resource	**β_{Day} (95% CI)**	**β_{Night} (95% CI)**	**β_{Day} (95% CI)**	**β_{Night} (95% CI)**
2° Roads	**0.30** (0.24, 0.37)	**-0.04** (-0.11, 0.02)	**0.52** (0.46, 0.58)	**0.21** (0.15, 0.28)
Conclusion	Avoid	No Avoid/Select	Avoid	Avoid

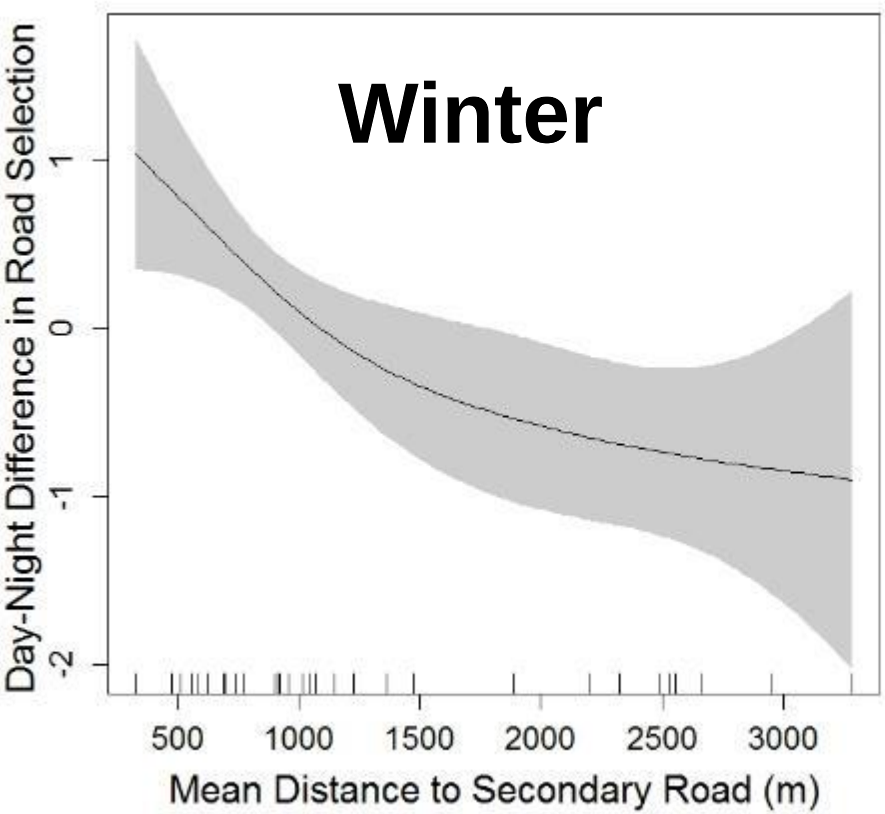
From Benson *et al.* (2015) *Oikos* 124:1164-1173.

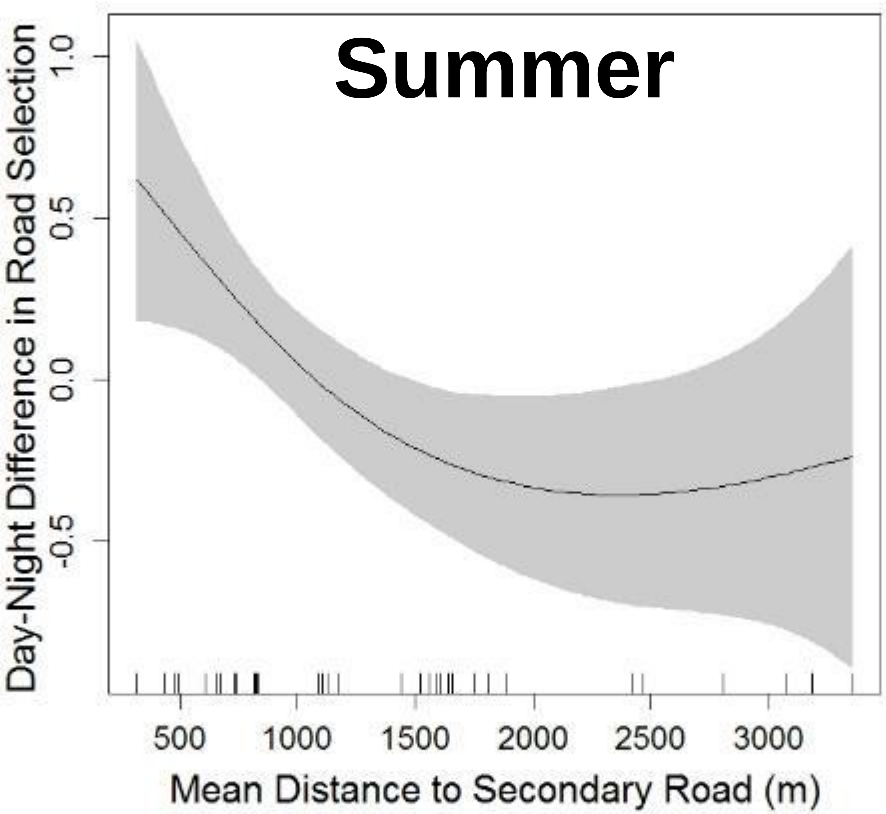
Q2: Do individuals change day-night behavior more at higher rd density?

