TUTORIAL - BEHAVIOR

Students come to behavior courses with diverse backgrounds. Some are knowledgeable about behavior, others have had courses on ecology. All have had some experience interacting with animals and have formed personal expectations about how animals behave. However, few participants have experienced the opportunity to integrate ideas about ecology and behavior, which is the goal of this course. Coming into this course, most students find it difficult to express their intuitive ideas about behavior, in the formal language of science.

This tutorial is designed to help everyone start on the same page. We can think about the process as learning to speak a shared language. One of the barriers to communication, is often the misperceptions about behavior, adaptation and natural selection. We absorb misperceptions from diverse sources: Discovery Channel, high school textbooks, popular magazines, and the stories we share with friends or family. In a similar vein, "ecology" has come to be associated with many ideas, ranging from "green" to "recycling". However, scientists have very specific meanings for the words "behavior" and "ecology".

The scientific statements we will be seeking to comprehend, make little sense when the reader understands technical words in terms "popular" meanings. We will use the term "Folk Psychology" to label these personal (popular) perceptions as myths. During this course, your job is to learn to distinguish between myth and science, This distinction is an important first step, necessary prior to learning how to explain behavioral ecology from a scientific perspective.

Why struggle with learning this technical language of science? The utility of the scientific perspective is the ability to make more accurate predictions, for a variety of species, in a full range of diverse settings. This is what we mean by "looking for the science behind the myths". It helps us with positive problem solving, when we encounter novel situations outside our current range of experience. An analogy might be a detective game; we will be constantly asking ourselves "what is the evidence?"!

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Tutorial: Behavior, Ecology & Natural Selection
I. Conceptual Framework for Behavior
Scientific Perspective - Tinbergen's 4 Questions

Animal behavior has been studied, and explained, using various perspectives. We will begin by looking at the scientific basis for studying animal behavior as clarified by Dr. Nikolaas Tinbergen. Each perspective is analogous to a "lens" that both focuses and filters each scientist's view of the reality of animal behavior. These four scientific perspectives contrast with Folk Psychology, which is not considered a scientific basis for the study of behavior (see next page). One convenient memory trigger is AB=CDEF: Animal Behavior is Causation, Development, Evolution, and Function..

- **Causation** (stimulus/response): How do individuals respond to stimuli in their environment?
- **Development** (ontogeny): How does behavior of individuals change as their bodies mature with age?
- **Function** (survival/reproduction): Why did the percentage of genotypes change between generations of a population?
- **Evolution** (phylogeny): Why have behavioral traits diverged among species during historical changes in populations?

Who was Tinbergen?
These four basic perspectives were defined as questions by Dr. Tinbergen, a Nobel prize-winning scientist who is known as one of the "fathers of ethology". His contributions were honored because he explained how the basic questions in biology could be applied to the study of animal behavior.

ACTIVITY: Use "http://en.wikipedia.org" to learn more about Tinbergen.

Tinbergen's Concept Map
To remember the four perspectives we gain from these questions, think in terms of "individual vs. population" and "pattern vs. process". It helps to think of the "individual" perspective as using a close-up lens in contrast to the "population" perspective being more like a panoramic lens. The technical terms are proximate (individual) and ultimate (population). To continue this analogy, "pattern" is more like a snapshot (one moment in time) and "process" is more like a video (a series of snapshots). Here is one way to visualize this concept map. Ready for a photo safari?

	PATTERN	**PROCESS**
INDIVIDUAL	Cause snapshot with a close-up lens	Development video with a close-up lens
POPULATION	Function snapshot with a panoramic lens	Evolution video with a panoramic lens

ACTIVITY: Use "http://en.wikipedia.org" to learn more about "proximate" and "ultimate".

Word Associations
These four basic perspectives appear in all fields of biology. You may have encountered the same ideas associated with a different set of words. Here is a more linear way of visualizing the distinctions among concepts.

