Behavioral Ecology of Vertebrates

Unit 1. Natural selection

Module 1 Introduction

j-packard@tamu.edu

Learning, Discovering and Sharing Knowledge

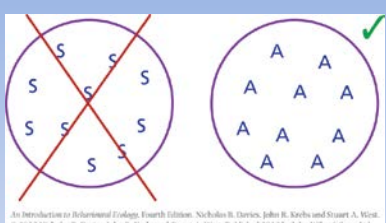
In this presentation, I will try to help you get the most out of Chapter 1 in (Davies et al. 2012). For best results, read the assigned chapter before each webinar, open your book and flip to the page numbers as we go through the presentation. Then reread those pages that you may have interpreted differently the first time through. It is natural that each of us will read the material differently based on the diverse backgrounds we bring to this course. My intent is to help with the leveling process so we all get on the same page as quickly as possible to strengthen the foundation for the rest of the course.

Learning Objectives (Davies et al. 2012:21)

1. **Natural selection**: logic for predicting individual behavior is based on genetic contribution to population
2. **Trade-offs**: predictions based on one motivational system (e.g. foraging) may be inaccurate due to interactions with other motivations (e.g. escape)
3. **Social conflicts**: predictions based on what is optimal for individuals are complicated due to genotypes carried by close relatives and competitors
4. **Ecological stage**: predictions based on a short time/space scale may differ from longer time/space scales

The take-home messages for Ch. 1 appear at the end of the chapter. They are easy to miss. I will elaborate on them because they are central themes throughout the book. If you read this chapter with these themes in mind, you will get more out of it. I have reworded these themes to be more consistent with the next chapter, which is about testing hypotheses in behavioral ecology.

Fig. 1.4



Analogy: selecting a script for a theater play

1. NATURAL SELECTION

You may have learned that natural selection is a “designer” process. To get us all on the same page, I will encourage you to think of it more as an editing process. Fig 1.4 illustrates Wynne-Edwards hypothesis that group selection would favor altruistic (A) over selfish (S) genotypes. His hypothesis was rejected because the evidence did not match the prediction. As an analogy, think of a genotype as a script for a theater play. If the script for “S” attracts smaller audiences than script “A”, then producers are more likely to select the script “A” over the script “S”. However, script “S” still remains in the library and some producer may rediscover it at a different time and place where it attracts a larger audience. This is the way in which we think of genotypes within the genetic “libraries” of populations. The “script” is the analogy for a “genotype”. The actual play presented by one theater company is analogous to “phenotype”, because the expression of the script is shaped by the environment in the production process.

1.1 Application (Davies et al. 2012:18-21, Fig. 1.11)

- Great tits forage for caterpillars
- Spring green up occurs at earlier dates
- Eggs are laid earlier in British population but not in Dutch population
- Dutch population is declining, not British

Lets start with an example of a scientific study that illustrates natural selection due to climate change. In Wytham Woods (Britain), females are laying eggs earlier, correlated with earlier dates of spring green up over the last decade. In Hoge Veluwe (Dutch), there has been no change in mean laying date, although spring green up is also earlier due to climate change. Great tits that lay late eggs have missed the peak of caterpillar availability and their nestlings starved. The Dutch population has declined but the British has not. Why? This does not fit our prediction of an optimal design!

1.2 Logic of Natural Selection (VHDP)

- **Variation** -IF there is variation in behavior within a population
- **Heritability** -IF the variation is heritable
- **Differential fitness**-IF some heritable variants survive/reproduce better than others
- **Proportion of genotypes change**-THEN there will be a change in a the gene pool of a population over generations

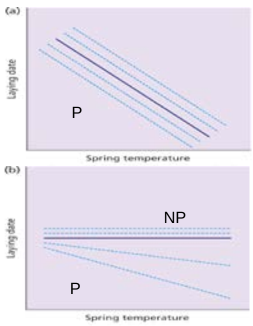
(Davies et al. 2012:5-6)

Lets apply the logic of natural selection to analyze this response to climate change that is different than what we might have predicted based on what would be an optimal design for the species. This is the way I will be talking about the logic of natural selection. It is implicitly the same as what is described in your textbook. I just find it easier to remember and apply to real world examples. I hope you will also.

