Lecture notes by Edward Loper

Course: 9.20 (Animal Behavior)
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Ecology: "Behavioral Ecology and Social Biology" online at

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http://link.springer-nm.com/link/service/journals/00265/tocs.htm
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1 Evolution

Defintion (in our context): change in characteristics of biological entities over generations. Exists among populations of entities. requirements:

1. populations made of variable individuals
2. variation is heritable
3. variation is random (esp. not directed by environment)
4. change in proportion of individuals with a characteristic in a population occurs. Dictated by chance (genetic drift) and by natural selection. Genetic drift more signifigant for smaller populations. Natural selection is differential reproduction & survival, and accounts for adaptation.
5. populations may subdivide (speciation)

2 History: Pre-Darwin

- Greeks: projection of archetype on world gives individuals. Basically, species don't change.
- Early Christian: species don't change. Also, there is a chain of perfection: God ← Angels ← humans ← [animals]. The chain is unchanging. Thus, no extinctions and no new species.
- Linnaeus: created taxonomy based on similarity of form. Not based on phylogeny.
- De Buffon: each species has an internal model of what it should look like. Closely related species may have had a common ancestor. Postulated that animals could be differentially modified by their environment.
- Lamark: Species naturally improve. Speciation occurs from the simplest animal:

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        /A4
       /
      / /A3
     / /     } species chain we see today
    / / /A2
   / / /
  / / / /A1
 / / / /
S S S S S ← simplest species (spontaneous generation)
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Believed that animals adapted differentially to the environment. Giraffe example.

3 History: Darwin (early 19th century)

- Travelled with the hms beagle on south american coast. In the gallopogos islands, found closely related species varying from island to island.
- Read pamplet by Malthus (who said that eventually there would be too many people to be fed – will lead to famine). Noticed that populations don't live up to reproductive limit. So if some individuals are more likely to reproduce, and traits are heritable, you can get natural selection..
- Spent 20 years thinking about implications etc. Recieved manuscript from Wallace. Presented both his and Wallace's papers, and finished his book.
- Theses of the book:

1. all species have arisen continuously from few 1st species
2. similar species have diverged from a recent common ancestor by accumulation of small changes
3. different groups diverged from a more ancient ancestor.
4. causal agent of evolution is differential reproduction.
5. Break-down of Theories presented by Darwin:
6. Evolution (change over time) exists
7. Common descent: even with humans
8. Gradualism: multiple small steps
9. Populational speciation: evolution occurs in populations
10. Natural selection: dictates how evolution occurs

4 History: Post-Darwin

- Agreement that evolution had occured, but dispute on mechanisms.
- Neo-Lamarkism: inheritance of acquired characteristics. Researcher showed that, even if you cut tails off mice, they won't ever give children with short tails.
- Mutationism: mendellians claimed that mutation accounts for speciation. Believed that any mutation that can survive will persist. Most mutations are bad, but occasionally one will create a new species.

5 History: Modern Synthesis

- Reconcilliation between genetics & darwinism & palentology etc.
- Tennants:
  1. Phoenotype (observed characteristic) differs from the genotype. Individual differences are partially
  2. Environmental effects on phoenotype are not transmitted to genotype
  3. Phoenotype is based on genes
  4. Genes mutate to different alleles randomly
  5. Evolutionary change is a populational process.
  6. Mutation is too slow to shift a population from one type to another: need some other form of selection.
  7. Natural populations are variable within a species. Differences are based on genetic effects.
  8. Natural selection occurs in nature (in the present). Differences in populations of species is adaptive. (e.g., house sparrows are an English species, which varies very little in traits 1..n. But it was released into US, and here there is lots of variation. 100 generations later, found correlation between body mass & climate, etc. Another example: in a year of drought, galopogos pigeon beaks grew by 5%, since only big nuts survived drought, and need big beaks to crack nuts. Another: Annolus introduced experimentally to several islands that didn't have any annolus's. Previously, annolus's that hung to big branches would have big hindlimbs, small branches would have small hindlimbs. Found that the average limb side went down for islands with small branches etc.
  9. There is a continuum between the small changes and speciation. Thus, genetically isolated populations can diverge enough from original populations to form a new species. (Species are defined as seperate (non-breeding) populations)
  10. Fossil record has gaps: there are specific conditions that need to occur for fossils to be created, so there simply aren't any fossils from some times & places. Nevertheless, there are still continuous changes etc.