What are you observing?	What are you looking for?	What question will you ask?	Examples of Answers
Individual (Proximate)	Pattern	Cause (Stimulus/ Response)	male starlings sing spontaneously from a perch, as well as in response to other starlings
Individual (Proximate)	Process	Development (Nature vs. nurture)	at puberty, male starlings instinctively produce simple notes and learn to put notes together in complex melodies by listening to other male starlings
Population (Ultimate)	Pattern	Function (purpose, those genotypes that.)	those males that produced more complex melodies were more likely to attract mates and repel intruders than those with simple songs
Population (Ultimate)	Process	Evolution (compare species => history)	the simple songs of grackles would have been more similar to the ancestral species of starlings, which have diverged in the trait of learning a complex melody

ACTIVITY: Use "http://en.wikipedia.org" to learn more about "cause", "development", "function" and "evolution", in the context of anatomical as well as behavioral traits. Read more about how Dr. Konrad Lorenz promoted the concept that behavioral adaptations evolved by the same process of natural selection as anatomical traits.

Tutorial: Behavior, Ecology & Natural Selection
I. Conceptual Framework for Behavior
Folk Psychology - A popular "not scientific" perspective

One of the ways we all relate to other "critters" (including humans and cars), is to assume that others experience the world in the same way we do. This is a form of "anthropomorphism", meaning "in the human form". Anthropomorphic explanations are based on the mental model that animals have desires, beliefs and emotions like people do. When they apply critical thinking skills, scientists note that each species has both similarities and differences in emotions, compared to humans. This distinction may be as simple as Folk Psychology being more of a "right brain" or intuitive process, and Science being more of a "left brain" or analytical process. Using both "sides of the brain" is valuable for understanding animal behavior, just in different ways.

ACTIVITY: Use "http://en.wikipedia.org" to learn more about "anthropomorphism".

What is folk psychology (FP)?
Example of anthropomorphic explanations, worded in the Folk Psychology perspective, include:

- **Desires:** The dog wanted to go outside.
- **Beliefs:** The dog knew that if he barked, Casey would open the door.
- **Emotions:** The dog was happy when Casey opened the door.

ACTIVITY: During your everyday activities, practice listening for Folk Psychology statements. Reflect on how these anthropomorphic statements are worded in terms of desires, beliefs and emotions. Practice rewording one statement in terms of the language of science, as you learned in the previous tutorial page.

When should we use Folk Psychology?
Folk Psychology is appropriate to use when we are trying to communicate with people who have not been formally trained in the scientific perspectives on behavior. People who have a lot of experience with animals, intuitively may think in terms of human psychology. With our canine companions, we feel comfortable explaining behavior in terms of beliefs, desires and emotions. For example, you may hear Folk Psychology explanations at:

- a dog training class
- public outreach programs at zoos and reserves
- introductory textbooks
- brainstorming sessions when scientists develop an hypothesis that could be tested by collecting data
- problem solving in individual case studies, with a plan for behavioral modification to increase "good" behaviors and decrease "bad" behaviors

ACTIVITY: As you listen for Folk Psychology statements, pay attention to the context or source of the information. Make a list of the places where you find these statements, and reflect on how it is important to match the message to the audience.

Tutorial: Behavior, Ecology & Natural Selection

I. Conceptual Framework for Behavior

c. Folk Psychology vs. Scientific Perspectives

Ethologists seek to understand animal behavior from the **scientific perspective** of the organisms within their natural habitat, the environmental conditions to which each species is adapted. Some aspects of behavior are due to the experience of individuals within the particular environment where they grow up. Other aspects are due to the genome, the historical genetic legacy of each species; in other words information in molecules of DNA accumulated over generations.

Those aspects that refer to expression of the genotype in the phenotype of each individual are included in the concept of **proximate**. Those aspects that refer to accumulation of diverse genotypes within the gene pool of a species are included in the concept of **ultimate**. Different types of evidence are used to test scientific hypotheses about **proximate** compared to **ultimate** concepts.

When we are not thinking like a scientist, most of us use **folk psychology** to make sense of animal behavior. In other words, we project onto animals our own feelings, desires and beliefs. It takes a conscious effort to distinguish between the myths of **folk psychology** and the reality of **scientific perspectives**. For those who work and live with animals on a daily basis, it is worth the effort to learn the **scientific perspectives** to be able to more effectively find solutions to behavioral problems that cannot be solved through **folk psychology.**

From the perspective of ethologists, both **proximate** and **ultimate** questions are interesting. However, behavioral ecologists tend to focus more on the questions related to the **ultimate** perspectives and comparative psychologists or neuro-ethologists tend to focus more on the **proximate** perspectives. These specializations are important to consider when you look for scientific sources of information on a particular behavioral trait in one or more species.