1.3 Variation (Davies et al. 2012:18-21, Fig. 1.10)

a) <u>British population</u>: wide variation in laying dates *(all correlated with spring green up "P")*

b) <u>Dutch population</u>: less variation in laying dates *(some individuals correlated with spring green up "P", some not "NP")*

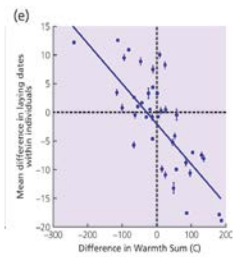


In the gene pool of this one species, the behavior of egg laying varies between populations. Each of the light blue lines in these graphs illustrate individuals and how their laying date (vertical axis) changed as spring temperatures increased over a decade (horizontal axis). In the British population, individuals varied in the initial laying date, but they all showed the declining trend of earlier laying as temperatures increased. In the Dutch population, some individuals showed no variation in laying date (horizontal lines) and some showed a declining trend. Overall, the mean date of laying (dark line) did not change in the Dutch population in contrast to the British population.

1.4 **Heritability** (Davies et al. 2012:18-21, Fig. 1.11)

a) British population:
   Genotype "**P**": plasticity *(individuals respond to environmental change)*

b) Dutch population:
   Genotype "**P**": plasticity
   Genotype "**NP**": not plastic *(individuals do not respond to environment)*

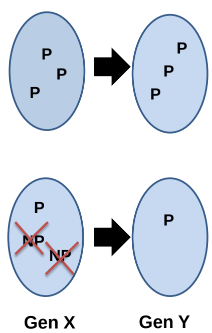


The variation in laying dates is due to individual plasticity in response to temperatures. This graph shows points for individual birds, plotting the differences between one year and the next year. This evidence does not fit the hypothesis that the phenotypic variation is due to genetic variation. So the mechanism to respond to changing temperature appears to be highly heritable in the British population, lets call this genotype "P" for plasticity. In the Dutch population, in addition to "A" there appears to be a second genotype, which is not responsive to temperature, lets call it "NP" for no plasticity.

1.5 **Differential fitness** (Davies et al. 2012:18)

a) British population:
   Genotype "**P**": no change in survival of nestlings

b) Dutch population:
   Genotype "**P**": no change
   Genotype "**NP**": nestlings more likely to die because they do not get enough caterpillars to eat



Although our textbook does not present the evidence, logically the "NP" genotype would be edited out of the Dutch population. We would not predict any difference in fitness among individuals in the British population, because the females are already tracking the environmental change. However, we would predict that females in the Dutch population who are not plastic will have lower fitness. Why? Their nestlings are less likely to survive compared to the females who are plastic and respond appropriately to the changing dates of spring green up. Remember that fitness is based on relative contributions to the gene pool of the next generation. The difference may be due to (a) survival of the breeder, (b) lifetime reproductive success, (c) survival of the breeders' offspring, and/or (d) the offsprings' reproductive success.

1.6 **Proportion** of genotypes change

- **H1**. Ancestral British population contained genetic variation like current Dutch pop
- **H2**. British population diverged from the Dutch population, with a decline in the % "**NP**" genotype so it is now mostly plastic "**P**"
- **H3**. In the future, the Dutch population will converge with the British population due to an increase in the % "**P**" genotype, and decrease in the % "**NP**" genotype

Following the logic of natural selection, we can propose three testable hypotheses. Remember that by definition, when the proportion of genotypes changes in the gene pool of a population, that is what we call evolutionary change. This logic is all about genotypes, not the "optimal design"! Remember our initial analogy that the genotype is like the script of a play. The "P" genotype is like a script to change behavior in response to the changes in the environment. The "NP" genotype is analogous to a script for "no change". The "P" script is more likely to be selected when the environment fluctuates.

1.7 Logic of Natural Selection (VHDP)

- **Variation** - egg-laying behavior varies in the degree of plasticity (response to temperature)
- **Heritability** – behavioral plasticity is highly heritable
- **Differential fitness**- more "plastic" individuals have more surviving offspring than "non-plastic"
- **Proportion of genotypes change**- "non-plasticity" has declined in the gene pool

So lets wrap-up with a recap of how the logic of natural selection applies to the example of the response of great tit populations to climate change.

