From biology to structured population models

EEE330 · Lecture 3

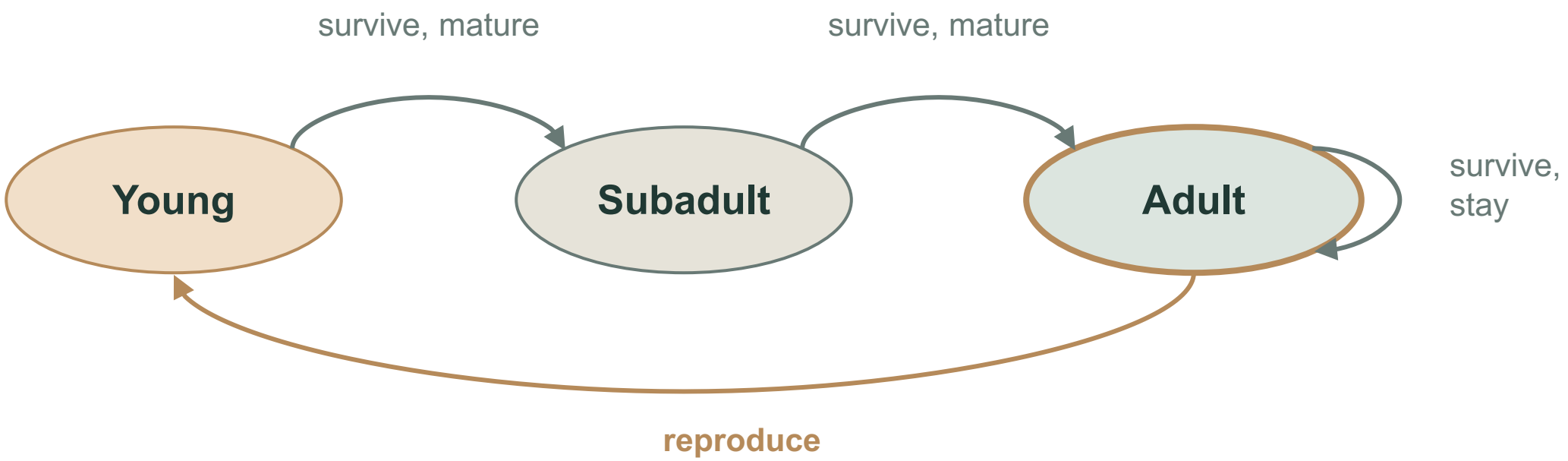
How do we turn a life cycle into a model of next year's population?



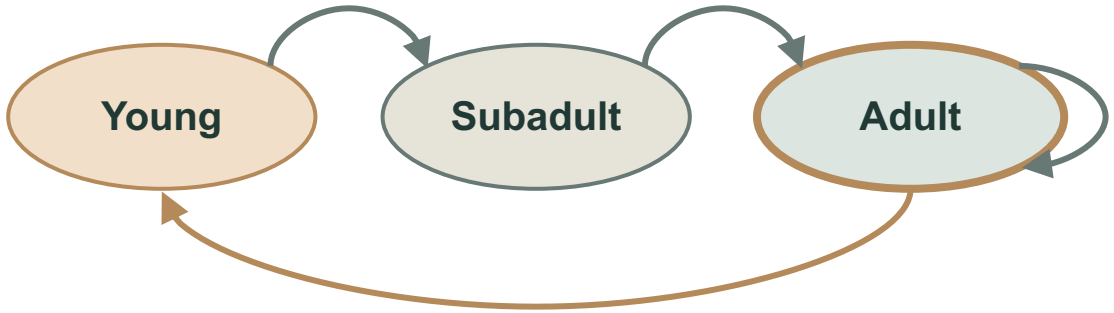
States need arrows

From Lecture 2: *Given these states, how do individuals survive, reproduce and move among them?*

Draw every way an individual can contribute to next year's census.



