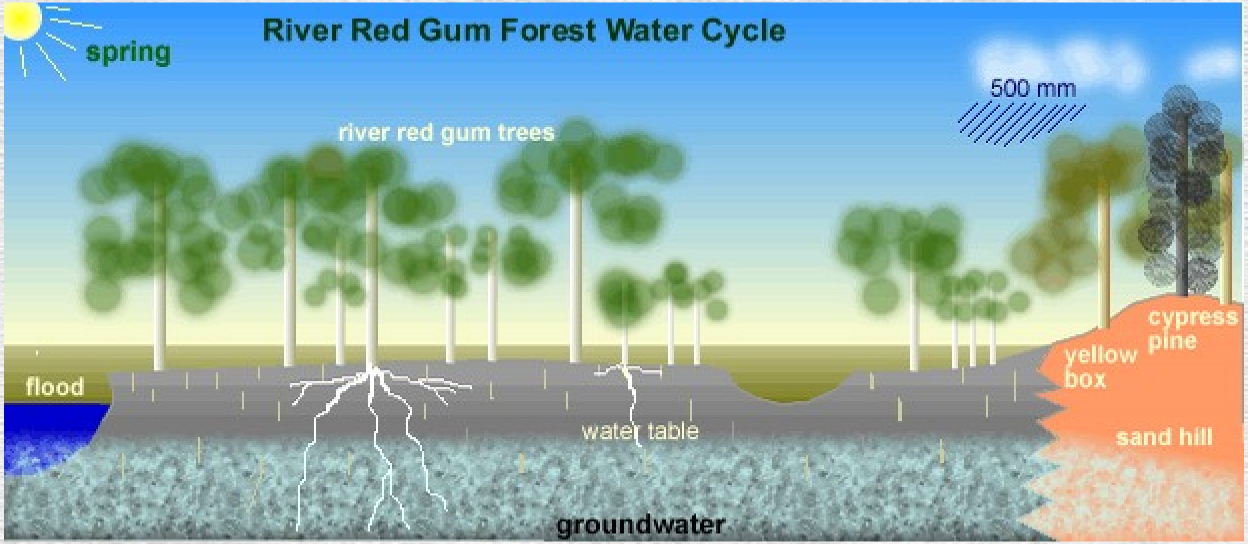
Survival estimation

Survival probability

- Probability of surviving from one time point to another
- At a population level, this can be number alive next year divided by number alive this year
- At an individual level, this is an expression of an individual's chances of still being alive next year

Estimating survival without marking

- If you can age individuals when caught, can use ratios of successive ages as your estimate
  - e.g. # three year olds/# two year olds
- Advantages:
  - Marking not needed
  - Can get age-specific survival estimates from a single year of sampling
- Disadvantage: confounds variation over time in survival with age-specific survival
  - Harsh conditions often affect the young more than the mature individuals
  - Bad conditions one year may reduce the survival of the young of that year, make survival at whatever age they are when you measure look low


River Red Gum Forest Water Cycle
spring
500 mm
river red gum trees
cypress pine
yellow box
flood
water table
sand hill
groundwater

Known fates

- Survival probability is simplest when the fate of every marked individual is known
  - Mark and release some individuals
  - Count how many are still alive next year
  - # alive next year / number caught and released is the survival probability
- Only need batch marks – don't need to be able to individually identify recaptures
- To be known fate, need to be able to positively document each individual's status (alive or dead) in the recapture
- When do you get this?




Encounter probability not usually 1

- Encounter probability is rarely 1 – some live individuals will be missed
- Some of the decline in number observed during recapture is due to live individuals that weren’t detected
- If we still use (recap)/(released), we call it “apparent survival” - biased (low) estimate of survival probability
- Apparent survival sometimes enough
  - Provided you can assume encounter probability is the same, even if you don’t know what it is
  - Comparison between sites, times
- But, we need an accurate estimate if we are going to estimate population growth – biased low by some unknown amount not good enough

The solution – capture histories and likelihood

- Can estimate survival probability with encounter probabilities using open population methods
- Based on capture histories of individually-marked organisms
  - Same kind of data as we used to estimate population size
  - Now re-captures are spaced further apart – usually 1 yr
- No longer assume demographic closure – mortalities occur
- Only work with marked animals
  - Set of individuals captured and marked at t = 0
  - Histories can be 111, 101, 110, 100
- Now we will have probabilities of survival for the time elapsed *between* captures, and encounter probabilities for the capture events