- Derive *individual-level* coefficients from random slope models for day and night
- $\beta_{day} - \beta_{night}$ = diff. in selection b/t day & night

Individual Selection Day - Night

From Benson *et al.* (2015) *Oikos* 124:1164-1173.





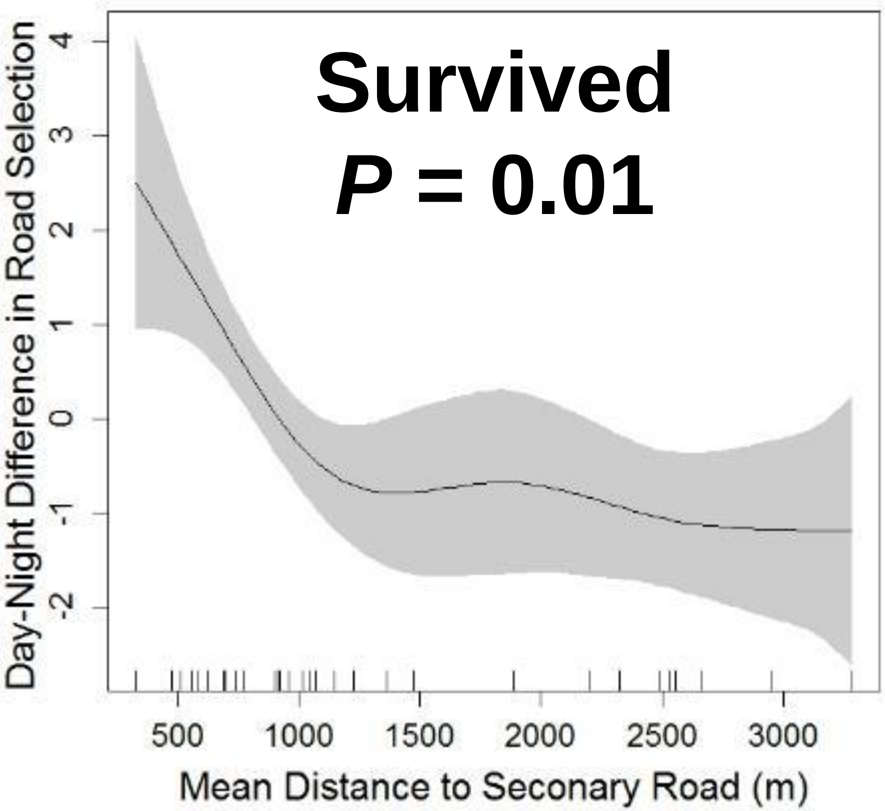
Diff. in day – night selection stronger at higher road density