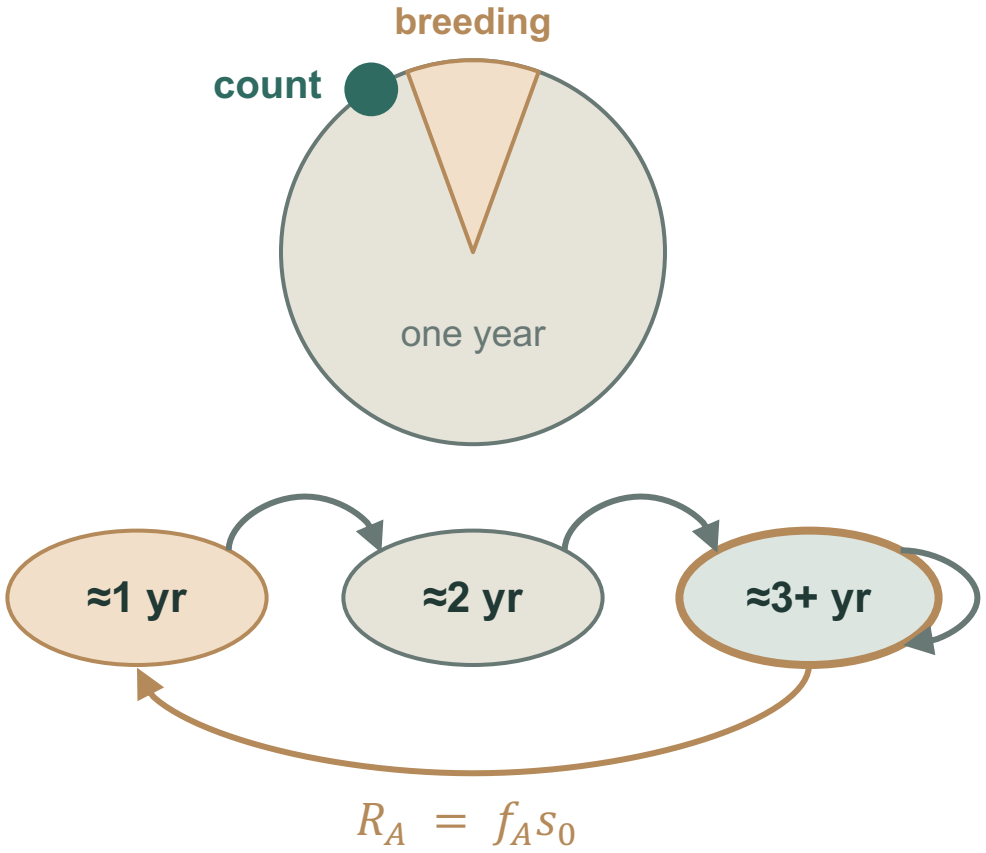
What an arrow means



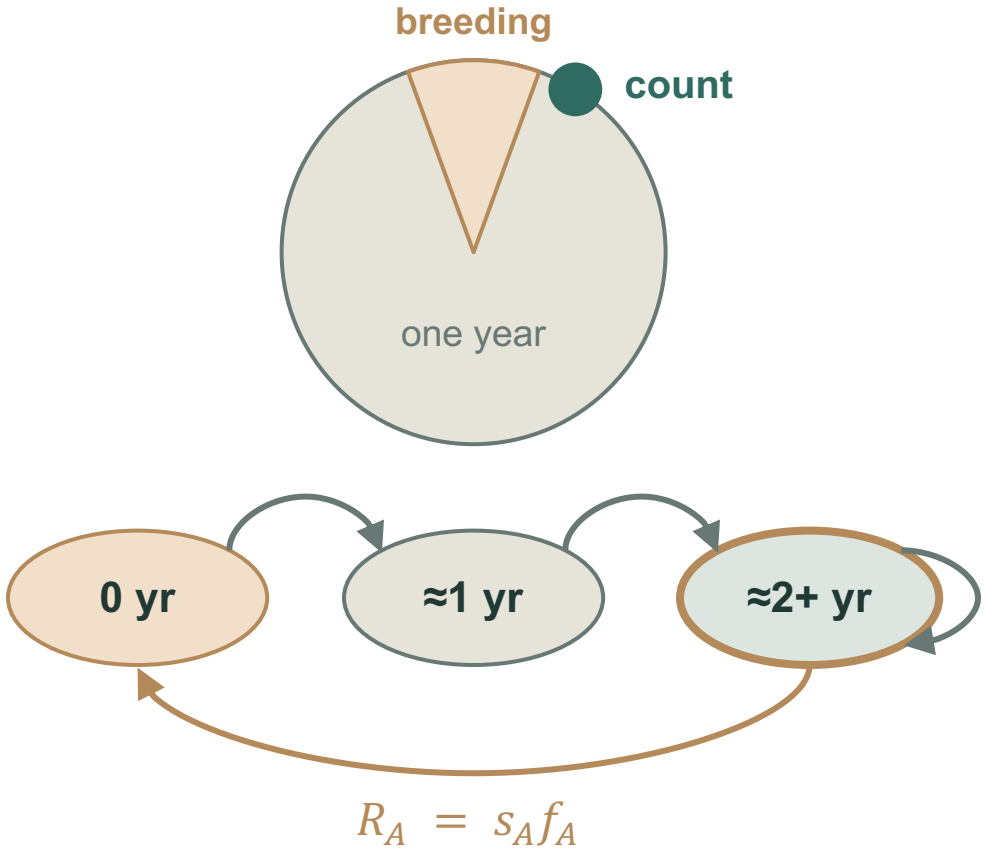
- A node is a state at the census.
- An arrow is the average contribution of one individual in that state to a state at the next census.
- Arrows for surviving individuals are probabilities: together at most 1.
- Arrows for reproduction count offspring: they can exceed 1.

When we count changes what the arrows mean

Pre-breeding census



Post-breeding census



Same number of states. The youngest is almost a year old before breeding, a few days old after.

Smurfs: a male-based model

Most demographic models follow females. We start with an exception.

Smurfs. Counted just before breeding. Live 4 years; none reaches age 5. Mature at age 4.









Draw the life cycle. Write each node's age.

Answer ›

Great tits





Great tits. Counted just before breeding. Breed from the end of their first year. Can live to 9, but data beyond age 5 are sparse: pool ages 5 and older.

Draw the life cycle.

Answer ›

Spotted owls: draw the life cycle



Northern spotted owls. Counted just after breeding, when this year's young have fledged. Females only.

- Young must survive their first year and disperse to find a territory.
- One-year-olds (subadults) do not breed.
- From age two, adults can breed every year and live for more than 15 years.

Draw the life cycle.

Answer ›

Teasel: draw the life cycle



Rosette



Flowering plant

Flowering plants produce seeds in late summer, then die. Seeds germinate into rosettes the next spring, or stay dormant in the soil. Rosettes grow, and eventually flower.

Draw the teasel life cycle, with one census each spring.

Answer ›



One arrow, one time step

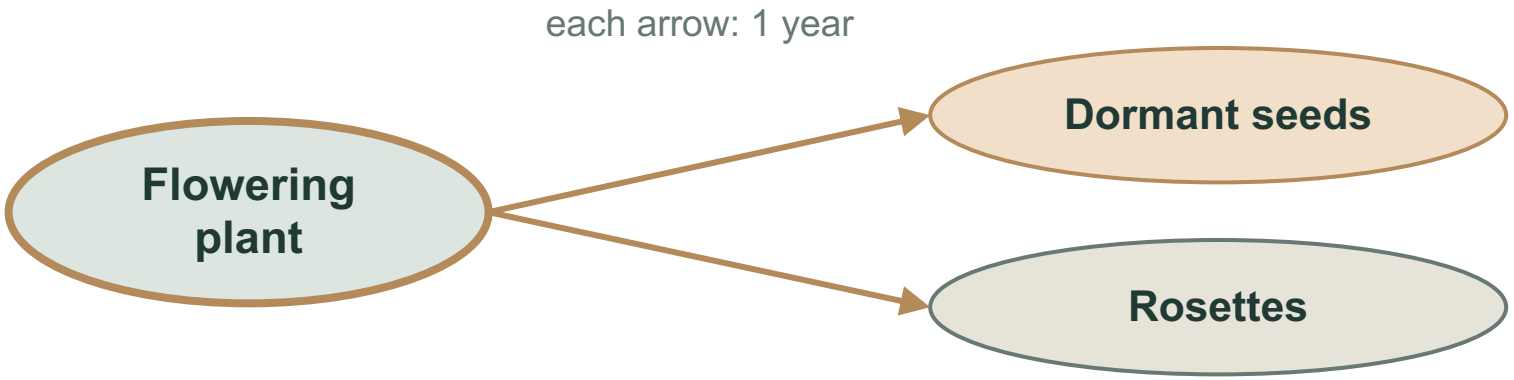
Flowering plants in summer produce seeds that germinate the next spring. What is wrong with this graph?