Simplest three year history is 111

$$
\begin{array}{ccccc}
t_0 & & t_1 & & t_2 \\
1 & \longrightarrow & 1 & \longrightarrow & 1 \\
 & \Phi & p & \Phi & p
\end{array}
$$

Model Φp

Model assumes equal survival probability each year (Φ)

Also assumes equal encounter probability each year (p)

Probability of this history is ΦpΦp

Missed the second year (101)

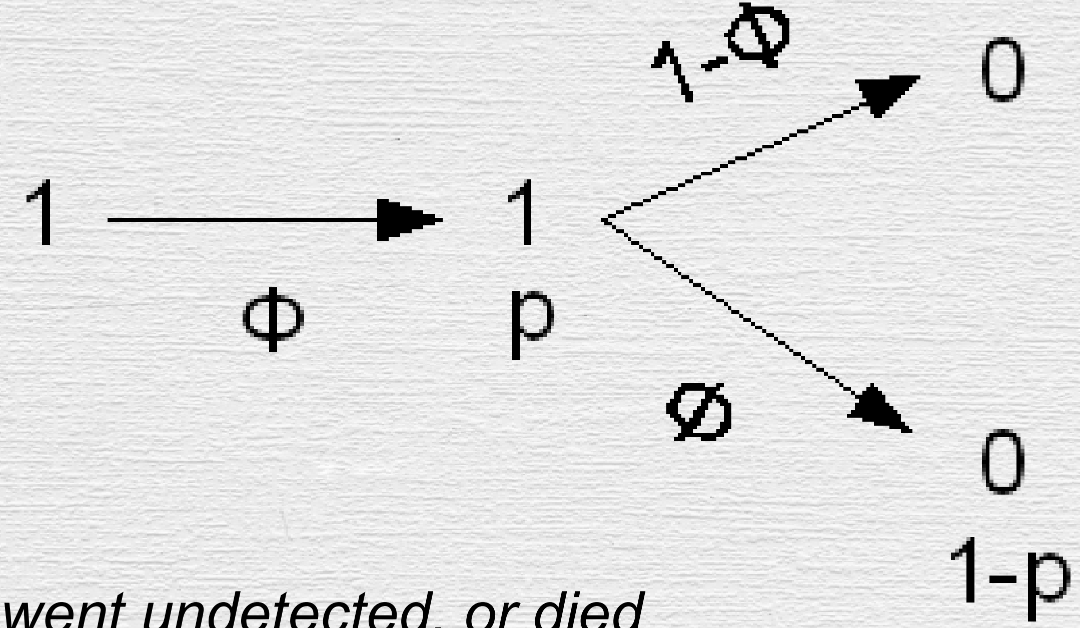
$$\begin{array}{ccccc} 1 & \longrightarrow & 0 & \longrightarrow & 1 \\ & \Phi & 1-p & \Phi & p \end{array}$$

Probability of a miss is 1-p

We don't need to account for the possibility that the animal died (why?)