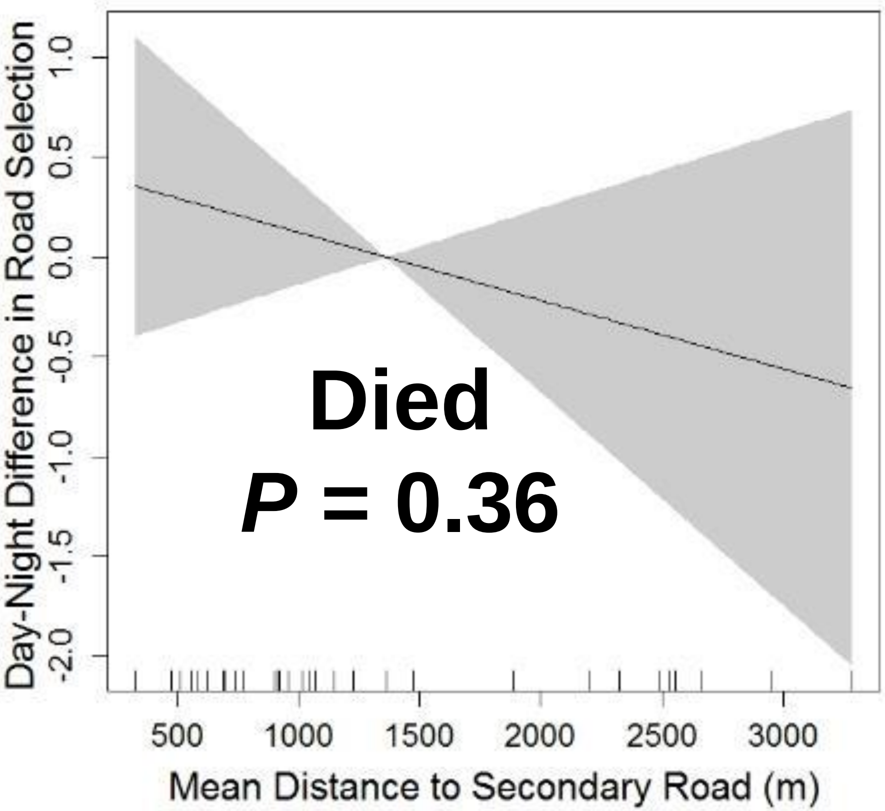
Q3: Do these patterns influence component of fitness (survival)

- Did animals that lived behave differently than animals that died?
- Specifically, did surviving animals change their behavior from day to night more strongly as a function of road availability than those that died?

Adaptive Behavioral Response

From Benson *et al.* (2015) *Oikos* 124:1164-1173.





