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

---

EDUCATORS' Example of Scientific Perspectives -Grackles Invade a Shopping Center
Observation | activity | Folk Psychology | Proximate Perspective | Ultimate Perspective
----

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 blackbird species of North America. 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

---

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

---

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 practises 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.