Wednesday, September 15, 1999

6 Problems with the Modern Synthesis

1. Traditionally, M.S. has a conception of an organism as a mosaic of traits, where each trait is independantly optimized. But animals are built up from what ancestors have gone through. The phylogeny constrains the evolutionary paths. Also, traits must be integrated within an organism. Thus, we shouldn't expect all traits to be "useful," since it may take lots of energy to restructure things to get rid of them. Also, traits can be byproducts of the way other things develop, or constraints of the way things happen. E.g., skull sutures are not adaptive, but are just a byproduct of the way the skull develops. Thus, it's important to consider a trait in the context of an organism (esp. it's phylogeny and ontology).

1. M.S. assumes that there is a short connection between genes and traits. But genes just code for protiens – many steps between genes and traits. These steps interact with genome and environment. Also, M.S. ignores the ability of animals to change their environment. Thus, heritable doesn't really mean genes – the parents give much more to the child than just the genes (e.g., modified environment, etc). As a special case, consider culture.

7 Natural Selection

7.1 Prerequesites for Natural Selection

1. Variation
2. Heritable variation
3. Some traits are better adapted to environment than others (Differential adaptation)
4. Individuals with these traits will consistantly leave more offspring in next generation (Differential reproduction)

Define fitness as the average rate of increase of a trait over generations.

7.2 "Selection of" and "Selection for"

Consider a toy which filters balls through progressively smaller holes. But big balls tend to be a different color than small ones. This toy selects $_f$or small balls, but there is still a selection of small-colored-balls. E.g., there is selection for opposable thumbs, with the incidental effect that there is selection of piano players. Note that we select $_f$or traits, not "for avoidance of extinction".

7.3 Levels of Selection

Group selection vs. G. C. Williams. Altruistic genotype will leave less offspring than non-altruists. Also, groups succeptible to cheaters. Thus, altruistic trait can't evolve by Darwinian (natural) selection. Then we resort to group selection (i.e., selection between groups). Groups with altruistic traits will tend to survive more than selfish groups.

But there are many problems:

- very hard to find populations which are so isolated that cheaters won't "contaminate" them.
- alternate explanations possible for seemingly altruistic behaviors.
- many many more individuals than populations. Individuals are born & die much much faster than populations do. Difference between individuals in a population tends to be much higher than differences

between populations. Thus, natural selection is much much faster than group selection. In general, natural selection will almost always win over group selection.

8 Adaptations

8.1 Definitions

Adaptation is both a feature of an organism, and a process...

1. An adaptation is a phoenotypic variant that results in the highest fitness than the alternative variants.
2. An adaptation is derived from ancestoral populations. Define adapation in terms of its history
3. Syntheis: An adaptation is a trait that has become prevalant or remains prevalant because of natural selection..

8.2 How do we identify an adaptation?

We can identify adaptations (heuristically) by:

- complexity
- seems to be "designed" to do something that increases fitness.
- experiments: artificially modify the trait in a population, and see if it affects fitness etc. (e.g., moths on polluted trees)
- comparitive method: animals that have come to the same solution, but by different unrelated species, then we expect that to show a common selection pressure.