Behavioral Response Linked to Component of Fitness

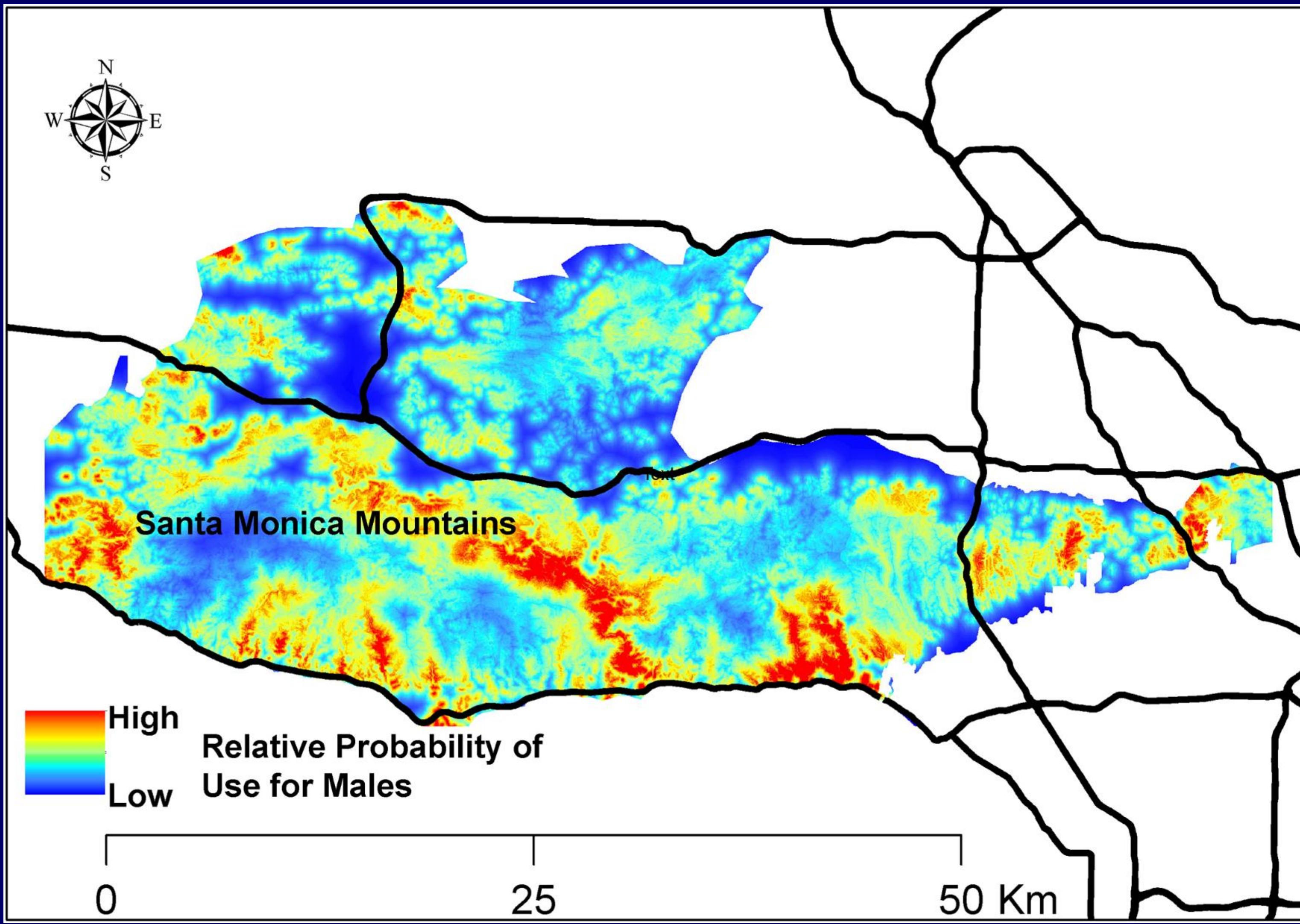
Implications

- Individuals respond to roads differently
- Different behavior had different fitness costs
- Canids can exploit roads while mitigating mortality risk = tradeoff

