UNIT 1. NATURAL SELECTION, ECOLOGY & BEHAVIOR

SOURCES *(for powerpoint format: http://wfsc.tamu.edu/jpackard/behavior/wfsc622/powerpoints.zip)*

required: Chapter 1 in Krebs & Davies (1993:1-22);

remedial: Halliday (1994:7-9, 23, 34, 44, 133-139); "Finding the Way" in The Trials of Life video series

supplemental: Dugatkin (2001: xi-xxii); Ch. 1-2 in Blumstein & Fernandez-Juricic 2010

PARTS OF THIS LECTURE OUTLINE

1. Behavior- orchestrated individual performance
2. Ecology- the stage setting
3. Natural selection- the "production process"

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1. BEHAVIOR- ORCHESTRATED INDIVIDUAL PERFORMANCE

1.1 **Tinbergen's four questions** *(these are also called "viewpoints" or "concepts"; Krebs & Davies 1993:4)*

F: function *(survival value & reproduction; fitness of genotypes in a population)*
C: causation *(stimulus & response; mechanisms; expression of a genotype)*
D: development *(ontogeny; change with age; genetic control of instinct/learning)*
E: evolutionary history *(phylogeny, comparative approach; ancestral/derived traits)*

1.2 **Example**: why do starlings sing? (Krebs & Davies 1993:4)

F: Those that sang, attracted more mates and produced more offspring
C: Two types of answers: external & internal
1. external context: daylength => hormones=> response to stimuli (mates/rivals)
2. internal mechanisms: airflow through syrinx => membrane vibrations

D: Instinct: in males, genes control the "sensitive age" for learning songs from parents &neighbors
E: Two parts to the answer: ancestral ("trunk" of the tree of life) & derived (divergent "branches")
1. ancestral trait (similarities among species): primitive birds had simple sounds (notes)
2. derived trait (differences among species): starlings have more complex song (melody)

1.3 **Concept map** "**A**nimal **B**ehavior is **C**ause, **D**evelopment, **E**volution & **F**unction" AB=C+D+E+F

Tinbergen's 4 Questions	**Snapshot** (pattern)	**Video** (process)
Close-up Lens on "Performer" (individual view, proximate)	**C**ause	**D**evelopment
Wide-angle Lens on Orchestra (populationview, ultimate)	**F**unction	**E**volution

TIP: for a tutorial, use the link on the upper right menu bar on the course homepage
http://wfsc.tamu.edu/jpackard/behavior/ wfsc622/Documents/tutorial.pdf

1.4 **Concept application** (**C**ause/**F**unction): as it applies to two "adaptive traits" that coevolved in lions

- Female trait: synchronized estrus and communal suckling of cubs (Krebs & Davies 1993:5-7)
- Male trait: infanticide directed to unrelated cubs during take-overs (Krebs & Davies 1993:7-8)

1.5 **Female lion** behavior trait: two ways to explain synchronized estrus (Krebs & Davies 1993: 8 Table 1.1)

1. "**performers**" *TIP: this is the **PROXIMATE** perspective (C: Cause "snapshot")*
   C: Female pheromones (chemical cues) may induce estrus in other females; when several females lose their cubs at the same time, after a few weeks, they all recycle & come in heat together
2. "**orchestra**" *TIP: this is the **ULTIMATE** perspective (F: Function "snapshot")*
   F: In the past, those genotypes that synchronized estrous would have had better cub survival due to the indirect fitness benefits of communal suckling; also their sons & "playmates" who left the pride together would have been more successful in "stealing" females from other males

1.6 **Male lion** behavior trait: two ways to explain infanticide by males (Krebs & Davies 1993: 8 Table 1.1)

1. "**performers**" is a PROXIMATE viewpoint
   Cause: when males attack other males during a take-over, they are likely to redirect the aggression toward the least intimidating individuals of the pride (i.e. the cubs); since the cubs are strangers, the attacking males are not inhibited; when their own cubs are born males are inhibited from attacking by the familiar odor of their own cubs
2. "**orchestra**" is an ULTIMATE viewpoint
   Function: In the past, those genotypes that killed unrelated cubs would have fathered more cubs than those that did not ("non-infanticide" genotypes waited longer until females came into estrus)

1.7 **Critical thinking skills**: two additional viewpoints on lions not elaborated by Krebs & Davies in Table 1.1