Probability of this history is $\Phi(1-p)\Phi p$

Missed the third year (110) – trailing zeros are ambiguous

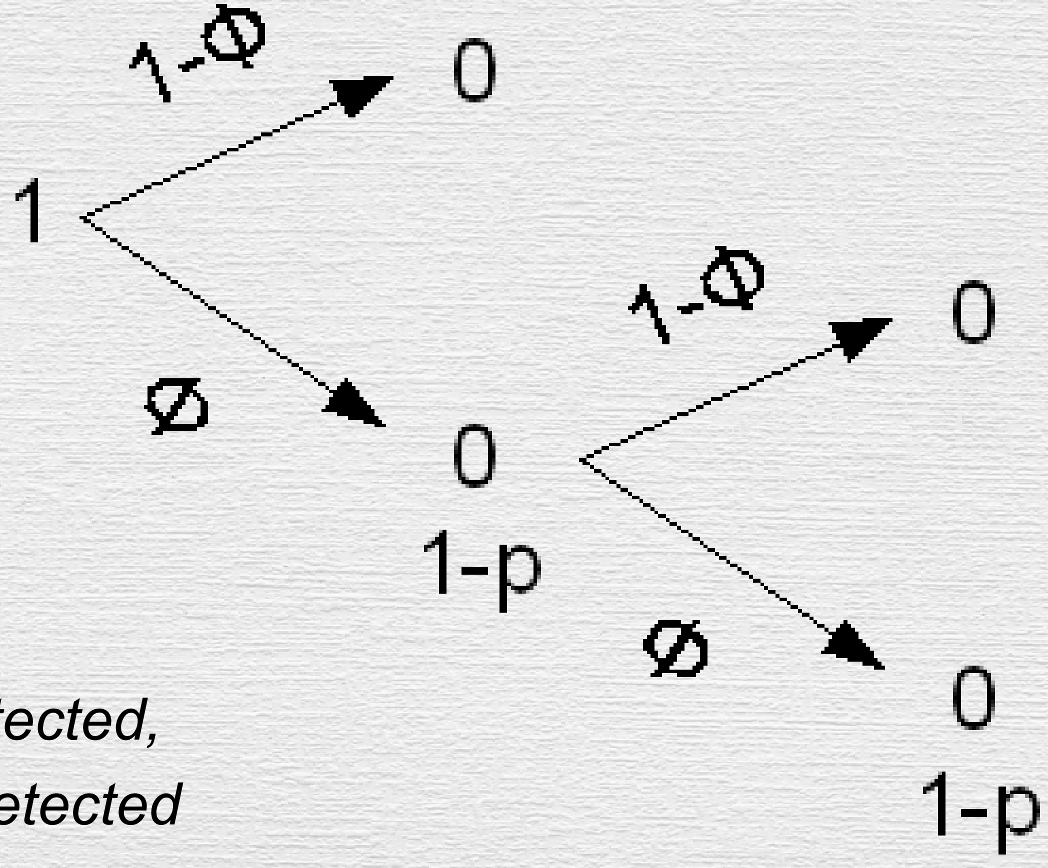


Either: lived and went undetected, or died

Probability of this history is sum of probabilities of the two paths:

$\Phi p(1-\Phi) + \Phi p \Phi(1-p) = \Phi p[(1-\Phi) + \Phi(1-p)]$

Not seen after first capture (100)



Either:

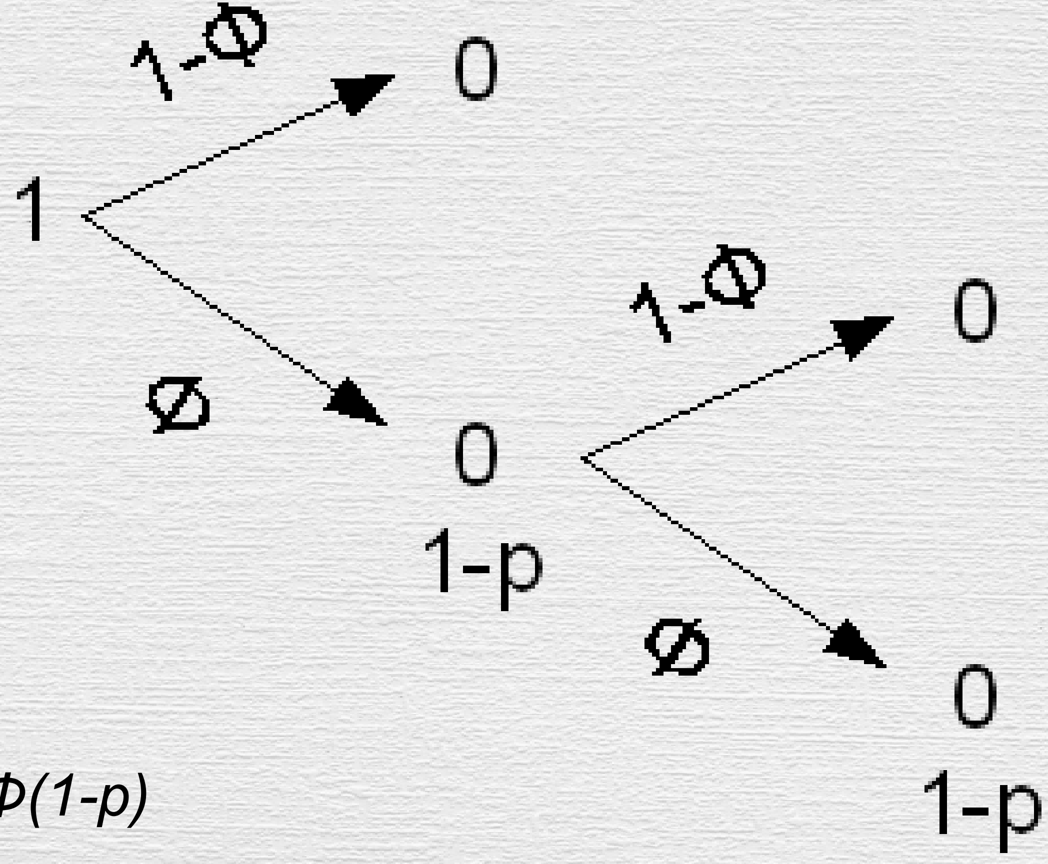
Died after first capture

Lived to second year, went undetected, and died before third year

Lived to second year, went undetected,

then lived to third year, went undetected

Not seen after first capture (100)



Probability of this history:

$(1-\Phi) + \Phi(1-p)(1-\Phi) + \Phi(1-p)\Phi(1-p)$

Maximum likelihood estimates of parameters

- You know the drill...
  - Tabulate frequencies of each history (111, 101, 110, 100)
  - Use the multinomial likelihood
  - Model the probabilities of each history using Φ and p
  - Find the values of Φ and p that maximize the log-likelihood
- Likelihood function is simpler – don't need the multinomial coefficient (counting part)

The likelihood for survival estimation

$$\ln\left(\left(M_{t+1}+x_{00}\right)!\right)-\ln\left(x_{00}!\right)+\sum \ln x_i\, p_i$$

No p's or Φ's

p's and Φ's are in here

So, this is all we need → $\sum \ln x_i\, p_i$

Example

Histories	Freq		Parameter	MLE	Betas		Multinomial probability of history	
111	29		phi	0.600	0.201		0.058	
101	43						0.086	
110	91		p	0.400	-0.201		0.182	
100	337						0.674	
Total caught	500					Sum	1	
							LnLikelihood	
							-476.2	

Multinomial probabilities:

111 = ΦpΦp = 0.6 • 0.4 • 0.6 • 0.4 = 0.058

101 = Φ(1-p)Φp = 0.6(1-0.4)0.6 • 0.4 = 0.086

110 = Φp[(1- Φ) + Φ(1-p)] = 0.6 • 0.4[(1-0.6) + 0.6(1-0.4)] = 0.182

100 = (1-Φ) + Φ(1-p)(1- Φ) + $Φ^2(1-p)^2$ =

(1-0.6) + 0.6(1-0.4)(1-0.6) + $0.6^2(1-0.4)^2$ = 0.674

Assumptions

- Geographic closure:
  - Immigration isn't a problem, only using marked individuals
  - No permanent emigration – live animals that can’t be captured
- Every marked individual has an equal probability of being captured at each time period (no trap response)
- Every marked individual has an equal probability of surviving from one time to the next
- Marks are not lost, gained, overlooked, incorrectly recorded, etc.
- No emigration, or only permanent emigration
- Independent fates

More elaborate models

- You knew this was coming...
- We are currently modeling the capture data with a single survival probability during year 1 and year 2 – reasonable?
- We are currently modeling the capture data with a single encounter probability for capture 2 and capture 3 – reasonable?

Making survival time-dependent
Model $\Phi_t p$

Hist.	Φp	$\Phi_t p$
111	$\Phi p \Phi p$	$\Phi_1 p \Phi_2 p$
101	$\Phi(1-p)\Phi p$	$\Phi_1(1-p)\Phi_2 p$
110	$\Phi p[(1-\Phi) + \Phi(1-p)]$	$\Phi_1 p[(1-\Phi_2) + \Phi_2(1-p)]$
100	$(1-\Phi) + \Phi(1-p)(1-\Phi) + \Phi(1-p)\Phi(1-p)$	$(1-\Phi_1) + \Phi_1(1-p)(1-\Phi_2) + \Phi_1(1-p)\Phi_2(1-p)$

Time-dependent encounter probability

Model Φp_t

History	Φp	Φp_t
111	$\Phi p \Phi p$	$\Phi p_1 \Phi p_2$
101	$\Phi(1-p)\Phi p$	$\Phi(1-p_1)\Phi p_2$
110	$\Phi p[(1-\Phi) + \Phi(1-p)]$	$\Phi p_1[(1-\Phi) + \Phi(1-p_2)]$
100	$(1-\Phi) + \Phi(1-p)(1-\Phi) + \Phi(1-p)\Phi(1-p)$	$(1-\Phi) + \Phi(1-p_1)(1-\Phi) + \Phi(1-p_1)\Phi(1-p_2)$