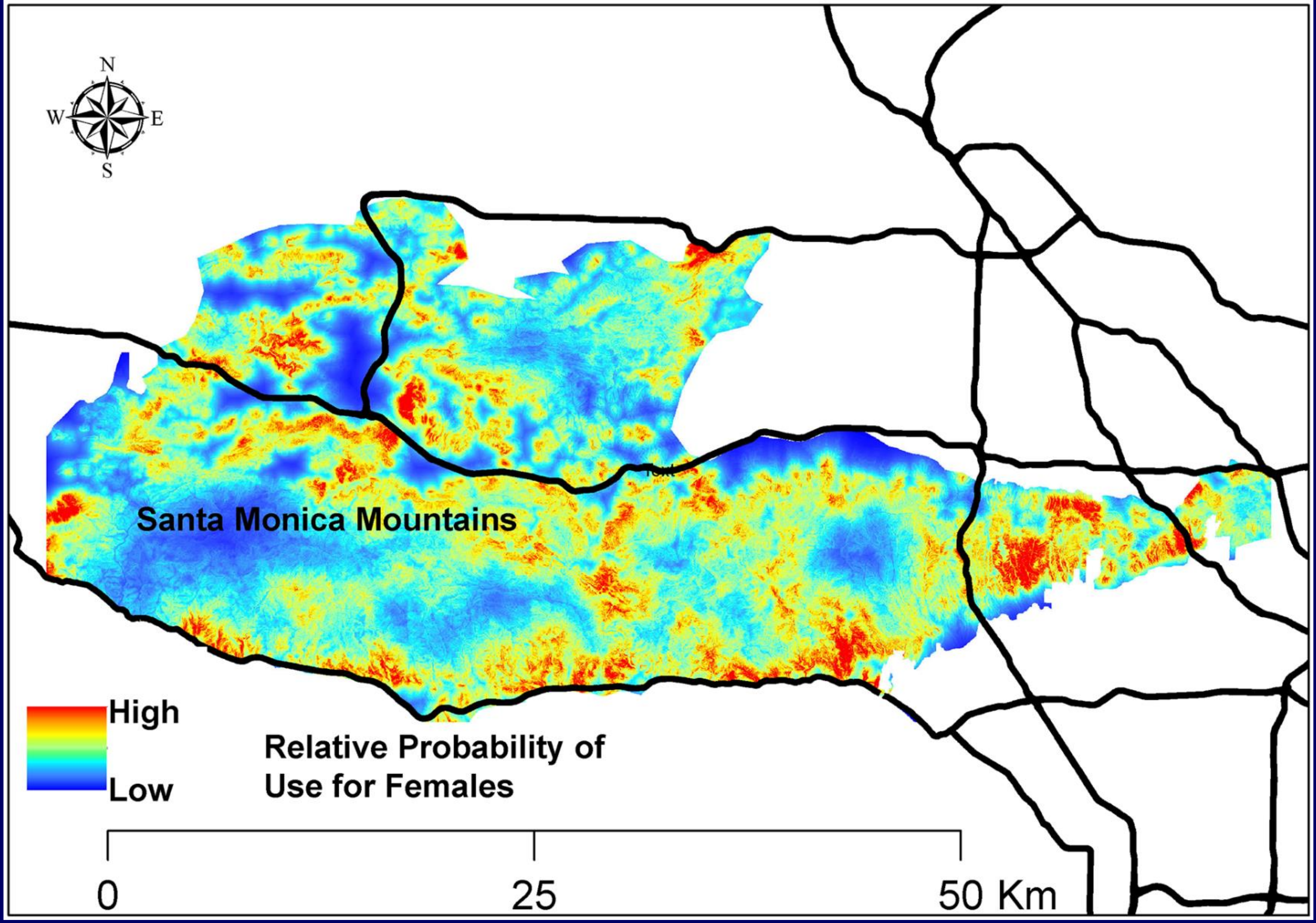
Relative Probability of Use

- Generate “heat” maps to predict areas that animals are likely to use
- These maps can then be used as layers for future models
- These can be done in ArcGIS or in R