1.8 Poll- lets see if you understand

Given global warming, if the plasticity in egg-laying behavior was not highly heritable, what would you predict about the future trend of the Dutch population of great tits?

a) Population increase
b) Continued decline in the population
c) No change in population size

Now lets see if you understand the implications of applying the logic of natural selection to the real-world application of managing biodiversity in the face of global climate change. Which is the correct answer? Why?

I would pick (b) because the phenotypes in the population are not adapted to a changing climate, they will have fewer and fewer surviving offspring, who also do not track the changes in spring green up. Some individuals may breed in the optimal time due to environmental influences, but if "plasticity" does not have high heritability, then their offspring will not. The population will decline to such a low level that it would be vulnerable to chance events (like a severe storm), which could wipe it out.

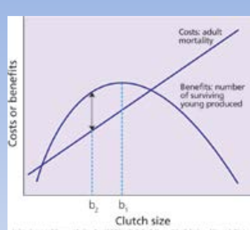


Fig 1.7

Analogy: Multiple themes in a script

2. TRADE-OFFS

The second theme running through our textbook is related to considering trade-offs in predicting how individuals behave. Scientists make these predictions based on optimality graphs, such as Fig. 1.7. These graphs may be "mind-benders" if you are not used to them. However, do not just "blow them off". The use of optimality models like these are pervasive in many areas of society, including economics, behavior, and ecological restoration. They are useful to analyze the trade-off between costs and benefits. You are probably most familiar with the trade-offs between growing your bank account by reducing costs or maximizing income. The same thinking has been applied to trade-offs in behavior based on costs (adult mortality) and benefits (surviving young). My analogy would be multiple themes in a script, e.g. the New York theater company might emphasize violent themes in a script and the Antioch theater company might emphasize themes related to caring family relationships.

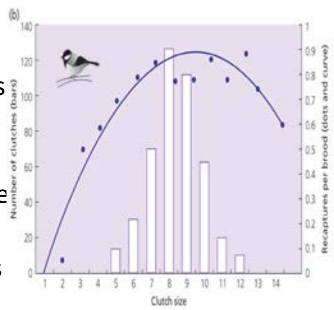
2.1 Application (Davies et al. 2012:13, Fig. 1.5)

- Nesting behavior of great tits in Wytham Woods near Oxford University *(60 yrs; Lack 1966)*
- Trade-offs influencing lifetime reproductive success of individuals
  - Adult mortality *(cost)*
  - # of offspring *(benefits; number of clutches and size of clutch)*

Our textbook uses a classic example of clutch size in great tits to illustrate the concept of trade-offs and the optimality models that have been used widely to make testable hypotheses in behavioral ecology. This is an amazing long term study. It also says a lot about the authors of the textbook, because they have been highly engaged in this study at Oxford University. So they use a lot of bird examples throughout the textbook. Good for our folks who are studying birds, but something to keep in mind in terms of picking supplements for other animals that you might find interesting but are not mentioned in the textbook. This is why we do the essays to encourage you to find the literature for the species with which you will be working.

2.2 Benefits (Davies et al. 2012:13, Fig. 1.5)

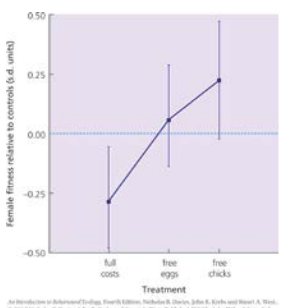
- Trade-off between size of clutch and survival of nestlings
- Offspring survival correlates with clutch size up to the tipping point at 9
- Modal clutch size is 8 eggs



We said optimality models examine trade-offs in terms of costs and benefits. Here is an example of a study that focused in on the benefits of clutch size in terms of offspring survival. Notice the humped shape of the curve similar to what you see in the diagrams of optimality theory (Fig 1.7). We will come back to that.

2.3 Costs (Davies et al. 2012:17, Fig. 1.8)

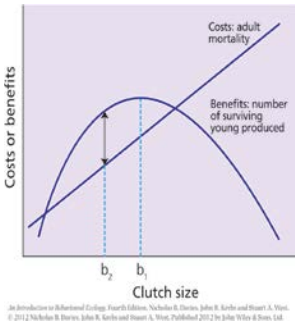
- Parental effort uses costly energy
  - Producing eggs
  - Feeding nestlings
- Relative to controls, female survival declines with costs of reproduction



Here is an example of a study that focused in on the costs of clutch size in terms of energy expenditure by the parent. Notice the straight line similar to what you see in the diagrams of optimality theory (Fig 1.7). Now lets look at the hump curve and the straight line together.