As first published



λ = 1.80

Corrected



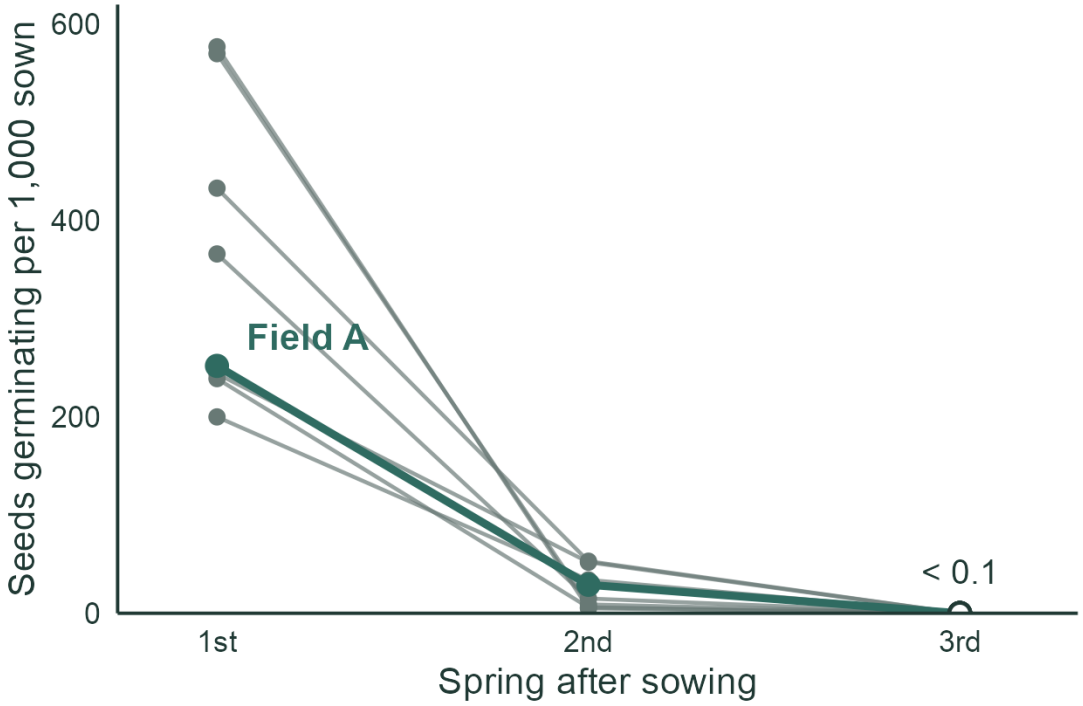
λ = 2.33

λ of the published Field A models: Caswell (1989), Example 4.1; data from Werner and Caswell (1977)

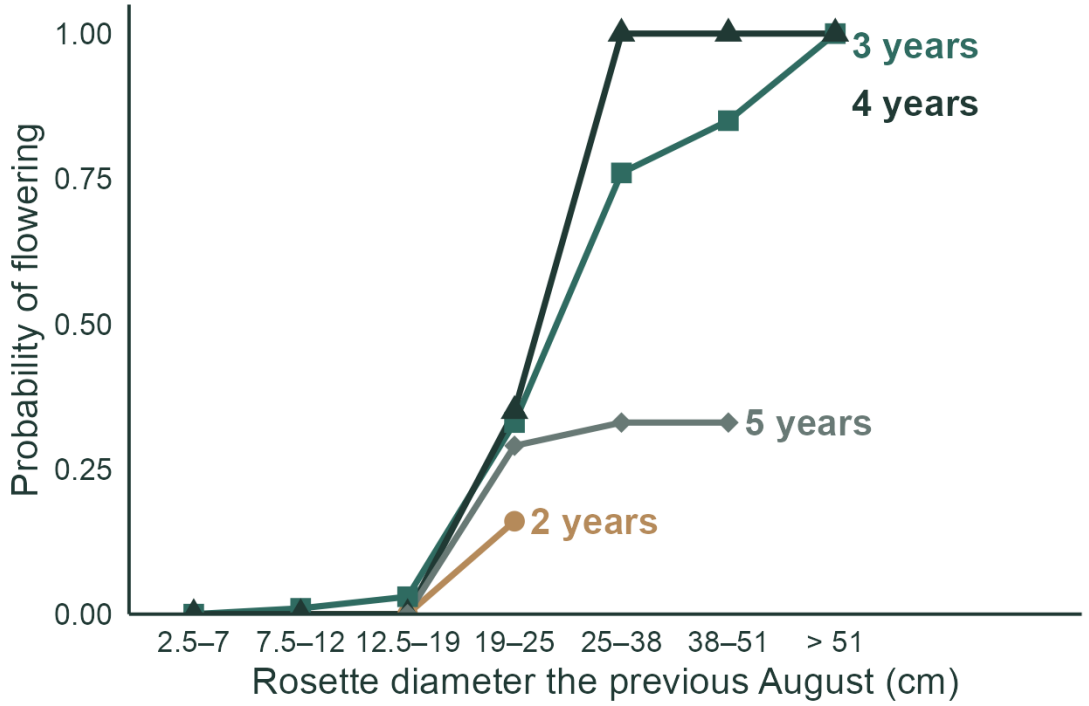


What the field data show

Seeds sown in eight fields, and rosettes of known age and size, were followed for years. When do seeds germinate? What predicts flowering?