Time-dependent survival and encounter

Model $\Phi_t p_t$

History	Φp	$\Phi_t p_t$
111	$\Phi p \Phi p$	$\Phi_1 p_1 \Phi_2 p_2$
101	$\Phi(1-p)\Phi p$	$\Phi_1(1-p_1)\Phi_2 p_2$
110	$\Phi p[(1-\Phi) + \Phi(1-p)]$	$\Phi_1 p_1[(1-\Phi_2) + \Phi_2(1-p_2)]$
100	$(1-\Phi) + \Phi(1-p)(1-\Phi) + \Phi(1-p)\Phi(1-p)$	$(1-\Phi_1) + \Phi_1(1-p_1)(1-\Phi_2) + \Phi_1(1-p_1)\Phi_2(1-p_2)$

Problem: with 4 histories we have 4-1 = 3 df, but there are now 4 parameters.

With more parameters than df we don't get unique solutions – need more df to fit this model

Increasing df

- We can add years
  - With four years the histories are 1111, 1110, 1101, 1011, 1100, 1010, 1001, 1000, which gives us 8-1 = 7 df, enough to fit $\Phi_t p_t$
- We can catch new individuals at second capture
  - 011, 010, 001
  - We would not model the first 0, start the probabilities at first capture
  - df would be 4+3 – 1 = 6, also enough for $\Phi_t p_t$

Complications

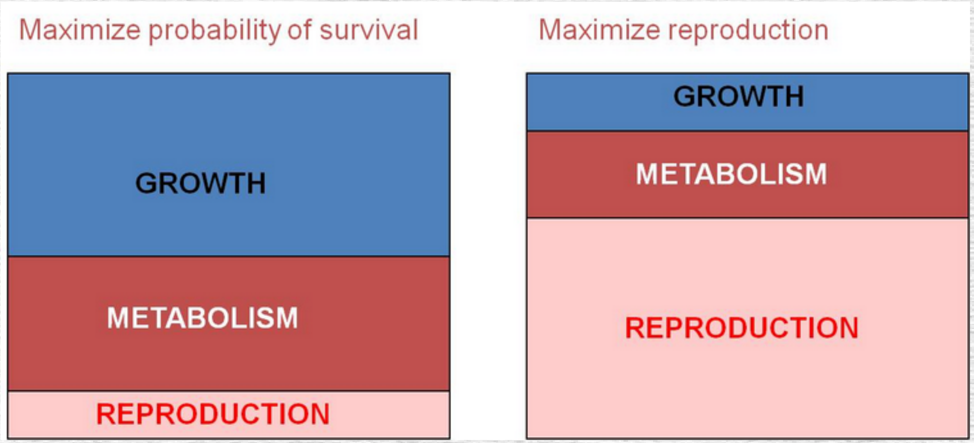
- Encounter probability and survival for more complex models can be confounded, impossible to estimate independently
- More years of trapping helps
- A small number of years means accepting simpler models

Extensions

- Covariates
  - Class covariates (male/female, habitat type)
  - Individual covariates (body mass, home range size, percent cover of trees, reproductive rate)
- Different designs
  - “Robust” design = short intervals between captures within a year to measure p, which is then used to estimate Φ between years
  - Censoring = eliminating animals that are removed from the study
- Applications in other fields, such as evolutionary biology

Trade-offs

- Life history evolution often assumes a “zero sum game”
  - A fixed amount of resources available
  - Organism has to decide whether to devote resources to survival or reproduction
  - Implies physiological constraints
- Evolutionarily speaking, we expect trade-offs between different components of fitness



Ecologically, we aren't working with a zero sum game

- Habitats vary in quality
- Different aspects of habitat may affect survival and reproduction differently
  - The best habitat for reproduction may also be the best for adult survival
  - The best habitat for reproduction may be the worst for adult survival
- Whether there is a trade-off or not ecologially depends on the effects of habitat on fitness
- We want to use the fitness of individuals using the habitat as our measure of habitat quality = habitat “fitness potential”

How to study this: individual covariates of survival

- Alan Franklin and colleagues' work on Spotted Owls
- Examined how the amount of old-growth forest within owl territories affected survival
- Used this along with measures of reproduction within territories to estimate habitat fitness potential for territories with different characteristics