2.4 Optimal trade-off (Davies et al. 2012:17, Fig. 1.7)

- Prediction based only on benefits to nestlings “b1”
- Prediction based on trade-off between costs & benefits “b2”
- Arrows show the optimal solution



For folks whose minds work like economists, this graph explains a lot. For most of us biologists, it takes too much time to figure out what it means! You will see this logic of optimality theory is used frequently in behavioral ecology, so I will take some time to explain it. If we just consider the benefits, we would predict clutch size would be “b1”. But the data from the field do not fit that prediction. If we consider the trade-offs between costs and benefits, we find the optimal solution in the area above the cost curve and below the benefits curve. The clutch size where this difference between the curves is the greatest (the line with arrows) is the optimal solution to this problem of trade-offs. In this diagram, it is “b2” . Notice that the optimal solution is smaller than what we would predict based only on the short term benefits. Basically this is telling us that genotypes that reserve a little energy from each clutch (by laying fewer eggs) are likely to live longer and have a higher lifetime reproductive success than those that produce larger clutches. Notice this only applies to iteroparous species who reproduce repeatedly in a lifetime.

2.5 Poll- lets see if you understand

Why is optimality theory so widely used in the discipline of behavioral ecology?

a) It allows scientists to make precise predictions so they do not have to go to collect field data
b) It allows scientists to test alternative hypotheses about trade-offs in costs and benefits
c) It is easier to publish if you base predictions on a conceptual model, testable based on field data
d) B & C

Now lets see if you understand the implications of applying the logic of optimality theory for making testable predictions about animal behavior. Which is the correct answer? Why?

I would pick (d). Publishing is all about testing hypotheses to figure out which ones are a better match to reality. Real animals behave as if there are complex trade-offs, based on past history of the species. Rarely does a simple hypothesis just based on one criteria (i.e. benefits) match how animals actually behave in the wild.

2.6 Critique (Davies et al. 2012:12-17)

1. Optimality models assume that the environment is static, unchanging
2. This is inconsistent with the reality that behavioral adaptations occur within a constantly changing environment
3. To address change, the trend in behavioral research is to move to game-theory models
4. To do so, we need to distinguish between the social and physical environment

Lets pause to examine what we have covered so far, (1) the logic of natural selection and (2) the trade-offs in behavioral decisions as modeled by optimality theory. Do you see the logical inconsistency? Optimality models were a theoretical break through for their time, because they allowed us to examine multiple factors. But they rarely result in accurate predictions because they are only relevant under conditions that are not changing. So in the next two parts of this lecture, we will look at how to deal with a changing environment. To do so, we will need to separate the components of the environment into two categories: (1) social and (2) physical.

Analogy: Actors roles compete for attention

3. SOCIAL CONFLICT

Lets look first at the social environment. Our textbook identifies this as the third theme that runs throughout behavioral ecology. To return to our analogy of genotypes as being like a script of a play, think about how the actors in a play may compete for attention. They all read the same script, but how one actor reads the script may depend on how other actors read their lines. In other words, the phenotype may be influenced by the social environment interacting with the genotype.

3.1 Application (Davies et al. 2012:2-5, Fig. 1.3)

- Invading male lions kill cubs
- How could this be adaptive?
  - Clearly not "for the benefit of the group" or species
  - Reduces the lifetime reproductive success of the mothers of the victims
- Is it a natural process or a side-effect of human impacts?

Our textbook uses a classic example of infanticide in lions to illustrate the concept of how the lifetime reproductive success of individuals depends on what others are doing in the population. Understanding the proximate and ultimate perspectives on this behavior helps managers decide whether this is a good or bad thing, and whether to take management action.

3.2 Tinbergen's 4 views (Davies et al. 2012:2)

Concept map	Snapshot (pattern)	Video (process)
"Close-up Lens" **Proximate** *(individual, "performer", genotype)*	**Cause**	**Development**
"Wide-angle Lens " **Ultimate** *(population, "orchestra", gene pool)*	**Function**	**Evolution**

(TIP: see Tutorial)

Lets look at this problem of infanticide from proximate and ultimate perspectives. Remember how these have been defined by Tinbergen as distinctively different ways of answering questions about behavioral decisions. To simplify, lets look at this just in terms of a snapshot in time, the pattern of cause and function.