1. **PROXIMATE "performers"** can also be viewed as a "**video**" at the individual level of analysis
   a. **D**evelopment: genotypes control age of reproductive maturity in lions; at puberty, females remain in their mother's group and males disperse
   b. The Development perspective looks at how genes control behavior (Krebs & Davies 1993: 10-14); we just do not yet have good studies of genes & behavior in lions
2. **ULTIMATE "orchestra"** can also be viewed as a "**video**" at the population/species level of analysis
   a. **E**volution: social behavior of cat species ranges along a gradient from solitary (i.e. bobcat, fishing cat, serval), through semi-social (i.e. cheetah), to highly social (lions); the "solitary" form of the trait is thought to be more primitive and "sociality" to be more derived; in all cats, males are infanticidal, hypothesized to be a trait that persisted through all species, thus an example of "phylogenetic inertia"
   b. The Evolutionary history perspective looks at how gene pools have changed over many generations; it is not elaborated in this chapter, but you may read ahead to learn more (Krebs & Davies 1993: 25-29)

TIP: To learn about more recent research on this topic, use the Web of Science to find the article by Mosser & Packer (2009) published in the peer reviewed journal Animal Behavior. This is an example of how to find "hot new research" for your personal weekly supplements you will be asked to identify in assignment 1. For instructions on how to use Web of Science, read the [technical help] link on the top menu bar of the course homepage.
http://wfsc.tamu.edu/jpackard/behavior/wfsc622/Documents/Technical_Help.pdf

Take-home message- orchestrated individual performance (useful analogy for a complex concept)

- In behavior studies, pay attention to the distinction between "proximate" (Cause, Development) and "ultimate" (Function, Evolution)
- 2 examples illustrate the distinction between proximate & ultimate, e.g. starlings and lions

Part 1	**Study Questions for Chat & Quiz 1 "The Behavior Viewpoint in Behavioral Ecology"**
1.1	What were Tinbergen's 4 major questions about behavior? (TIP: use the keywords for CDEF)
1.2	What are examples of answers to Tinbergen's 4 questions about starling song (CDEF)?
1.3	In your own words, what are the similarities and differences among Tinbergen's 4 questions? (TIP: describe the concept map for CDEF)
1.4	Why do male lions kill cubs, in scientific terms? (TIP: apply CDEF concepts & avoid Folk Psychology; see tutorial)

2. ECOLOGY-THE STAGE SETTING FOR BEHAVIOR

TIP: This perspective is implicit in the assigned reading (Krebs & Davies 1993: 14-21); however, it is easy to overlook if you have not learned about time/space scales in a previous course in ecology. This section is a more explicit elaboration so you can pick out what you need to remember as foundation concepts in this course. If it does not make sense, read the tutorial.

2.1 **Behavior => ecology**: How do we explain adaptations to a changing environment?

Types of adaptive explanations	**Time scale**	**Example (Krebs & Davies 1993: 14)**
learning	an individual's lifetime	Trial & error learning in one individual bird building a nest; the actual movements or sequence of action may differ between individuals
cultural transmission	a social group's "lifetime"	Some individuals observe a more experienced bird building a nest and copy the actions; actions may differ between cultural groups
evolution	a species' "lifetime"	All individuals hatch with the genetic coding that causes them to respond instinctively to the stimulus of nest materials, prior to learning or observing others; the genetic coding may differ between species

2.2 **Change in environment**- ecological variation analogous to a "stage setting"

1. time scale- process of change over time ("video")
   a. individual's lifetime
   b. social group's lifetime
   c. a species' lifetime
2. space scale- distribution across the landscape ("snapshot")
   a. an individual's home range (resources may be clumped or evenly distributed; high or low abundance)
   b. distribution of a subpopulation relatively disconnected from others (protected areas of habitat)
   c. a species' global range (all the subpopulations in patches of habitat more or less connected)

TIP: Does the above "video" and "snapshot" analogy sound familiar? This is similar to the two columns in our concept map of CDEF! It is the way we can link the behavior to the ecology in behavioral ecology. It is also the way that we can get to the scientific perspectives behind the Folk Psychology of "group thinking" about explanations of behavioral adaptations. For a critique of "group thinking" read (Krebs & Davies 1993: 14-15). This is particularly difficult to understand if you have learned about behavior and/or ecology from a source based on the conceptual foundation of the 1970's (many of our wildlife management textbooks are outdated). It will take extra effort to "unlearn" concepts of group thinking and replace them with this "selfish gene" way of thinking that became standard in behavioral ecology after the 1980's. If you want more elaboration, look up "Stephen Jay Gould" on http://www.wikipedia.org/. Several of his essays are available in the library course reserves. To access course reserves, use the library link on the right side of the course pages. Also, reread Krebs & Davies (1993: 1-3). The following sections of this outline are elaboration of an analogy that (hopefully) we all can relate to, drawing on our own lifetime experiences attending plays, movies and selecting entertainment videos.