Werner (1977), Ecology 58:840–849, Table 2

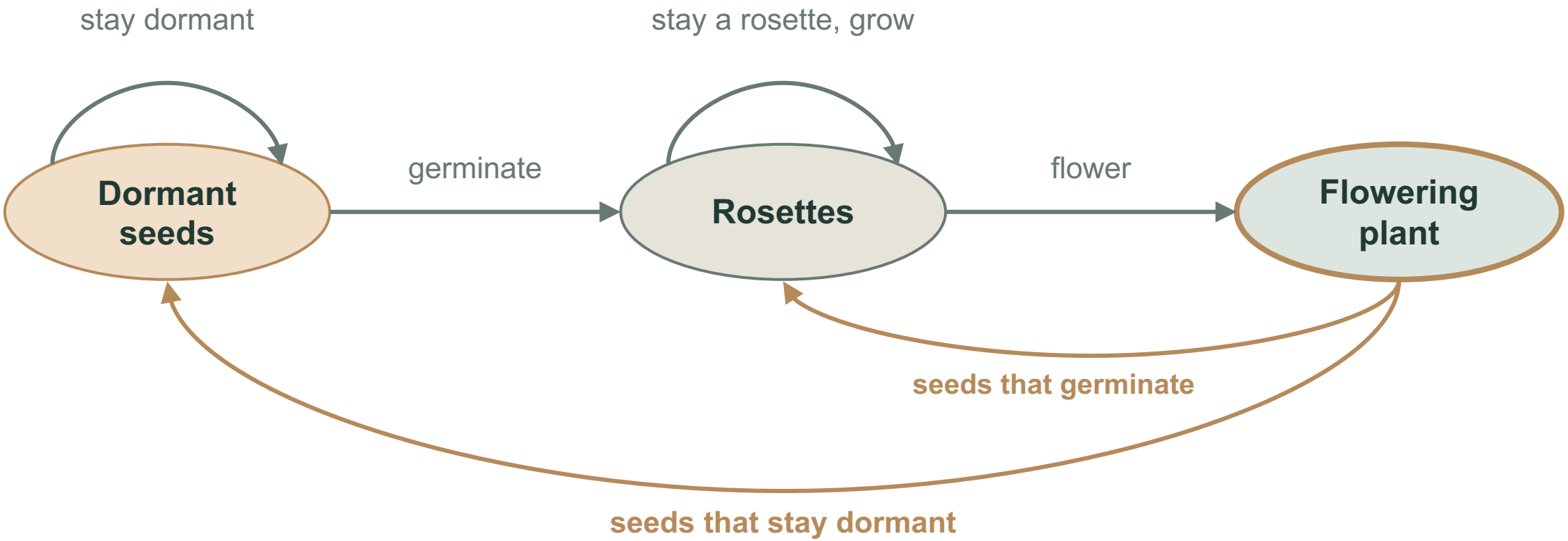


Werner (1975), Oecologia 20:197–201, Table 1



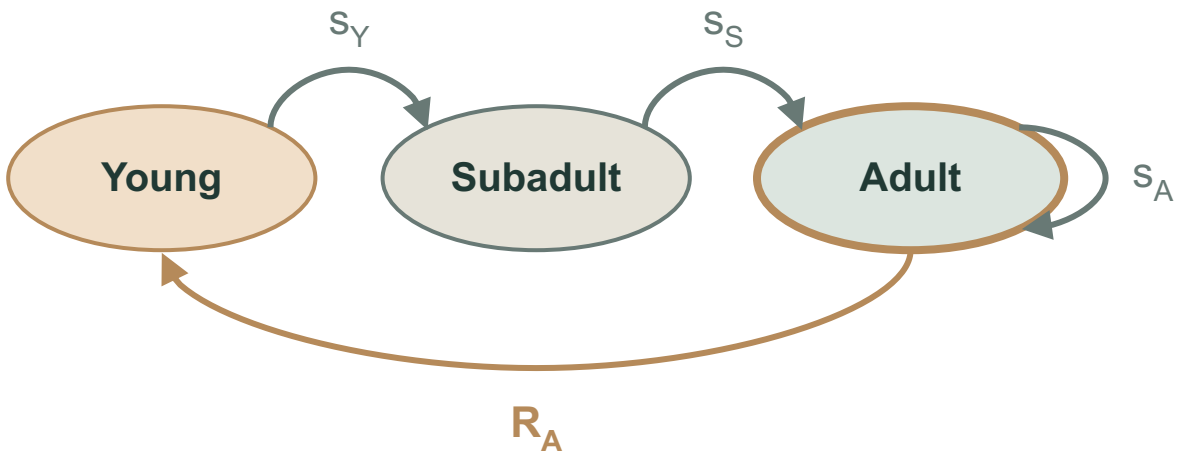
Teasel: change the life cycle

Seeds germinate in their first or second spring, never later. Flowering depends on size. How would you change the life cycle?



Answer ›

The matrix is the graph as a table



Column = **from** · Row = **to**

to ↓ from →	young	subadult	adult
young	0	0	R_A
subadult	s_Y	0	0
adult	0	s_S	s_A



Reading a real matrix

Find staying, growing, skipping and reproduction. Why can one entry be as large as 322?

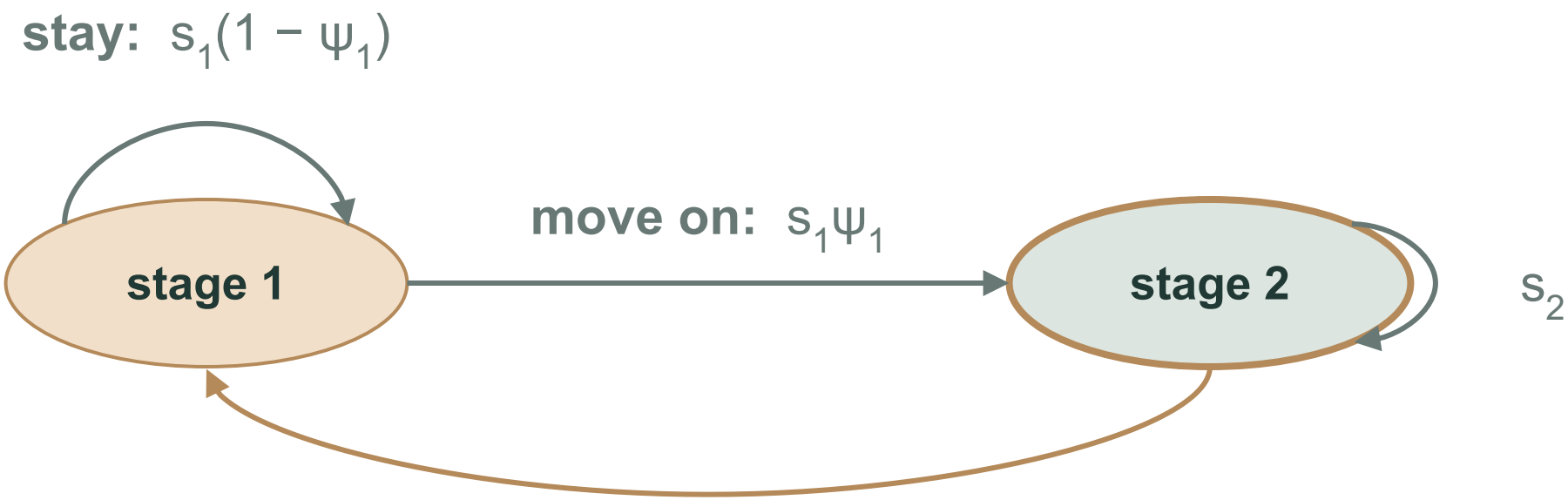
to ↓ from →	dormant 1	dormant 2	small	medium	large	flowering
dormant 1	0	0	0	0	0	**322.38**
dormant 2	0.966	0	0	0	0	0
small	0.013	0.010	**0.125**	0	0	**3.448**
medium	0.007	0	0.125	**0.238**	0	**30.17**
large	0.008	0	0.038	0.245	**0.167**	**0.862**
flowering	0	0	0	0.023	0.750	0

Teasel, Field A: Werner and Caswell (1977), Ecology; corrected matrix in Caswell (1989), p. 49

Staying medium → medium 0.238 **Growing** medium → large 0.245 **Skipping** dormant 1 → large 0.008

Reproduction flowering → dormant 1: 322 seeds per flowering plant, a count, not a probability

Entries are built from vital rates



counted before breeding: $R_2 = b_2 f_2 s_0$

counted after breeding: $R_2 = s_2 b_2 f_2$

s survival ψ move on, given survival b breed, given survival
f offspring per breeder s_0 offspring survival to the first count

Polar bears: draw the life cycle

- Counted each April, when mothers with cubs of the year leave the den. Females only.
- Young stay with their mother for two years and become independent at age 2.
- Females can first breed at age 5.
- A breeding female is accompanied first by cubs of the year, then by yearlings.
- A mother who loses her cubs of the year may breed again.