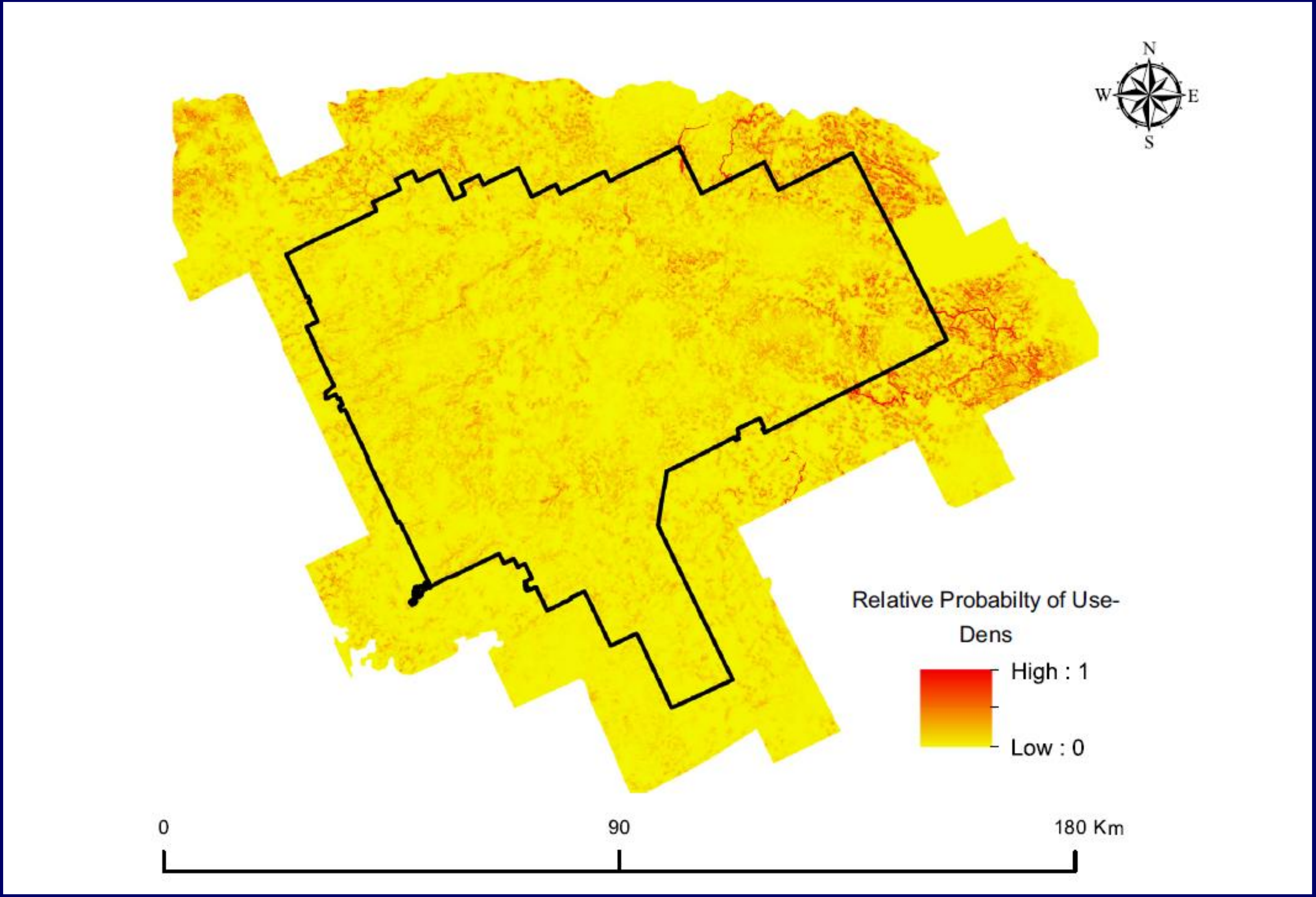
Deer Kill Sites of Mountain Lions



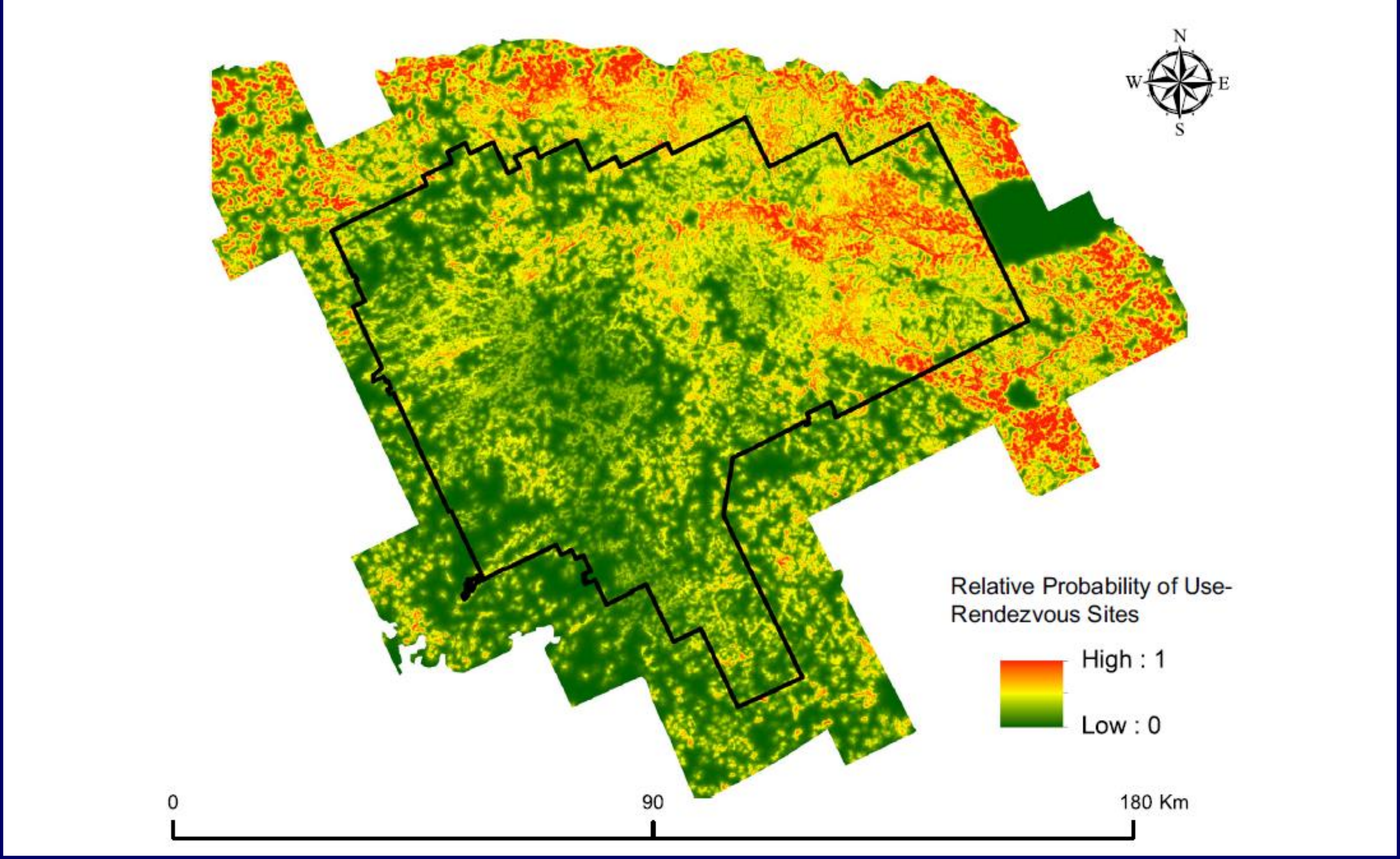
Deer Kill Sites of Mountain Lions



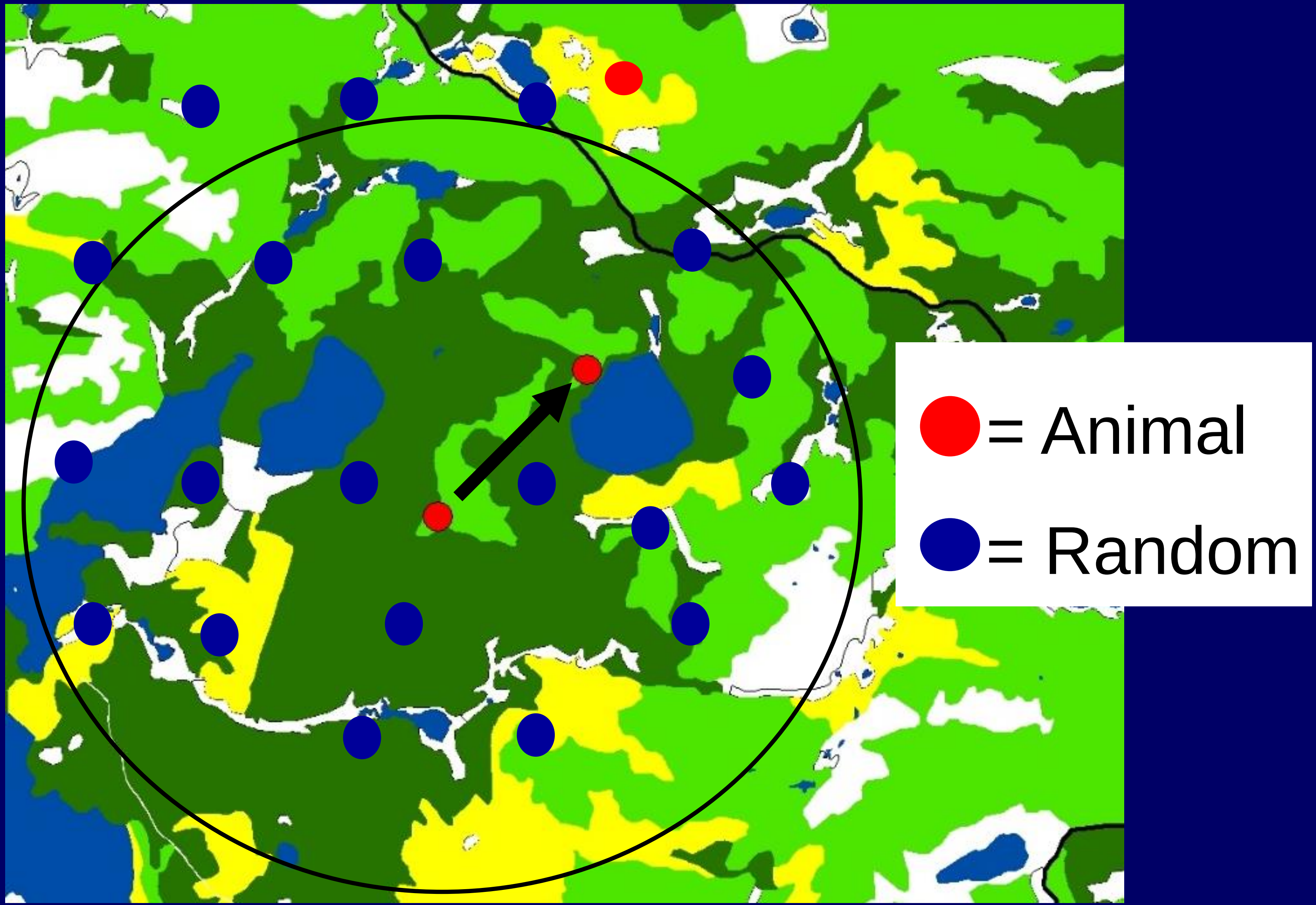
Den Sites of Wolves



Rendezvous Sites of Wolves



Step Selection RSF



Simple, but Quirky Models

- RSFs are being published at a crazy rate
- Lots of mistakes being made
- Lack of basic understanding of regression
  - e.g., reference categories
- Failure to properly apply hierarchical habitat selection
- Failure to appreciate importance of availability