More examples follow…. for educators, practitioners, scientists

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EDUCATORS' Example of Scientific Perspectives -Grackles Invade a Shopping Center
Observation | activity | Folk Psychology | Proximate Perspective | Ultimate Perspective
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Observation: Large flocks of black grackles converge on the supermarket parking lot in the evening in our city. They land in the trees, ridges along roofs and cars. They sing loudly and fly from one spot to another. They feed on whatever they can find under the cars, such as old French fries or potato chips. They drink from the puddles of water that drip off air-conditioners under the cars. I've seen a panting grackle move from the hot sun to the shade under a car. Typically, when one male lands next to another, he points his bill up at the sky. The other may respond in the same way, then they separate. When a female is nearby, typically a male spreads his tail, puffs his neck and sings. If she hops away, he follows.

Activity*: Observe blackbirds at a location where you have noticed them in flocks and write notes on what you actually see, hear, and smell. Interview others about what they have observed and how they feel about it. Analyze your observations from the following ethological perspectives: (1) Folk Psychology, (2) Tinbergen's Proximate Perspective, and (3) Tinbergen's Ultimate Perspective. Compare your analysis with the following examples written by an ethologist. Discuss what is similar and different. Summarize what you have learned about the distinction between Folk Psychology and Scientific Perspectives.*

Folk Psychology

The birds want to be safe from predators and they believe they will be less vulnerable if they roost in flocks. They are scared to roost alone. They want people to feed them with crumbs from the store, and harass people by flying at them. When they point their bills into the air, it is like turning away their weapons. They believe the other guy will be nicer or will be bluffed into turning away. Males are trying to attract females so they can pass on their genes to the next generation. Females are coy so the males will fight over them and females can choose the suitors with the best genes, to help survival of the species.

Tinbergen's Proximate (Causation & Development)

Each individual grackle is attracted to move closer to other birds of the same species. However, individuals learn to sit out of reach of the bill of each nearby bird. When they land too close, they get pecked. They fly in flocks, where the movements of the group result from individual decisions about orienting relative to each other. A small group may be attracted to food crumbs in a parking lot. More groups may join the small groups as night falls. They are attracted to other grackles and to trees with thick leaves and open branches where they perch. Nets placed over the trees reduce the attractiveness of roosts. In response to movements or noises typically associated with predators, they fly up, then settle in another tree. Disturbance may be more likely from an exposed site than from a sheltered, warmer site.

Tinbergen's Ultimate (Function & Evolution)

Genetically, grackles are more related to the species of weaverbirds in Africa, than they are to the starlings of Europe. The genome of grackle species has become adapted to environmental conditions of seasonally flooded coastal prairies, where they nest in scattered clumps of trees inaccessible to ground predators. Invasion of urban habitat provided by humans is fairly recent in the history of grackle species.

Flocking behavior is associated with two functions: finding patches of food and avoiding predators. The seeds providing food for blackbirds are likely to vary in location from week to week as the plants mature, from season to season as rainfall changes and from place to place depending on patchy rain and soil conditions. Those grackles that were attracted to other birds were more likely to find food than those that foraged alone. Those that roosted together were more likely to escape predators. To the extent that there is a heritable basis to flocking behavior, over the past history of the species, genotypes that favored flocking behavior would have persisted in the genome. Non-flocking genotypes would have been edited out of the gene pool.

PRACTITIONERS' Example of Scientific Perspectives - Nesting Behavior of Warblers

Observation | activity | Folk Psychology | Proximate Perspective | Ultimate Perspective