Draw the female life cycle. Which states do you need?

Answer ›

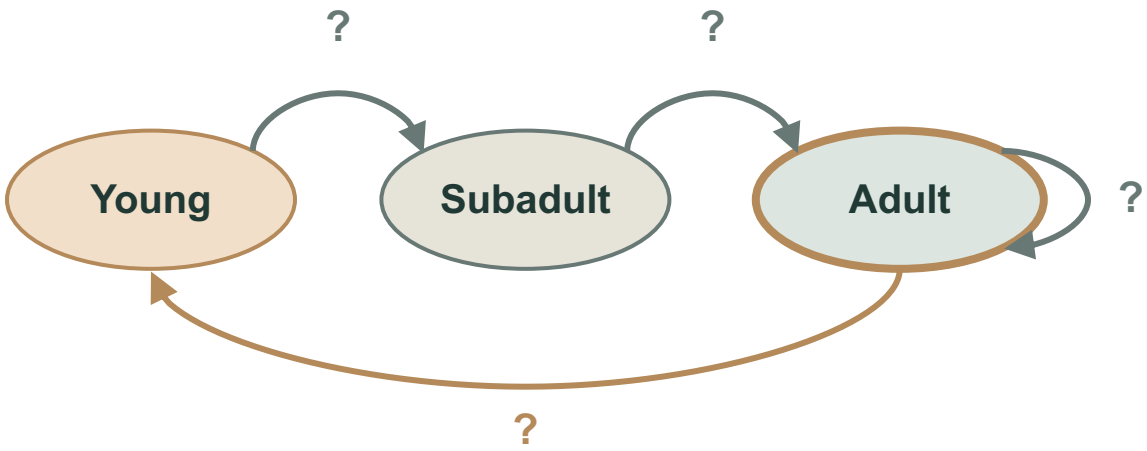
Spotted owls: estimating the arrows



Counted after breeding. Females only. Adults are banded.

	Young	Subadults	Adults
Year t	250	31	500
Year t + 1	113	27	493

Of the 493 adults in year t + 1, 471 were already adults in year t.



Estimate the arrows and write down the matrix.

Answer ›

What the model assumes

Which of these would fail first for the polar bear?

	Relaxed in
• Rates stay constant from year to year.	L06
• Rates do not depend on population size.	L07
• Females only, or males do not limit reproduction.	L08
• No immigration or emigration.	L09
• Rates are known without error.	L10
• All individuals in a state share the same rates.	beyond this course

From life cycles to matrices

What did we learn today?

- A life-cycle graph shows how each state contributes to each state at the next census.
- When we count decides what each state and each reproduction arrow contains.
- Every arrow spans exactly one time step.
- The matrix is the graph as a table: columns "from", rows "to".
- Entries are products of vital rates; states follow the biology that decides fate.

We have the owl matrix. How do we project the population forward?

Further reading



Climate change threatens polar bear populations: a stochastic demographic analysis

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Abstract. The polar bear (*Ursus maritimus*) depends on sea ice for feeding, breeding, and movement. Significant reductions in Arctic sea ice are forecast to continue because of climate warming. We evaluated the impacts of climate change on polar bears in the southern Beaufort Sea by means of a demographic analysis, combining deterministic, stochastic, environment-dependent matrix population models with forecasts of future sea ice conditions from IPCC general circulation models (GCMs). The matrix population models classified individuals by age and breeding status; mothers and dependent cubs were treated as units. Parameter estimates were obtained from a capture–recapture study conducted from 2001 to 2006. Candidate statistical models allowed vital rates to vary with time and as functions of a sea ice covariate. Model averaging was used to produce the vital rate estimates, and a parametric bootstrap procedure was used to quantify model selection and parameter estimation uncertainty. Deterministic models projected population growth in years with more extensive ice coverage (2001–2003) and population decline in years with less ice coverage (2004–2005). LTRE (life table response experiment) analysis showed that the reduction in 3 in years with low sea ice was due primarily to reduced adult female survival, and secondarily to reduced breeding. A stochastic model with two environmental states, good and poor sea ice conditions, projected a declining stochastic growth rate, $\log \lambda_S$, as the frequency of poor ice years increased. The observed frequency of poor ice years since 1979 would imply $\log \lambda_S \approx -0.01$, which agrees with available (albeit crude) observations of population size. The stochastic model was linked to a set of 10 GCMs compiled by the IPCC; the models were chosen for their ability to reproduce historical observations of sea ice and were forced with "business as usual" (A1B) greenhouse gas emissions. The resulting stochastic population projections showed drastic declines in the polar bear population by the end of the 21st century. These projections were instrumental in the decision to list the polar bear as a threatened species under the U.S. Endangered Species Act.

Key words: climate change; demography; IPCC; LTRE analysis; matrix population models; polar bear; sea ice; stochastic growth rate; stochastic models; Ursus maritimus.

INTRODUCTION

Climate change is projected to have significant effects on population dynamics, species distributions and interactions, food web structure, biodiversity, and ecosystem processes (Convey and Smith 2006, Parmesan 2006, Grosbois et al. 2008, Keith et al. 2008). The climate is changing faster in the Arctic than in other areas (Serreze and Francis 2006, Walsh 2008). For Arctic marine mammals, the most critical of these changes involve the sea ice environment (Laidre et al. 2008). The extent of perennial sea ice in the Arctic has been declining since 1979 at an average rate of 11.3% per decade (Stroeve et al. 2007, Perovich and Richter-Menge 2009). The summer minimum sea ice extent in 2005 set a new record, which was broken again in 2007; the ice extent in 2008 was the second lowest on record. This trend has led to concerns about Arctic species with strong associations with sea ice. The polar bear is one of the most ice-dependent of all Arctic marine mammals (Amstrup 2003, Laidre et al. 2008). As a top predator, it is also an important indicator of effects on the Arctic ecosystem (Boyd et al. 2006).

Arctic sea ice changes have been associated with negative effects on individuals and populations of polar bears (Stirling et al. 1999, Obbard et al. 2006, Regehr et al. 2006, 2009, Rode et al. 2010). Such observations alone, however, provide few insights into future impacts of climate, which can be assessed only by linking population growth models, environmental effects, and

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2883

ONE PAPER

Hunter et al. (2010), *Ecology*
Polar bears and sea ice: a life cycle built from vital rates.

Focus: Introduction, "Demographic model structure", deterministic results (pp. 2883–2888); Fig. 2 with Appendix A (the matrix in vital rates); Fig. 3.

Skip: the bootstrap, the LTRE, the stochastic model and the sea-ice forecasts.