8.3 Caveats (What not to expect)

1. An adaptation doesn't have to be necessary for survival.
2. Don't expect perfection
3. Don't expect "progress"
4. Don't expect harmony or balance, just stability
5. Evolution is ammoral

9 The Study of Animal Behavior

9.1 Observation and Description

You must begin by observing and describing an animal's natural behavior. This both generates questions, and allows us to tell more about what the animal is doing. Have to deal with abstraction and bias. When and where to observe? Behaviors change over time and place. Also, what behaviors to observe? Distinguish function and mechanism. When we ask "why" an animal sings, we can talk about evolutionary reasons, or immediate causes (mechanisms). Also, examine in terms of ontogeny (development) or phylogeny: birds sing because their ancestors did; birds sing because they developed in certain ways that lead to that.

9.2 Tinbergen's Questions

The following four questions are all valid, and none can be reduced to the others. We can answer any of them about adaptations or behavior etc.

1. causation: proximal mechanism
2. ontogeny: how it developed
3. phylogeny: how it evolved

4. survival value: how it affects fitness

Book groups 1-3 as proximate, and 4 as ultimate (distal?).

9.3 The Importance of Keeping Questions Seperate

These 4 questions can't be reduced to each other. Be sure to differentiate them, and not confuse them.

Monday, September 20, 1999

10 Animal Behavior: Two Traditions

There have traditionally been two separate traditions of study for animal behavior: ethology and animal (comparative) psychology.

Ethologists were trained as zoologists, and studied a wide variety of animals. Their emphasis was on instinct and evolved behavior. Methods were careful explanation and field explanation. Ethologists were mainly from Europe.

Animal psychologists were trained as psychologists, studied mainly mammals, and especially lab rats. Their emphasis was on learning and the development of theories of behavior. Methods were lab work, control of variables, and statistical analysis.

10.1 The Research Emphasis of Ethology

Developed in 30's $\rightarrow$ 50's. The study of evolution of behavior & instinct. Instinct = adaptive behaviors used to solve problems in the natural world. Instinctual behaviors were thought of as being adapted, and not learned. Took each species at face value (not a model of a human behavior, & no "scala natura"). Emphasis on complex behavior. Documented behavior very well, but tended to avoid experimentation.

10.2 The Research Emphasis of Animal Psychology

Search for a general set of rules that could be applied to all animals to describe their behavior. Emphasis on the modifiability of behavior (learning). Early emphasis on studying many different animals, but this went away. Animal psychologists ultimately wanted to understand human behavior, & incorperates the "scala natura". Domesticated mouse, and inbred them to reduce variability between individuals. Wanted to eliminate subjective reporting, & advocated control. Simplified behavior & examined one variable at a time.

11 Conceptual Stances of Ethology and Animal Psychology

11.1 Ethology

Interested in mechanism and by evolution of behavior.

Fixed Action Patterns

A stereotyped sequence of actions that happen in a rigid, predictable, highly structured way. Complex patterns, not just simple reflexes. Characteristic of a single species, and true of all animals of that species (under the correct circumstances). Behavior elicited by specific and simple stimuli. (self-exhausting: eventually you'll stop doing it) Behavior is triggered, and once begun will occur independantly of the environment. Behavior is independant of experience.

e.g., egg rolling: if a goose spots an egg out of its nest, it orients, goes through a series of motions to roll the egg back to the nest. This movement is very stereotyped – will continue without feedback (even if egg is removed). (however, the stabalizing aspect of the behavior wasn't as stereotyped).

Sign Stimulus

Simple but specific stimulus that elicits a specific response. Also known as a ”releaser”. e.g., the egg in goose example. A ”super-normal” stimulus (e.g., a really big egg) may elicit a stronger response. Ethologists studied what aspects of a sign stimulus were the crucial ones.

Innate Releasing Mechanism

”Innate releasing mechanism” is responsible for detecting the sign stimulus and releasing the fixed action pattern (no one's found one yet).

The Umwelt

”The world around me”: each animal has its own world view, and different animals are sensitive to different things in their environment. e.g., humans are blind to many stimuli that other animals use. Bees can detect uv and some fish, electric signals.