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Observation: Endangered yellow-cheek warblers choose nest sites close to mature stands of Ashe juniper on the Fort Hood Military Reservation, Texas. Warblers use fibrous strands of juniper bark and sticky spider webs to build nests. They forage for insects on the emerging leaves of oaks early in the growing season and later include the evergreen junipers. Nest sites are primarily in patches of mixed oak/juniper habitat (Magness et al. 2006). Nest success declines in smaller patches (<15 ha; Butcher et al.2010) possibly related to predators at the forest edge (Peak 2007). Based on studies of other species, nests that are in open sites and with more parental activity are more vulnerable to nest parasitism by brown-headed cowbirds (Aviles et al. 2006, Banks & Martin 2001). Migratory males arrive first in March, advertise and defend territories against other males. Males use a high-pitched, short call near females in the interior of the territory at the beginning of the nesting season (Bolsinger 2000). Nesting behavior varies, some reports assume males choose the nest site, other observations indicate that pairs choose nest sites together (Graber et al. 2006). Later in the nesting season, males

more frequently sing a complex song type, perched at the edge of a break in the forest canopy (Bolsinger 2000). No effects of military training activities could be detected on nesting behavior and the warbler population increased over 10 years (Anders & Dearborn 2004), despite a wildfire that burned 4,000 acres, likely reducing juniper density in burned patches for decades (Reemts & Hanson 2008). Causes of nest failure were similar between urban and rural forests (Reidy et al. 2008).

Activity: *Read more about the natural history of golden-cheeked warblers and listen to their two song types using links on Wikipedia. Read more about the Fort Hood Recovery Credit System in the news release "Army Finds Way to Recover Golden-cheeked Warbler". Imagine that you are in an outreach program and your job is to communicate with landowners around Fort Hood. Write down your ideas about how you would explain warbler nesting behavior. Apply what you have learned about Folk Psychology and Scientific Perspectives. Compare your descriptions with the following paragraphs and discuss similarities or differences.*

Folk Psychology

Warblers need juniper trees for nesting. They want to build their nests at the center of large patches of trees to avoid predation on nestlings. Males sing in order to defend a territory and attract a mate. Females want mates that have the best genes to pass on to their offspring. This helps the survival of the species. Conservationists believe that if all the oak/juniper habitat was cleared for agriculture, the species would go extinct. This warbler species nests only in Texas and could be wiped out by competition from cowbirds, because clearing juniper trees to improve cattle pastures will favor cowbirds, not golden-cheeked warblers.

Tinbergen's Proximate (Causation & Development)

Nesting behavior of golden-cheeked warblers is highly instinctive, meaning that they will pick a nest site, choose a mate of the same species and build the typical nest with juniper bark and spider webs without learning from others of their same species. Seasonal cues influence their migratory behavior in spring and fall. Starting in March, golden-cheeks return from over-wintering sites in central America, to the oak/juniper habitat of central Texas. With the decline in daylength in the fall, migratory restlessness increases in both adults and juveniles, stimulating individuals to fly south to wintering sites. Along this migratory path, both experienced and inexperienced birds pass over many different types of vegetation, responding specifically to settle in the oak/juniper habitat patches. The evidence for this is that golden-cheeks are not found nesting in other types of vegetation.

The hypothesis that golden-cheek males respond positively to the singing of other territorial males, is currently under investigation. The idea is that inexperienced yearling males fine-tune the choice of territory by choosing habitat patches where experienced males have settled, a mechanism of social facilitation. Each male learns to stay away from territorial neighbors after experiencing chases, indicating choice of territory is a complex combination of instinct and learning.

Although black-capped vireos nest in the same habitat patches as the golden-cheeks, the golden-cheek females are not attracted to the songs of other species, only to the soft calls of courting golden-cheek males. Golden-cheeks tend to choose nest sites surrounded by more branches, rather than open sites. Previous experience of the male and female of a pair likely influence variation in nesting behavior.

Tinbergen's Ultimate (Function & Evolution)

Nesting behavior of golden-cheeked warblers has diverged from other warbler species in their specialized adaptations to the oak/juniper vegetation. Those that nest in other vegetation or at the edges of oak/juniper patches are less likely to have successfully raised young. The function of nesting in the center of dense thickets appears to be reduction of predation and brood parasitism. In comparison to the golden-cheeks, vireos that nest in more open bushes are more vulnerable to

predation and parasitism in the same habitat patches.

Periodic disturbance by fire has been a part of the phylogenetic history of this species, which is adapted to an ecoregion typical of the edge between prairies and woods, maintained by fire. Although the entire southwestern region of the continent was covered with woods during previous glacial periods, the edge of the woods retreated in a northeasterly direction in the current inter-glacial period.