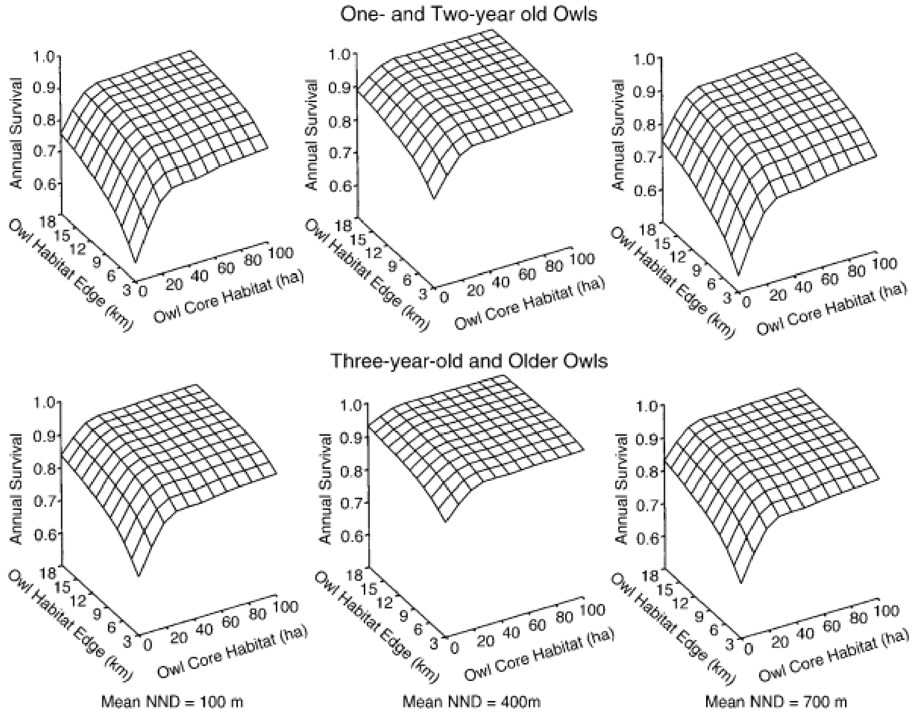


FIG. 6. Annual apparent survival (ϕ) of 1- and 2-yr-old and ≥3-yr-old Northern Spotted Owls in relation to the amount of core habitat, edge between spotted owl and other habitats, and nearest neighbor distance (NND) between patches of spotted owl habitat on territories in northwestern California. Estimates of apparent survival are based on model $\{\phi_{a2'+LSOCOR+LSOEDG+SODIS+(SODIS)^2}, p_{c+ELEV}\}$.