Function or Survival Value of Behavior

What's the survival value of a behavior? E.g., egg-shell removal experiment. White on eggs increases predation. Eggs with shells near them are more likely to be eaten. Thus, function is to decrease predation.

11.2 Animal Psychology: Themes and Personalities

Process of Learning (Thorndike's Law of Effect)

Thorndike put cats in puzzle boxes, where the cat must do something to open the door. Looked at how long it took animals to figure out to escape. Over time, animals got better at escaping. Thorndike's law: if an action A is followed by a reward R, then A will be more likely to occur in the future (operant conditioning).

Insight/Animal Intelligence (Kohler)

Kohler thoguht animals have insights that allow them to solve problems. E.g., chimpanzees stacking boxes to get banannas. More of a cognitive approach, and less of a stimulus-response one.

Content of Learning and Animal Thought

What types of things can animals learn?

Lashley tested whether mice could distinguish different visual cues. Used doors with different pictures, and even relatively similar pictures (dots of 2 sizes) could be distinguished. Also, they could learn to pick the odd-door-out of 3 doors.

Tolman said we should be asking how a behavior allows an animal to accomplish its goals. Animals learn things other than stimulus-response connections. Latent learning: animals learn (e.g., spacial information) even when there's no reward or punishment: If you train a rat in a maze with a cheese reward, they'll get better and better. However, if you just place a rat in a maze without cheese, and then place it in a maze with a cheese reward, they'll get better much faster. Tolmen claimed animals have complex representations of their environment (e.g., a ”map” of the spacial layout). In contrast to learning things like ”left right right left left”. Tolman tested this with a plus-maze (tubes to N, S, E, W). Blocked off N, placed rat in S, and put food in E. Later blocked off S, placed rat in N, and food in E. According to map theory, rat will go to the right place. According to the stimulus-response theory (rat just learned ”turn right”), it will go to the wrong place (W). (But if you give the rats no visual cues outside the maze, they will go to the wrong place (W).)

Behaviorism and its demise

Behaviorism ran opposite to ethology. Claimed:

- only observable behaviors should be theorized about
- measure only external variables (not internal states)
- all behaviors are learned S $\rightarrow$ R associations
- operant conditioning
- equipotentiality: all behaviors follow the same principles of learning (regardless of animal & task)

Behaviorism died out (replaced by cog. psych.). Equipotentiality is false (e.g., much easier to associate tone w/ shock or food with indigestion).

12 Comparative Psychology and Ethology

12.1 Interactions and Conflict

Cog. Psychologists interested in some of the same things as ethologists. Psychologists didn't like the fact that ethologists didn't do experiments. Ethologists didn't like the lack of variety in cog. psych., nor their lack of interrest in adaptation and evolution.

12.2 Common Ground

Eventually realized that much of their conflict came from confusing what questions they were trying to answer. Cog. psych. studied mainly mechanism, and ethology mainly evolution.

13 The Splintering of Animal Behavior: Tinbergen's 4 Questions

13.1 Survival Value – The Rise of Behavioral Ecology

Understanding the relationship between an animal's ecology and its behavior.

1. Economic Models of Behavior: the design of a particular

behavior is designed to be an optimally efficient solution. Must consider the trade-offs between different costs & rewards of all the different behaiors

1. Evolutionarily Stable Strategies: the behavior of one

animal depends heavily on the behaviors of the animals in its environment.

1. Evolution of Social Behavior (Sociobiology)

13.2 Immediate Causation – Neuroethology and Physiological Psychology

Neuroethology – studying how neural configurations cause behavior physiological psychology – studies of hormones, etc.

13.3 Ontogeny – Developmental Psychobiology

13.4 Evolution (or Phylogeny) – ignored till recently

14 The Beginning of a Re-Integration

Wednesday, September 22, 1999

15 The Comparative Approach

Why do we find the differences between species that we do? (e.g., why is species A solitary and species B gregarious). Compare groups of related species, and figure out how differences in behavior reflect differences in Ecology.