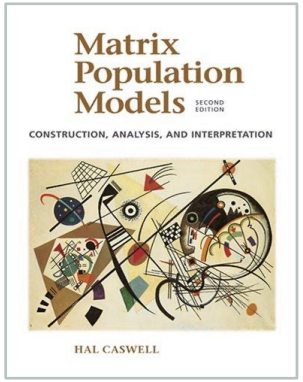
Later: the LTRE after L5; the stochastic model and Fig. 5 after L6.

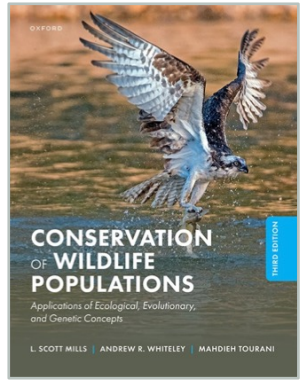
RESOURCES

Mills, Whiteley and Tourani (2025), Conservation of Wildlife Populations, Ch. 6: census timing and stage-structured projection.

Caswell (2001), Matrix Population Models, 2nd ed., Chapters 2–4: life cycles, graphs and matrices.

Kendall et al. (2019), Ecological Modelling: common errors in building matrix models.





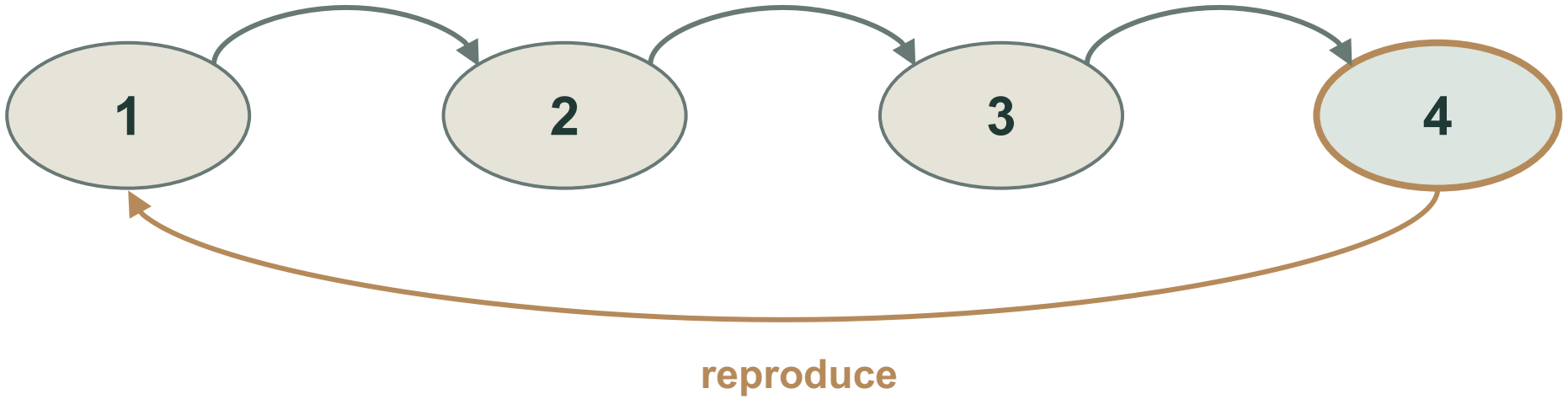