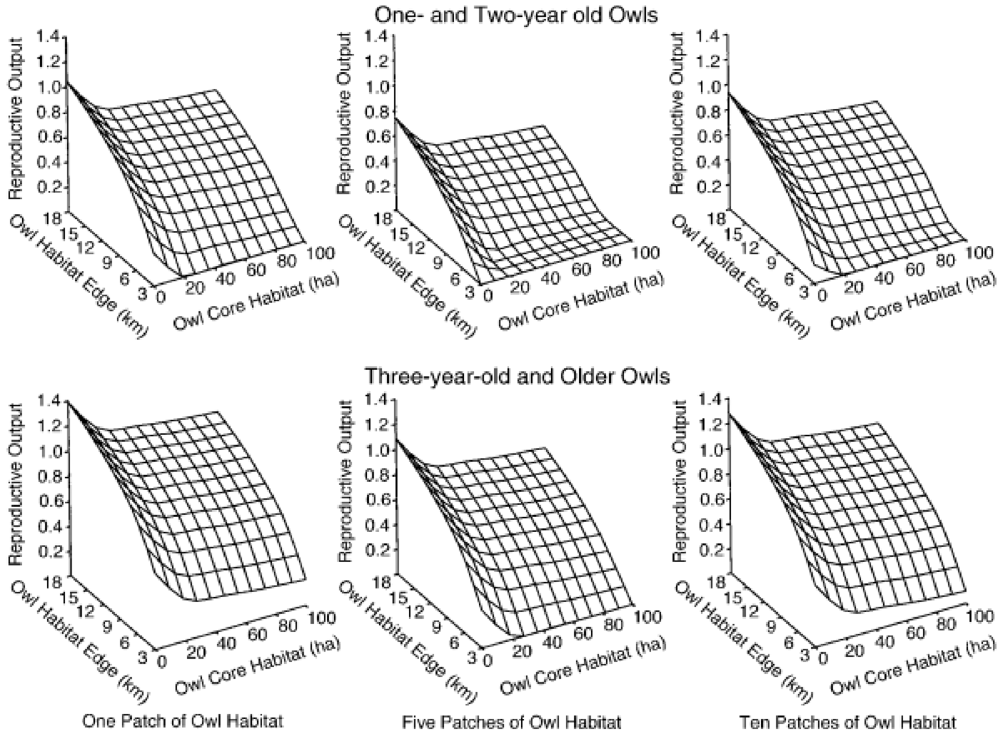


FIG. 7. Reproductive output (R) of 1- and 2-yr-old and ≥3-yr-old Northern Spotted Owls in relation to amount of core spotted owl habitat, edge between spotted owl and other habitats, and number of patches of spotted owl habitat on territories in northwestern California. Estimates of reproductive output are from model $\{R_{a2'+LSOCOR+LSOEDG+SONP+(SONP)^2}\}$.

The best habitat for survival has high levels of core habitat, low edge

Best habitat for reprduction has low core habitat, lots of edge – why? That's where the woodrats are

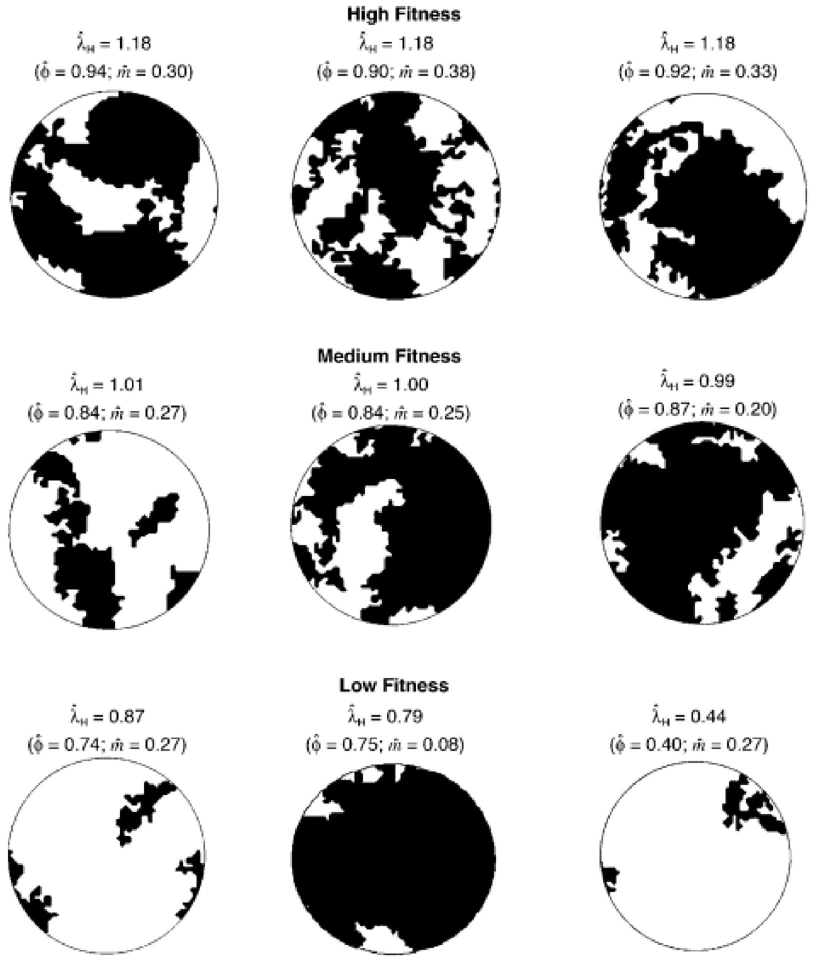


FIG. 10. Landscape habitat characteristics (within 0.71 km radius circles used to define Northern Spotted Owl territories) at three levels of habitat fitness potential in northwestern California. Dark areas are Northern Spotted Owl habitat; white areas are other vegetation types. Estimates of ϕ (apparent survival) and m (fecundity) are for owls ≥ 3 yr old.

Homogeneity is not good, even if it's uniformly old growth