The migratory path of golden-cheeks is similar to other warbler species, a taxonomic group labeled "neo-tropical migrants". In comparison, other warbler species show behavioral adaptations that are associated with more generalist nesting strategies occupying a wider variety of vegetation types and larger regions than golden cheeks.

Although the physiological mechanisms controlling nesting behavior have not been studied in golden-cheeks, these mechanisms are well understood in other passerine species that have been studied. Based on these general models of avian reproductive physiology, we would hypothesize that (1) the migratory restlessness is controlled by photoperiod, (2) territorial singing by males stimulates male reproductive hormones, and (3) courtship singing and displays by males stimulate female reproductive hormones. Consistent with the concept of phylogenetic inertia, these reproductive traits appear to be ancestral in the avian genome, in other words the genetic systems relating social stimulation, hormones and behavior are shared among all species in the taxonomic family of Aves.

SCIENTISTS' Example of Scientific Perspectives - Infanticide in African Lions

Observation | activity | Folk Psychology | Proximate Perspective | Ultimate Perspective

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Observation: Although lions can breed throughout the year, females tend to give birth close to the same time (Krebs & Davies 1993:5). A short-term study reported only 20% of lion cubs survive to the age where they can reproduce (Krebs & Davies 1993:6). A long-term study reported 56% of male cubs survive to 9 months in the absence of male conflict in contrast to 14% of cubs exposed to male takeovers (Packer 2000). Groups of 6-12 mothers, daughters and sisters live together in locations where hunting success is good. One or more breeding males defend these groups of females and their cubs for 2-3 years, fighting off other males until they themselves are defeated. Young males disperse around the time of puberty and wander alone, or in small bachelor groups, until they are successful at ousting the aging breeding male(s) from the territory of a group of females. During these fights, infrequent attacks on cubs have been recorded (Krebs & Davies 1993:7). When a female loses her cub, hormonal changes in her body will bring her back into breeding readiness within 9 months. Otherwise, the interval between births is about 25 months for lactating females.

Activity: *On YouTube, search for videos labeled "Lion infanticide". As you watch the video clips, listen carefully to the narrator and take notes on phrases that are worded in terms of folk psychology and scientific perspectives. Apply what you have learned about Tinbergen's questions and write your own narrative from three perspectives: folk psychology, proximate and ultimate. Compare your narrative with the following paragraphs written by an ethologist. Discuss similarities and differences.*

Folk Psychology

On websites and even textbooks, lion infanticide is often described in terms of folk psychology. Some examples are: "Male lions use infanticide to get rid of offspring in a newly acquired pride that are not genetically related to the male coalition" (Shelburne 2004). "[A]ny individual that practices [sic] infanticide when he takes over a pride will father more of his own offspring and therefore the tendency to commit infanticide will spread" (Krebs & Davies 1993:7). "She needs protection from male harassment of her cubs for over 2 years in order to rear her cubs successfully" (Krebs & Davies 1993:7). "High sexual activity in females may therefore incite male-male competition and so result in

the best protectors taking over the pride" (Krebs & Davies 1993:8). "Infanticide has evolved simply because of its advantage to the male that practises it." (Krebs & Davies 1993:14). Statements like these contain a grain of truth, elaborated so they will be more appealing and intuitive to readers. However, they largely reflect views of sexuality and sociality prevalent in the cultural context of the authors. Readers who filter the information through a cultural lens of folk psychology are less likely to comprehend the scientific perspectives in the same source. Practicing skills of critical thinking helps informed readers to distinguish between folk psychology and scientific perspectives.

Tinbergen's Proximate (Causation & Development)
Repeated physical stimulation of the cervix is the physiological mechanism causing reflexive ovulation in lions. Without the stimulus of repeated copulation, the ovulatory reflex does not occur, meaning ova are not released into the oviduct even though a female may be in a hormonal state of breeding readiness (estrus). During estrus, when females crouch, roll and rub in response to male advances, copulation may occur as often as 15-min. intervals. Duration of estrus usually varies from 2-4 days; shorter periods of courtship activity rarely result in pregnancies. Since the hormones of lactation suppress the mechanisms of ovulation, estrus is unlikely until yearling cubs are weaned. When several females lose cubs simultaneously, the internal state of estrus is more likely to be synchronized and to cycle monthly until pregnancy occurs. Although females seek isolation at birth, when they return to the group with cubs, they may not distinguish between other familiar cubs and their own while nursing. Compared to males that disperse alone, young males that disperse together are more likely to survive and successfully challenge the breeding male(s) defending another group of females. During male invasions, unfamiliar cubs are more vulnerable to attack than females and yearlings. Familiar pheromones and defense by females may inhibit resident male attack on cubs born into the group during stable periods between male conflict.