Answers

EEE330 · Lecture 3

Smurfs: a male-based model

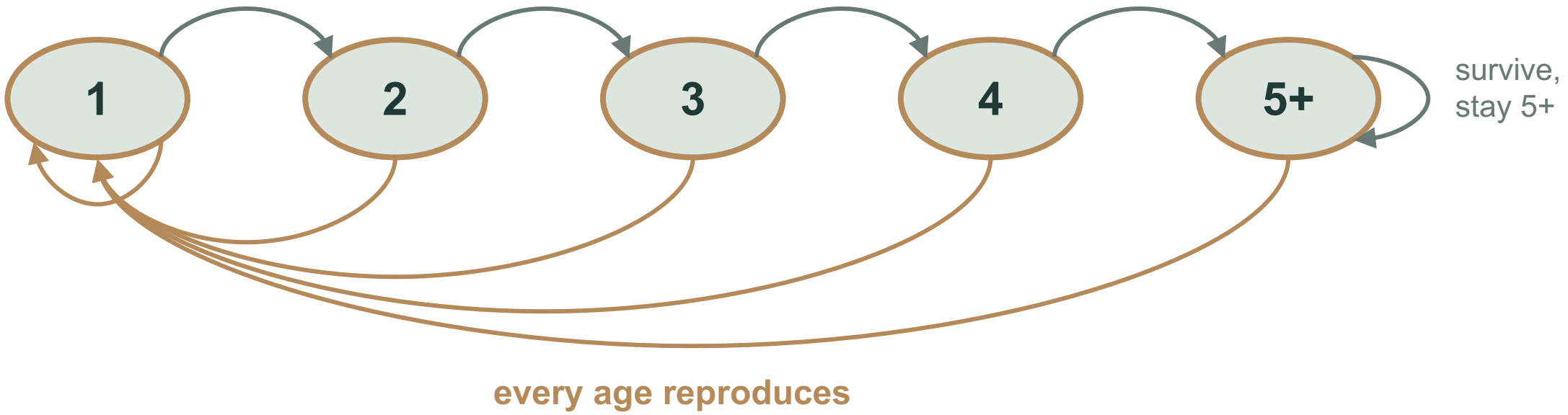




Great tits

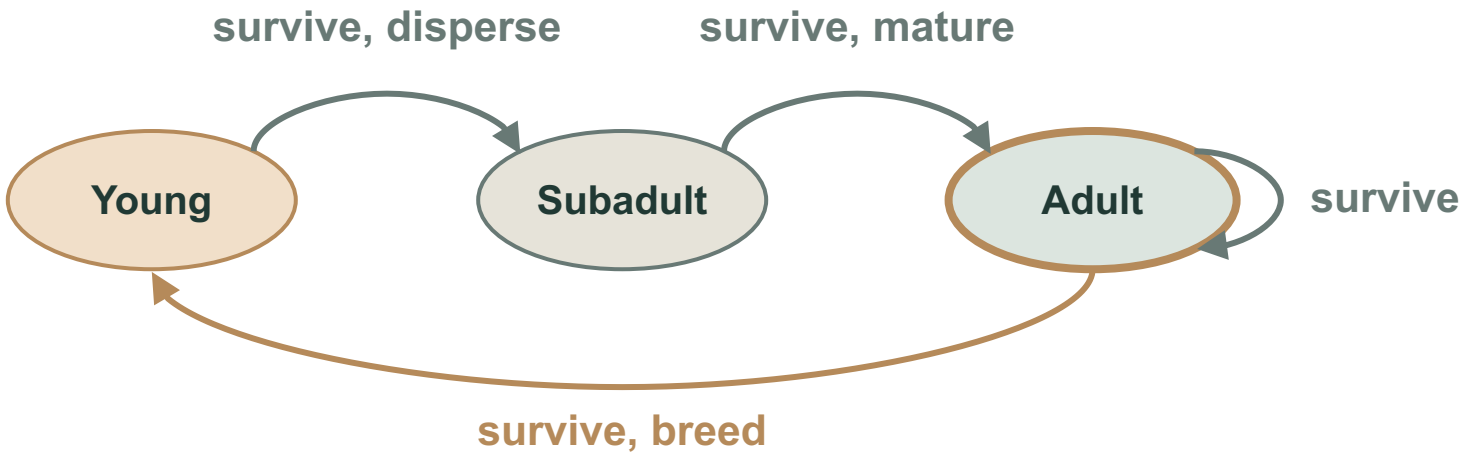




‹ Question

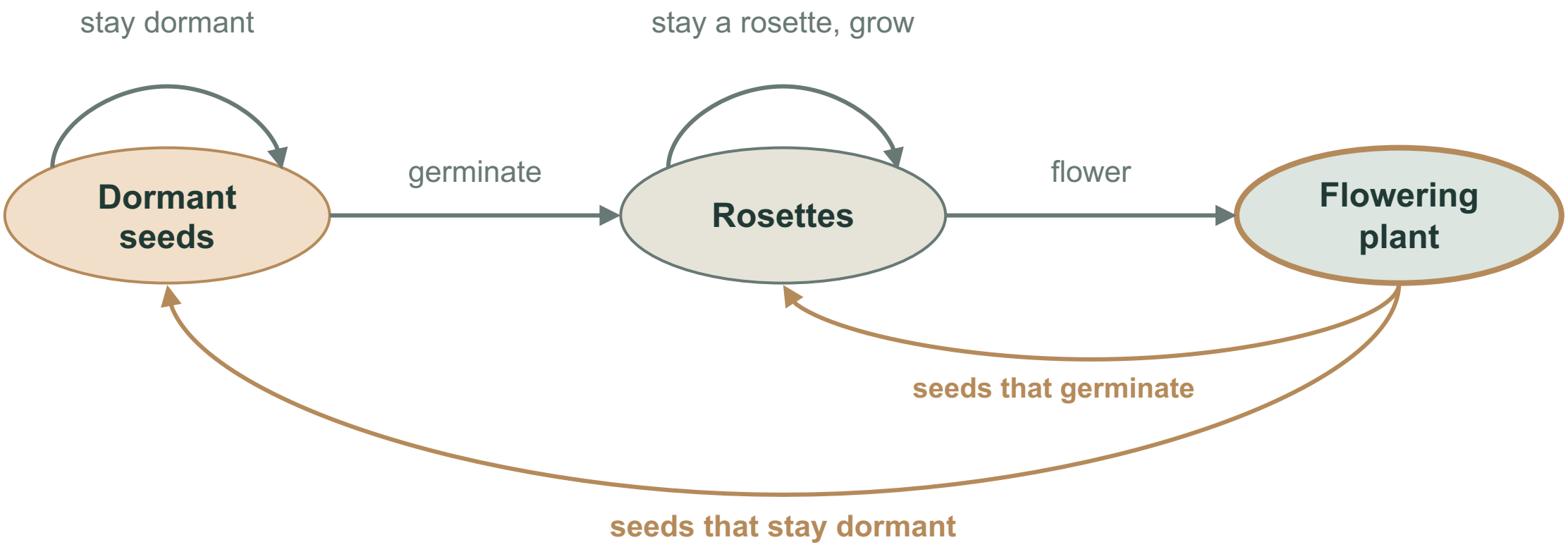
Spotted owls: draw the life cycle





Teasel: draw the life cycle

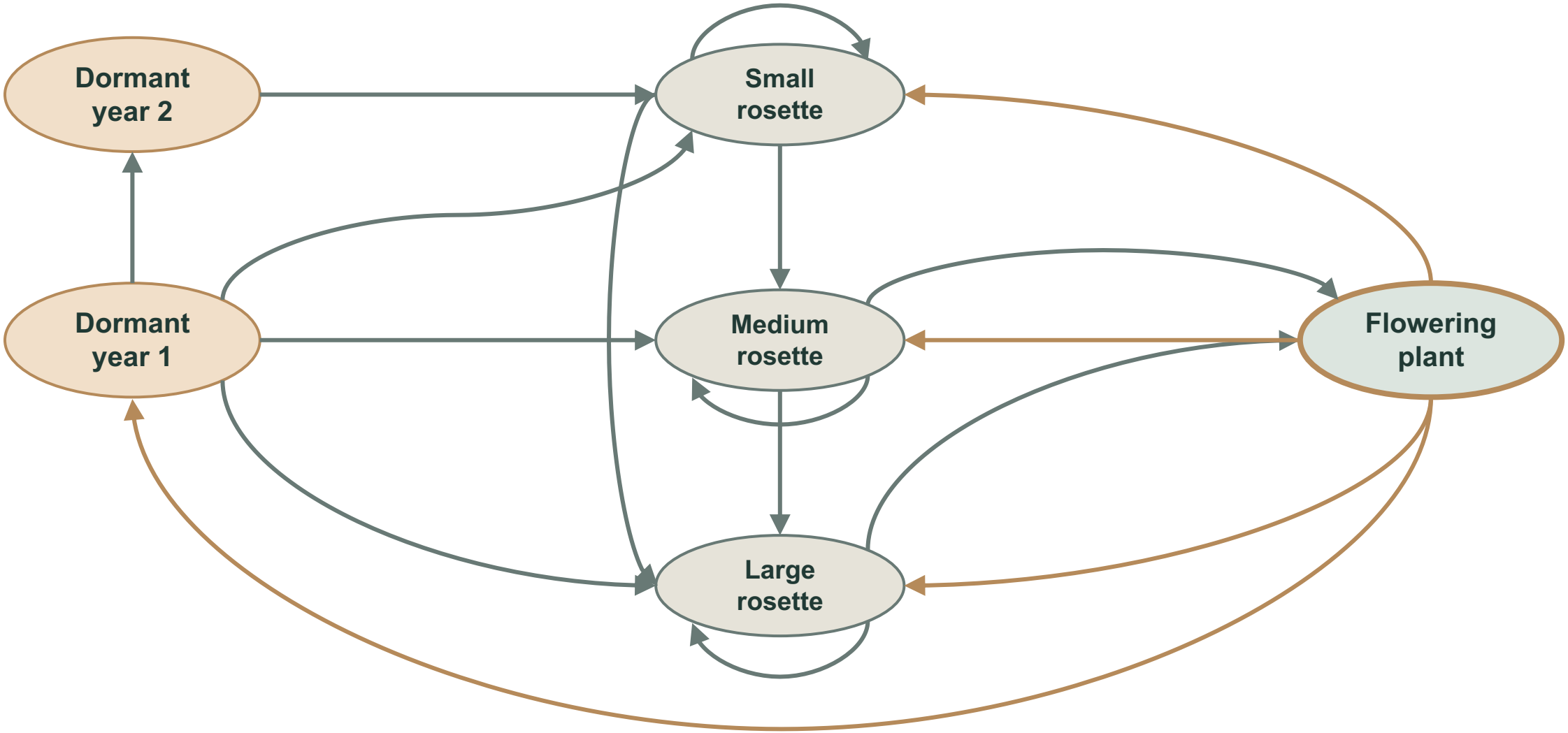




‹ Question

Teasel: change the life cycle

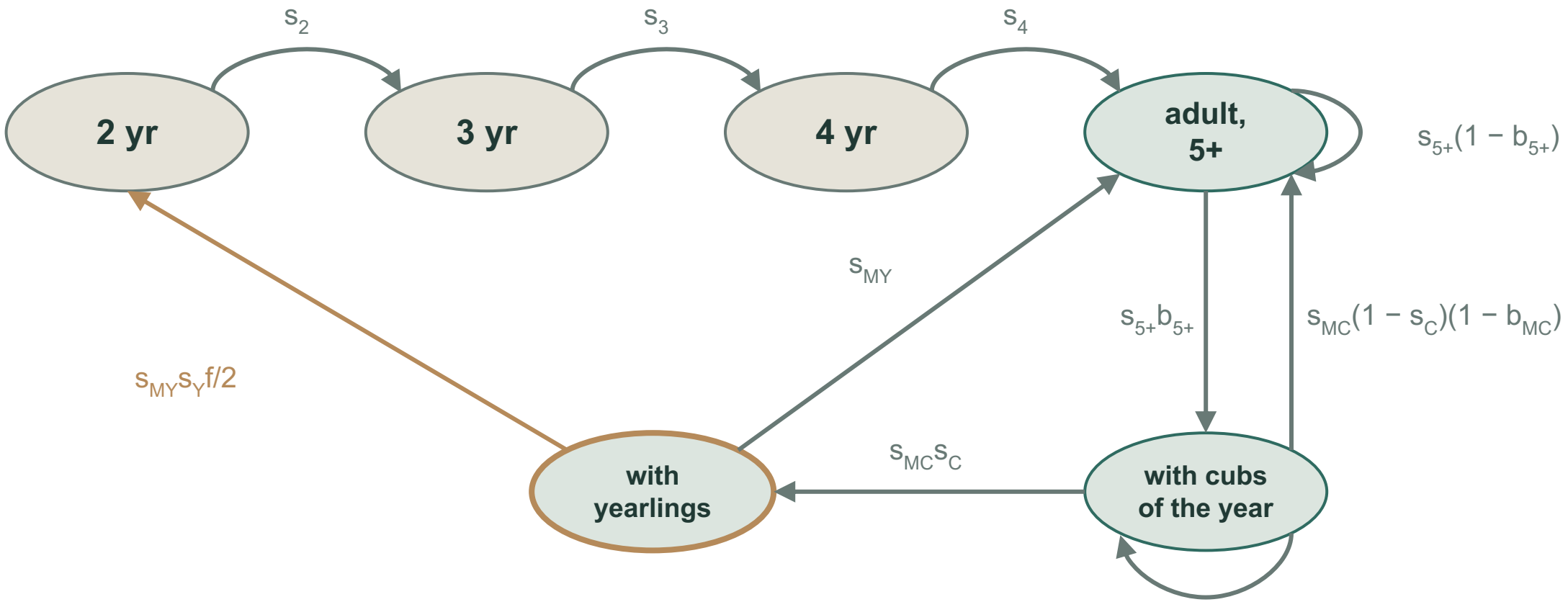




‹ Question

Polar bears: draw the life cycle





Female life cycle redrawn from Hunter et al. (2010), Ecology 91:2883–2897