2.3 Time scale: analogy of the stage setting for a play *(Krebs & Davies 1993: 20-21)*

Time scale	Analogy of a play	Example from studies of magpies (similar to crows)
short	One scene in one stage setting	caterpillars available in one brood season of one pair
medium	All the scenes with several stage settings during the entire play	territory quality over many seasons during the reproductive lifetime of one pair
long	Remakes of the same play during the last century (i.e. changing directors)	changing food during glacial periods, e.g. Pleistocene climatic fluctuations affecting many generations of the species

2.4 **Space scale**: analogy of the stage setting for a play *(Krebs & Davies 1993: 16-20)*

Space scale	Analogy of a play	Example from studies of great tits (similar to chickadees)
narrow (close-up lens)	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 the Wytham Woods patch of habitat near Oxford University in the British Isles
broad (wide-angle lens)	House lights on the whole theater	All the patches of woodlots with nesting pairs in the British Isles

TIP: Does the above "close-up lens" and "wide-angle lens" sound familiar? This is similar to the two rows in our concept map of CDEF, helping us link behavior and ecology in scientific studies. This concept map is pretty basic to modern biology. You may have learned it using different words in other classes. Here we are just trying to help you relate the jargon that we will be using in behavioral ecology, to concepts that you have already learned in other classes and/or lifetime experiences. The analogy of a play is just to help you get a "gut feeling" understanding. If it does not work for you, no big deal.

2.5 **Adaptation** - predictions of optimum brood size in great tits depends on what the researchers assume about the time/space scale *(Krebs & Davies 1993: 17-18)*

1. Assumption 1: narrow space & short time (1 pair in 1 season) => predict 12 eggs
2. Assumption 2: broad space & long time (several pairs over their lifetimes) => predict 8 eggs
3. Result: the average brood size was 10 eggs, with a range from 2 to 14 *(Fig. 1.5)*
4. Interpretation of result:
    a. due to variation in both space and time, optimal conditions are not always present;
    b. natural selection favored multiple genotypes coding for a range of clutch sizes;
    c. the most frequent genotype codes for 10 eggs;
    d. in good years, genotypes that laid more eggs did better (produced more chicks)
    e. in bad years, genotypes that laid fewer eggs did better (adults survived longer).

2.7 **Take-home message**- the ecological setting of behavior = variation in 2 dimensions

1. time dimension is also called "process" in ecology (e.g. season, lifetime, glacial era)
2. space dimension is also called "pattern" in ecology (e.g. territory, wood-lot, British Isles)
3. e.g. variation in brood size in Great Tits & Magpies matches ecological variation

Part 2	**Study Questions for Chat & Quiz 1 "The EcologyViewpoint in Behavioral Ecology"**
2.1	What are 3 hypotheses about how behavior becomes adapted to ecology?
2.2	What are two scales used by ecologists to investigate environmental change?
2.3	In a species of your choice, how does brood size relate to time and space scales?
2.4	How are the 3 hypotheses about behavioral adaptation related to time and space scales?

3. NATURAL SELECTION- THE "PRODUCTION PROCESS"

3.1 **How** is an animal's behavior **adapted** to its environment? Answers have changed over decades

1. Darwin's theory (1859):
    a. myth: nature red in tooth & claw; survival of the fittest
    b. science: heritable variation with competition for survival and reproduction
2. Neo-Darwin theory (1920's, as popularized by Dawkins 1976 cited in Krebs & Davies 1993:):
    a. myth: selfish gene; individuals are vessels for gene replication
    b. science: selection causes changes in gene frequency
3. Why did the theory change? discovery of genes! *(Krebs & Davies 1993:9)*

TIP: Even though you have read about this previously, this is not the time to skip over it. Pay special attention to the logic that is outlined below. It is the essence of the difference between "Folk Psychology" and the scientific perspective on testing hypotheses in behavioral ecology. Throughout this course, you will be rewarded with points for the scientific perspective and will lose points for "Folk Psychology" (also referred to in the next chapter as "adaptationist story-telling", see page 29-31). Here the logic of natural selection is "boiled down" to a few phrases that are easier to remember than the wordy points on page 9. It's basically the same idea. For those of you who are more familiar with evolutionary theory, this is based on the "shifting balance" model Fisher (1930), Wright (1931), Haldane (1932) as cited in Wilson (1975:63)

3.2 **Process of Natural Selection (NS= V + H + D => P)** *(Krebs & Davies 1993:9-10)*