Tinbergen's Ultimate (Function & Evolution)
Reflexive ovulation in the taxonomic family Felidae is an example of the concept of phylogenetic inertia, meaning a heritable trait that has persisted from the more ancestral solitary species to more recently derived social species like African lions. Also an example of phylogenetic inertia, the tendency for males to kill cubs is similar in both solitary and social species of felids. The social lions differ because resident males do not kill familiar cubs, the ones born during the 2-3 years that they defend the female group from other intruders. In solitary species, males do not remain with females outside estrous periods. Logically, the inhibition of killing would be hypothesized to be a more recently derived behavioral trait, and the tendency to kill strange cubs theoretically would be more ancestral, having persisted in the felid genome for millions of years.

Reflexive ovulation is also an example of the concept of a divergent trait when compared with other carnivore families such as the Canidae. For example the genome of jackals and African wild dogs codes for mechanisms of (1) spontaneous ovulation and (2) male care of familiar pups, even those that are not direct offspring. Although the recently evolved sociality of group-hunting in lions and wild dogs fits the concept of convergent evolution, reflexive ovulation and paternal care diverged much earlier in the phylogenetic history of the carnivore genome.

Infanticide behavior is associated with testable hypotheses about several functions: (1) Those male lions that were more likely to kill unfamiliar cubs and inhibit killing familiar cubs would have had higher lifetime reproductive success than those that did not kill unfamiliar cubs. (2) The genotypes of males that did not kill familiar cubs would have increased in future generations compared to those that killed their own cubs. (3) The sons of males that killed unfamiliar cubs would have been more likely to survive and reproduce because they were more likely to form successful male coalitions.

Tutorial: Behavior, Ecology & Natural Selection
III. Natural Selection: The Process
Elaboration: Examples of the application of Tinbergen's Conceptual Framework

In the first chapter of your textbook, several examples are used to illustrate the scientific perspective on behavior. However, the concepts are implicit and hard to pick out of the reading. It's a balance between a "good read" and introducing new perspectives. Here we try to make the concepts more explicit so they are easier to compare and to learn. If these concepts were presented in other terms in your previous courses, be aware that "learned filters" may make your comprehension of the material more difficult. Sometimes "old habits" have to be unlearned before the new concepts can be absorbed and applied.

Components of the Logical Argument

CDFE=> VHDP

- Variation in the trait
- Heritability of the variation
- Differential fitness of genotypes
- Proportion of genotypes changes in population over generations

Logic of natural selection as applied to starlings

- If individuals vary in complexity of songs they sing.
- If the ability to learn complex songs is highly heritable.
- If complex songs are more likely to attract mates and repel rivals.
- Then starlings would have diverged over evolutionary time, showing an increase in the heritable ability to learn complex songs.

Logic of natural selection as applied to lions

- If individuals vary in attacking cubs;
- If the ability to learn to distinguish between strange and familiar cubs is highly heritable;
- If infanticide of strange cubs is more likely to bring females into estrus sooner, and tolerance of familiar cubs is associated with higher offspring survival;
- Then infanticide would have persisted in social species, such as lions, along with genotypes associated with learned inhibition against killing familiar cubs.

Tutorial: Behavior, Ecology & Natural Selection
III. Natural Selection: The Process
Starlings Example

Not all birds sing in the spring, but those that do, contribute to one of the joys of the season. This experience raises the intriquing question of why some birds sing and other do not. From a Folk Psychology perspective, we might just explain "birds sing because they are happy". Applying critical thinking skills, a scientist would ask "how do we measure happiness"? How could we test an hypothesis that relates happiness to singing? It would be very difficult because it is so hard to measure "happiness" even in our own species! Starlings are a good example, because they have spread all over the world and most of us have shared the experience of listening and watching these blackbirds or related species such as grackles. So lets apply Tinbergen's four questions to the behavior of singing in starlings. As we do this, look for the logic of natural selection and how the answer to each question relates to the next.