Sea-ice loss lowers survival and breeding. Which arrows change?

‹ Question

Spotted owls: estimating the arrows

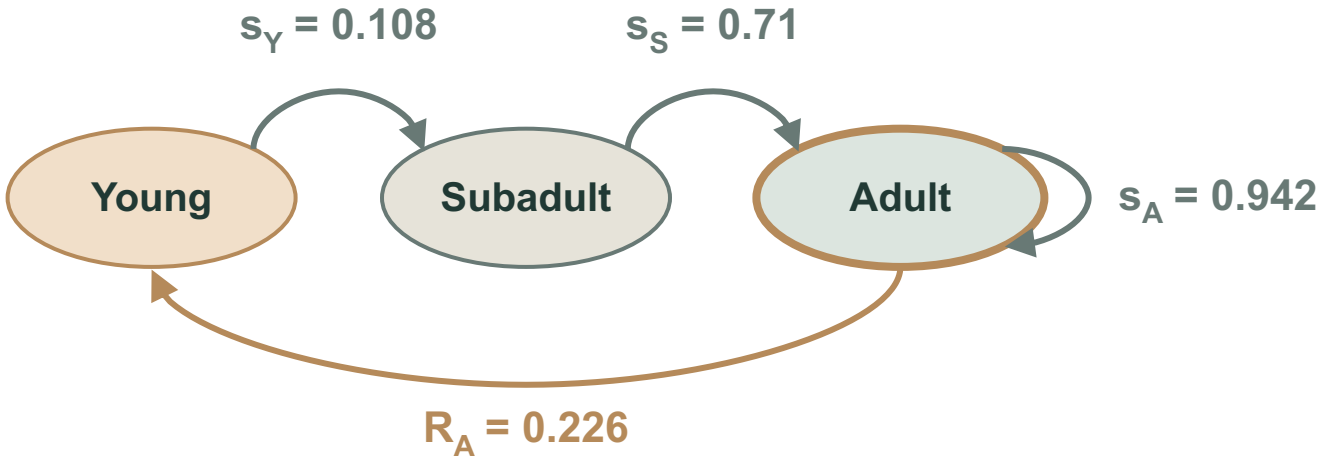


$R_A = 113 / 500$

$s_Y = 27 / 250$

$s_S = 22 / 31$

$s_A = 471 / 500$



$$\mathbf{A} = \begin{bmatrix} 0 & 0 & R_A \\ s_Y & 0 & 0 \\ 0 & s_S & s_A \end{bmatrix} = \begin{bmatrix} 0 & 0 & 0.226 \\ 0.108 & 0 & 0 \\ 0 & 0.71 & 0.942 \end{bmatrix}$$

Rates of Lande (1988), Oecologia 75:601–607; counts hypothetical

‹ Question