2. Theoretical Distributions

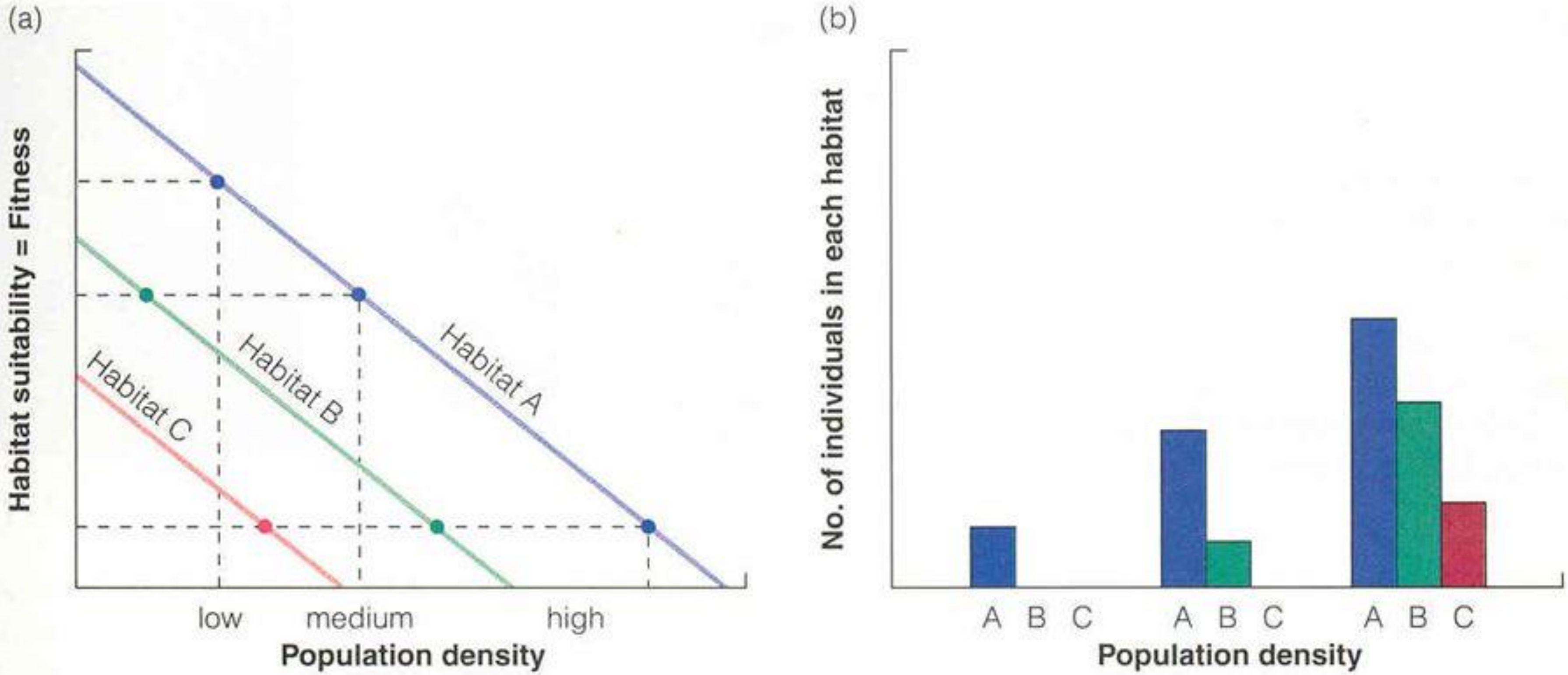
a. Ideal free
b. Ideal despotic
   – Ideal pre-emptive

Ideal Free Distribution

Fretwell & Lucas 1970

- Predicts how animals distribute themselves to achieve the greatest fitness
- Number of individuals in each patch is proportional to amount of resources in each
- Thus, if 2x as many resources in patch A as patch B there will be 2x number of individuals
- Individuals select habitat by balancing quality-density to maximize fitness

Ideal Free Distribution Model Of Habitat Selection



At very high densities, all habitats have equal suitability.

Assumptions

1. Animals have complete & accurate knowledge of distribution of resources (ideal)
2. Free to move to the highest quality site (free)
3. All individuals are competitively equal
4. Best sites are occupied first

- As best sites fill up, animals begin to select sites with *fewer resources but less competition*
- **Best sites support most animals, but individuals achieve = fitness in different habitats**

Other Distributions

- **Ideal despotic distribution** (IDD): best competitors monopolize best resources
  - Departure from key assumption of IDF that all competitors are equally matched
- Individuals settle in the best areas first and exclude others (e.g., via territoriality)
- Still ‘ideal’ as animals have complete knowledge
- But not ‘free’ as restrictions on best patches
- ➢ Large differences in fitness b/t haves & have nots

Empirical Support?

- Support has been found for both IFD and IDD
- Assumptions of IFD usually do not hold
- Like a lot of theories (e.g, marginal value) IFD valuable for testing predictions & learning
- What is practical implication of IFD?
- That density is a good indication of habitat quality