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

3.3 **Test of theory**: migratory behavior of **Blackcap Warblers** *(Berthold et al. 1990 cited in Krebs & Davies 1993: 12-13)*

1. **V**: variation in French population (40% migrators, 60% non-migrators)
2. **H**: highly heritable (polymorphic alleles for direction & restlessness)
    a. M: migratory adults=>migratory offspring (German population)
    b. NM: non-migratory adults=> non-migratory offspring (Cape Verde)
    c. hybrids showed intermediate restlessness
3. **D**: differential reproduction in 2 lab groups
    a. lab group M- only migratory birds bred, others were culled
    b. lab group NM- only non-migratory birds were bred
4. **P**: proportion of genotypes changed- 6 generations
    a. group M- increased % migratory (40%=> 100%)
    b. group NM- decreased % migratory (40%=> 5%)

3.4 **Variation**- examples of behavioral polymorphism *(Krebs & Davies 1993:10-12,16)*

1. garter snakes: slug eaters vs. non-slug eaters (coastal 73:27; inland 35:65)
2. fruit flies: fast maters vs. slow maters
3. lions: (males) infanticidal vs. non-infanticidal; (females) synchronizers vs. non-s
4. tits: (females) large clutch layers vs. small clutch layers

3.5 **Heritability**- tested by hybridizing, mutations, line-breeding, *(Krebs & Davies 1993:10-12)*

1. garter snakes: hybrids of coastal & inland parents were intermediate (50:50)
2. fruit flies: not all behavioral variations are highly heritable
    a. high H: selective breeding of fast-maters resulted in a fast-mating strain
    b. low H: "stuck" variation is the result of a mutagen (radiation)
3. lions: heritability of infanticide has not been tested experimentally

3.6 **Differential fitness** (survival and/or reproduction of genotypes) *(Krebs & Davies 1993:10-12)*

1. Garter snakes: more slugs in coastal rainforest than dry inland habitat
    a. Coastal population: those that ate slugs were better nourished & produced more offspring
    b. Inland population: no difference in fitness of slug-eater genotype vs. non-slug eater genotype
2. lions: those that killed unrelated cubs had more offspring than those that did not
3. warblers: harsher winters in northern habitat compared to southern
    a. northern populations: those that migrate were more likely to survive winter
    b. southern populations: those that don't migrate produced more offspring

3.7 **Proportion of genotypes changed** *(Krebs & Davies 1993:10-12)*

1. garter snakes: % slug-eating genotypes increased in coastal compared to inland population
    a. assumes coastal population was derived from inland ancestral population
2. passerines: % genotypes with large clutches increased in gene pool of hole-nesting species compared to non hole-nesting species (assumes hole-nesters were better protected from predators)

3.8 **Take-home message**: process of natural selection resulting in pattern of adaptation

- IF **V**ariation + IF **H**eritability + IF **D**ifferential fitness THEN **P**roportion of genotypes changes
- Examples (migratory restlessness in Blackcap warblers, slug-eating in garter snakes)
- consciously strive to reword myth: "for the good of the species" in terms of science: **NS=VHDP**

Part 3	Study Questions for Chat & Quiz 1 "Natural selection in Behavioral Ecology"
3.1	What are four components to the modern theory of natural selection (VHDP)?
3.2	Using an example of your choice, what is meant by behavioral variation (V)?
3.3	Using an example of your choice, what is meant by heritability of behavior (H)?
3.4	Using an example of your choice, what is meant by differential fitness (D)?
3.5	Using an example of your choice, what is meant by the proportion of genotypes (P)?

SUMMARY

1. **Behavior**- orchestrated individual performance implies individuals do not act alone
    1. AB= (**C+D**)+(**E+F**) = ("individual": proximate) + ("orchestra":ultimate)
    2. e.g. starling song; lion infanticide and communal suckling

2. **Ecology**-the stage setting for the performance varies in pattern & process
    1. process: time scales- short (season), medium (lifetime), long (glacial periods)
    2. pattern: space scales - narrow (1 territory), medium (woodlot), broad (British Isles)
    3. e.g. brood size (egg-laying behavior) in Great Tits & Magpies

3. **Natural selection**-the "production process" results from interaction between behavior & ecology

- NS= **V + H + D** => **P**
- e.g. migratory behavior in warblers, slug-eating in garter snakes
- natural selection of genotypes is the science behind the myth of group selection

Summary	Study Questions for Chat & Quiz 1 "Natural selection, Ecology & Behavior"
4.1	Without plagiarizing, what are the 3 take-home messages of this lecture outline?
4.2	In your own words, what is the meaning of "behavioral ecology"?