Causation (Stimulus/response)?
The reproductive hormones of male starlings are stimulated by the light:dark ratios in the spring, also called seasonal photoperiod. When testosterone is high, males are much more likely to respond to mates and rivals with a burst of melodic song. This sound is produced by air vibrating as it passes through the trachea. Changes in the shape of the trachea cause the pitch of each note to change, as controlled by muscular activity in the throat and diaphragm. The short-term "trigger stimulus" is another starling, the "action response" is a melodic song. The probability of this response is modified by internal hormonal state (mood). The "priming stimulus" is photoperiod, which has an effect over several weeks of exposure to lengthening daylight. When testosterone is very high, the threshold for response may be very low, such that males sing spontaneously, even at times when no other bird is visible.

ACTIVITY: Could you think of ways to test the relation between these various cause and effect variables?

Development (Ontogeny)?
Individual starlings do not sing melodic songs instinctively, without any learning. When they first learn to produce sounds, the notes are in simple combinations, analogous to "baby talk". At a certain age, they listen to the males singing around them, and begin to produce more complex songs. If an individual is isolated during this sensitive period of development, the learned song will be different than individuals raised with the sound of adult males singing. We hypothesize that the ability to learn is highly heritable, i.e. the "nature" part of development. The actual song is learned, shaped by the sounds in each individual's environment, i.e. the "nurture" part. Producing single notes is instinctive, as is the ability to learn. The melodic song is not instinctive, rather the result of a genotype interacting with the environment. The sons of isolated males do not inherit their father's simple songs, they learn the complex songs of the adults in the environment where they develop.

ACTIVITY: Could you think of ways to test what is learned and what is inherited about the singing behavior of starlings?

Function (Adaptation)?
Those starlings that sing complex melodies are more likely to attract mates and repel rivals than those that produce single notes. Within a population, individuals more likely to attract mates and repel rivals are more likely to reproduce. Their genotypes are more likely to be represented in the gene pool of the next generation. However, if the difference between singing "complex melodies" and "simple notes" is more a matter of learning (phenotype) than heritability (genotype), there will be no change in the proportion of genotypes passed from one generation to the next. Lets try a thought experiment about behavioral adaptation. Imagine there was a genotype that coded for "complex song", and another that coded for "simple notes" in the population. Imagine that a new river split the population of starlings in two, and starlings did not cross the river. If the females on one side of the river were more attracted to males that learned to sing more complex songs, we would predict the % genotype "complex song" to increase in the population, compared to the % of the "simple note" genotype. If the females on the other side of the river did not favor "complex" over "simple" songs, then we would predict no change in the % of "complex" or "simple" genotypes.

ACTIVITY: Could you think of ways to test the adaptive function of song-learning ability in starlings?

Evolution (Phylogeny)?
Starlings are a passerine species in the order "Passeriformes", a taxonomic family that includes thousands of species of perching birds and songbirds. These species vary in the complexity of song-learning. When we use the word "species", we are referring to a distinctive "gene pool" of a population, not to be confused with each of the individuals that carry the genotypes within the population. The Superfamily "Passeroidea" includes the family "Icteridae", the grackles, blackbirds and orioles of the New World. Starlings are one of the blackbird species. TIP: Use en.wikipedia.org to learn more about passerines. The grackle, blackbird and oriole species share a common ancestral species in their phylogenetic history. We hypothesize that the simple song was an ancestral trait, since it is shared by all species in this family. However, the songs of blackbird species are more complex than grackle species. The songs of orioles are more melodic than blackbird species. The hypothesis is that blackbirds diverged from grackles, due to a change in the social environment of their ancestors. Over thousands of generations, genotypes coding for the ability to learn complex songs increased in the ancestral populations of blackbirds but not of grackles. We do not know of an hypothesis as to which specific change in the environment resulted in this divergence of the trait. Logically, the change would somehow have been related to the choosiness of females or the "intimidation" factor between males.

ACTIVITY: Could you think of ways to test the divergent evolution hypothesis about the differences in singing traits of blackbirds and grackles? Blackbirds and orioles?