TIP: for a tutorial, use the link on the upper right menu bar on the course homepage

3.3 Proximate causes (Davies et al. 2012:5, Fig. 1.3)

- Females have strong social bonds
  - *Remain in mother's group*
  - *Synchronize estrus*
  - *Nurse cubs communally*
  - *Cycle again soon after the loss of a cub*

- Brothers form coalitions
  - *Disperse from mother's group*
  - *Fight with males of another pride*
  - *Attack vulnerable infants*
  - *Defend females from other males*

From a proximate perspective, the mechanisms influencing reproduction in females are different than males. As in all the cat species, females show indeterminate heat cycles, meaning that when they lose an infant they can cycle again without waiting for a breeding season. However, lions differ from solitary cats in that they are social and females remain together throughout their lifetimes. The male genotype is very different, in that brothers disperse from their mothers group and hang out together until they are successful at ousting the males of a different group. During the social conflict, vulnerable cubs are likely to be the victims of aggressive behavior. However, once the conflict settles down, the cubs are not a stimulus for attack by males. The males direct aggression to potentially dangerous rival males outside the group.

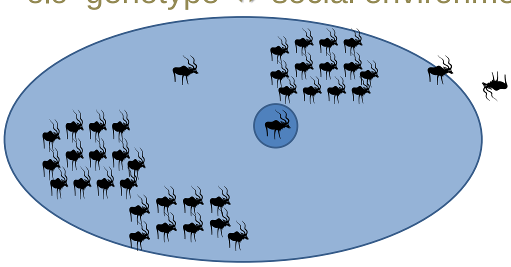
3.4 Ultimate function (Davies et al. 2012: 5; Fig 1.2)

- Female genotype "social"
  - *__Benefits__: better cub survival with communal nursing; sons more competitive at reproductive age*
  - *__Costs__: cubs killed in take-overs*

- Male genotype "fighters"
  - *__Benefits__: competitors cubs are killed; replaced by own cubs*
  - *__Costs__: males breed for only 2-3 years before they are ousted*

Our textbook uses a classic example of infanticide in lions to illustrate the concept of how the lifetime reproductive success of individuals depends on what others are doing in the population. Understanding the proximate and ultimate perspectives on this behavior helps managers decide whether this is a good or bad thing, and whether to take management action.

3.5 genotype ⇔ social environment



Take home message: Individual success depends on others in the group & population

The idea that I hope you will hold in your mind with respect to this third major theme in the textbook "social conflict", is that the lifetime reproductive success and the phenotypes resulting from any one genotype will depend on what others are doing in the social environment. This will vary between a population that has been wiped out and is still in a growth phase with little competition between individuals, compared to an established population where density is so high that individuals are competing for resources (e.g. food, mates, safe places). This applies not only to lions, but also to all social species (addax in this diagram)

3.6 Poll- lets see if you understand

Why is the social environment important for making predictions re. behavioral ecology?

a) The social environment dictates what is best for the species to survive
b) The phenotype is the result of interactions between the genotype and social environment
c) A changing social environment influences which genotypes make more copies of themselves
d) B & C

Now lets see if you understand the implications of considering the social environment when making testable predictions about animal behavior. Which is the correct answer? Why?

I would pick (d). In the example of lion infanticide, we saw that both female and male behavioral traits were shaped by the social environment in a proximate sense. From the ultimate perspective, the lifetime reproductive success of individuals depended on the behaviors of others in the population.

Rudnick et al. 2012

Analogy: The stage setting for a theater play

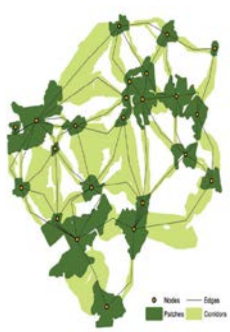
4. ECOLOGICAL STAGE

Now lets turn to the last of the four themes, related to changes in the physical environment. The analogy in the textbook is the “ecological stage”, implying that the expression of the “script” (genotype) also depends on the physical setting “theater stage”.

4.1 Application

(Rudnick et al. 2012, Fig. 5)

- Habitat fragmentation and increased disease transmission
- How do individuals make dispersal decisions?
  - *When to leave a patch*
  - *Connective travel corridors*
  - *Impenetrable edge barriers*



Our textbook is missing a good example to illustrate how this concept of the ecological stage is important in managing populations. For a good explanation of why behavioral ecology is important in the consideration of habitat fragmentation and connectivity, I recommend reading a recent review by Rudnick et al (2012). The dark patches in this network analysis represent habitat fragments and the light green are dispersal corridors potentially connecting the fragments.

4.2 Space scale (pattern, “snapshot”)

scale	analogy	e.g. great tits
narrow	Spotlight on the leading couple	Territory of one nesting pair in one woodlot
medium	Stage lights on all actors	All the territories of nesting pairs in one patch of woods near Oxford
broad	House lights on the whole theater	All the patches of woodlots with nesting pairs in the British Isles

The previous example of connectivity illustrates how important the choice of scale can be in behavioral ecology. For example, predictions about behavioral adaptations would be different depending on your choice of scale for spatial distribution. Remember our example of the two great tit populations responding to climate change. If you just looked at the Dutch population, you might predict the species would go extinct. On a broader scale, clearly there are other populations that will persist, so you would not predict species extinction. As an analogy, think about how much space is illuminated by a spotlight, stage lights and house lights in a theater.

4.3 Time scale (process, “video”)

scale	analogy	e.g. Great tits
short	One scene	Caterpillars in one nesting season
medium	All the scenes in the play	Territory quality over all seasons of a pair
long	Remakes of the play	Food changes with glacial cycles

In ecological studies, we also consider different scales in time. The succession of plants invading a sandbar that has been wiped clean by a flood might be an example of how plant communities change over time. Likewise, your choice of a time scale will influence your predictions in behavioral ecology. As we learned with the great tits, the optimal clutch size predicted for one nesting season is higher than what would be predicted considering the trade-off with mortality over the reproductive lifetime of a breeding pair.

4.4 Ecological change (stage-set)

Space scale (pattern; “snapshot”)

- Individual home range
  - *e.g. habitat patches*
- Subpopulation
  - *e.g. fragmentation, connectivity*
- Global range of a species
  - *e.g. ecoregions, biomes*

Time scale (process; “video”)

- Short cycles within an individual's lifetime
  - *e.g. El Nino drought cycles*
- Long cycles in a social group's lifetime
  - e.g. fire recovery cycles
- A species' history
  - *e.g. glacial cycles*

Throughout this course, we will be talking about the ecological setting in terms of changes in both the time and space scales. This will be very important for you in terms of applying what you learn in behavioral ecology to applications in the real world.

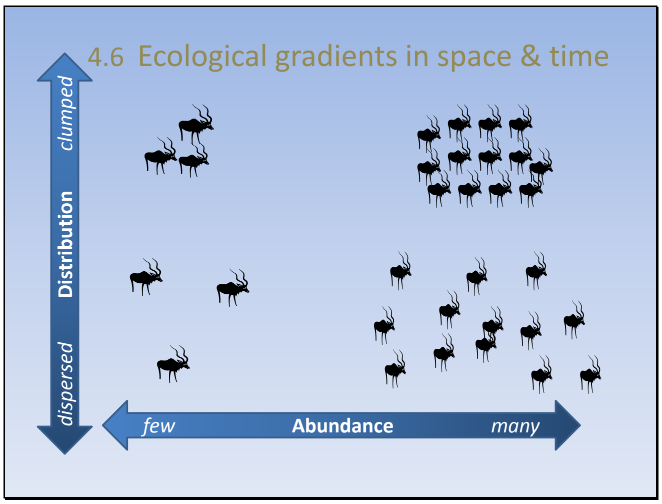
4.5 Tinbergen's 4 views (Davies et al. 2012:2)

Concept map	Snapshot (pattern)	Video (process)
"Close-up Lens" **Proximate** *(individual, "performer", genotype)*	**Cause**	**Development**
"Wide-angle Lens " **Ultimate** *(population, "orchestra", gene pool)*	**Function**	**Evolution**