Tutorial: Behavior, Ecology & Natural Selection
III. Natural Selection: The Process
Lions Example

By applying the same logic of natural selection to another example, you will understand more deeply how the conceptual framework of Tinbergen's 4 questions provide a set of umbrella concepts with general utility. Although many of us have only observed African lions in zoos or on TV, their regal bearing and shear power are fascinating. Are they merely an overgrown domestic cat? Do they really live together for the good of the species? Why do both tomcats and lions kill cubs?

Causation (Stimulus/response)?

When rival males fight for control of a group of females (a pride of lions), sometimes cubs are killed. These cubs are likely unfamiliar to the intruding males, and fearful of the strangers. They are a weaker target than the other subadults and females in the group. The stimulus is the strange cub and the response is the male's bite or a swatting blow with a forepaw. The context of this behavior is likely to be the confusion associated with the conflict between males. The intruding males are likely to be in an internal state of high testosterone and activity of the adrenal (fight/flight) system, a "neurendocrine cocktail" in the brain associated with an excitable "mood".

ACTIVITY: Could you think of a way to test the hypothesis that male lions are more likely to kill strange cubs than familiar cubs?

Development (Ontogeny)?

When male lions are born into a group, they grow up with other cubs and learn what to predict from the behavior of subadults and adults within the pride. As they reach puberty, they are likely to disperse, often with members of the same age cohort, their "playpals". They wander, looking for females in breeding condition who are not protected by vigorous males. When they find a group of females, they are likely to challenge the defending males, assessing their own strength relative to the strength of the defenders. Given signs of weakness in the defenders, the intruding males are likely to escalate conflict and fight until the defenders are intimidated, leave, or die. This is the context in which strange cubs may trigger infanticide by intruding males. After the intruding males have reproduced with the females, they are unlikely to kill familiar cubs. However, they are not presented with many opportunities due to the maternal protectiveness of the mothers.

ACTIVITY: Could you think of a way to test the hypothesis that infanticide is not always an instinctive response to all cubs, i.e. tolerance of familiar cubs is learned?

Function (Adaptation)?
When an intruding male lion kills a cub, the cub's mother will cycle within months. The result is that intruding males reproduce sooner when they kill cubs than when they do not kill cubs. Those that killed cubs would have been more likely to produce more offspring, within the few years that they were vigorous enough to defend the pride of females from rival males. Let's try a thought experiment about behavioral adaptation. Imagine there is a genotype that is "equally tolerant" of strange and familiar cubs. Imagine a "killer" genotype that attacks both strange and familiar cubs. Imagine a third genotype that "distinguishes" between strange and familiar cubs, killing strange but not familiar cubs. From one generation to the next, we would predict the "distinguisher" genotype to increase in percentage within the population compared to the "killer" and "tolerant" genotypes. Think out the logic. The "killer" genotypes would have killed off their own offspring. The "tolerant" genotypes would have produced fewer offspring, in the same amount of time, compared to the "distinguisher" genotypes.

ACTIVITY: Could you think of a way to test the hypothesis about the shifting balance of genotypes in a population of lions, using computer modeling?

Evolution (Phylogeny)?
African lions are classified within the Felidae family, which includes 41 species. Based on genetic evidence, the living species diverged from a common ancestral species about 10-11 million years ago. African lions are classified in the genus Panthera, which retains more ancestral genetic characteristics compared to the genus Felis. Domestic cats are in the genus Felis, so may be described as more recently diverged from the ancestral lineage. Compared to other species of Panthera, lions are more social than jaguar, leopard or tiger. To the best of our knowledge, the males of all species of cats show cub-killing behavior. So we would hypothesize that it has persisted in the genome due to "phylogenetic inertia", a term that means a slow rate of change over time. Logically, we hypothesize the genotype was present in the ancestors of modern cat species and nothing changed in the environment that would have resulted in a decrease of the "infanticide" genotype over evolutionary history of these species. Based on the logic of natural selection, we would hypothesize that tolerance of familiar cubs is a derived trait, associated with the divergence of the social lions from an asocial ancestral species. In general, we hypothesize that sociality is a more derived trait. However, we need to keep an open mind, because changes in environments could result in convergent evolution among asocial species, such that a previously social species "loses" its social traits.

ACTIVITY: Could you predict the changes in the environment that might have been associated with the divergence of sociality within the genus panthera?