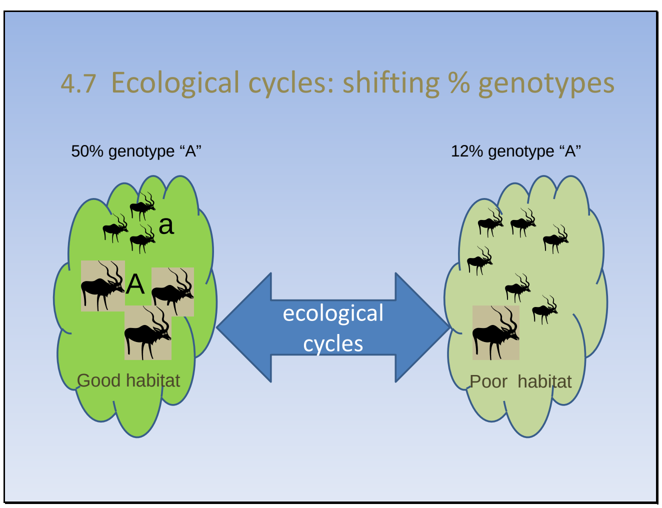
(TIP: see Tutorial)

Notice that this corresponds to the same distinction between pattern and process as we saw in the two columns in Tinbergen's concept map. These are broad concepts that apply across both ecology and behavior. Understanding pattern & process helps us link ecology and behavior.

TIP: for a tutorial, use the link on the upper right menu bar on the course homepage



To help you visualize the effects of space and time, at each scale we will examine the distribution of resources, and how that influences the distribution of animals. So we will be making different predictions based on whether resources are "clumped or dispersed", "few or many". The "distribution" interactions with the "abundance". We will be considering how animals make behavioral decisions when resource distribution changes seasonally, e.g. between winter & summer.



The shifting abundance and distribution of resources are very obvious with ecological cycles such as floods and droughts. What may be good habitat at the peak of the cycle may be poor habitat in the low of the cycle. This has implications for natural selection and the shifting balance of genotypes in the gene pool of a population. Let's say "a" is a skinny genotype and "A" is a fat genotype. The fat genotypes do better under good habitat conditions and the skinny do better under bad conditions. As conditions shift with ecological cycles, we would predict the % genotypes would shift.

4.8 **Take-home message** (ecology)

- Ecological setting of behavior: 2 scales
  - time scale is also called "process" in ecology *(e.g. season, lifetime, glacial era)*
  - space scale is also called "pattern" in ecology *(e.g. territory, wood-lot, British Isles)*
- Ecological change influences behavior
  - Variation in distribution & abundance of resources
  - Implications for shifting proportions of genotypes

To recap, the fourth theme that appears throughout this textbook is related to the physical environment (as distinct from the social environment). This theme is implicit in Chapter 1, so I have tried to make it more explicit in this presentation by relating it to 2 scales (time/space) and the variation in resources at each scale (distribution/abundance). The ecological setting turns out to be very important in making predictions about shifting proportions of genotypes due to the process of natural selection.

4.9 Poll- lets see if you understand

When behavioral ecologists talk about the ecological setting, what do they mean?

a) Changes in distribution and abundance of resources
b) Implications of time and space scales for predicting behavioral decisions of individuals
c) A and B

Now lets see if you understand the implications of the physcial environment for making testable predictions about animal behavior. Which is the correct answer? Why?

I would pick (c). The ecological setting for each prediction about behavioral decisions of individuals is based on a choice of scale for the time and space dimensions. Within the particular scale that is chosen, the predictions will be based on resource distribution (clumped/dispersed) and abundance (few/many).

Summary (Davies et al. 2012:21)

1. **Natural selection**: variation, heritability, differential reproduction/survival, % genotypes change in gene pool
2. **Trade-offs**: optimality models allow for predictions based on several factors; but they assume static conditions
3. **Social setting**: in a changing social environment, the success of individuals depends on behavior of others
4. **Ecological setting**: predictions based on a short time/space scale may differ from a longer time/space scale (e.g. changes in distribution/abundance of resources)

In summary, there are four major themes that appear throughout our textbook. If you keep these in mind, it will be much easier to "see the forest for the trees" when we talk about specific examples of research in behavioral ecology. This chapter clarifies the concept map for behavior (Tinbergen's four questions), the concept map for ecology (space and time scales) and how these two are integrated by the logic of natural selection. It provides a roadmap for analysis of questions in behavioral ecology.