15.1 Useful in the search for Adaptations

Differences between related species suggest adaptations.

15.2 Early Studies (John Crook, 1964)

Studied about 90 species of weaver bird. Varying social organizations. Some build individual nests, others build huge group nests. Some species monogomous, some polygomous. Looked for correlations between ecology and social organizations: types of food, abundance of food, predatory pressure, nest-site location. Showed that weaver birds could be classified in 2 basic categories:

Forest-dwellers eat insects, live in solitude, defend large territories, build hidden cryptic solitary nests, and are monogomous, and are monomorphic (both sexes look the same).

Savanah-dwellers eat seeds, feed in flocks, nest colonially in the open (not hidden), and are polygomous. Males tended to be more brightly colored and ornamented.

Hypothesized that predation and food drive the social organization. In forest, insects are dispersed food resources. Need large territory to get enough food. Need two parents to provide enough food for children ($\rightarrow$ monogomy). Both sexes are camoflogued, as is nest. In savanah, seeds are patchy and super-abundant locally. Finding patches best done in a group. Enough food in the patch to go around. In the open country, you can't hide nest very easily. Safe nesting sites are a scarce resource – colonial sites. Within a nest site (tree), there are some better nest sites than others. Competition for the best nest sites leads to polygony: females tend to mate with males in better nesting sites.

15.3 Problems with this approach:

Alternative Hypothesis

It's a little too easy to explain the data without testing – there are many different possible explanations, and even though one sounds reasonable, it may not be correct.

Cause and Effect

Can't tell which is cause, and which is effect. For example, diet of seeds could be a cause instead of an effect.

Confounding Variables

If A correlates with B, it may just be because they both correlate with C. E.g., body size can be a confounding variable.

Different Solutions

Differences you see between species may not reflect differences in ecological pressure – may just represent two different solutions to the same problem. E.g., ram horns derived from skin, and deer horns from bone; but this is probably not caused by different ecological pressures.

15.4 The Big Problem: "We forgot about Phylogeny"

The evolutionary history of an animal needs to be taken into acount. This has been called "the problem of independance of data points."

Hoglund, 1989

Testing the hypothesis that differences were caused by Lek-ing: large area, but during mating all males congregate in a small location, and females come to observe females. Found that in Lek-ing species, males were more likely to be larger and to have plumage than in non-lek-ing species. However, when he examined phylogeny, he found a very high correlation between lek-ing and dimorphism in one particular group of animals – biased the whole analysis. Basically, he showed that the correlation between lek-ing and dimorphism might be explained by common ancestors.

How do we fix it?

Conservative approach – use higher taxanomic groups. That way, we can hopefully rule out the common-ancestor explanation. But this disregards lots of useful data.

Independant contrasts; e.g., DeVoogd et al, 1992: First, construct a phylogenetic tree (don't use the characteristics you're looking at). Take contrasts between two different nodes (D&E or F&G or DE&FG).

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D  E  F  G
 \/    \/
  \    /
   \  /
    \/
(This is a Cladogram)
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In particular, compare how differences in the characteristic you care about relate to the "distances" between different species.

For example, for songbirds, compare the differences in HVC volume and in song repetoire sides (after compensating for brain size etc) between different nodes. Then look for correlation. For example, with Leking and dimorphism, measure both between each pair of nodes, and then plot the correlation.

16 Phylogeny and the Evolution of Behavior

Phylogeny:

- Allows you to generate hypotheses for future studies.
- Allows you to test hypotheses with variables you can't really manipulate (polygomy)
- Find out how a trait evolved

16.1 Behavior does not fossilize

It's very difficult to find any information about the behavior of previous species.

16.2 Cladistics

Reconstruct Phylogeny

But you can try to use behavior to reconstruct a phylogeny.

Trace evolution of behavior from phylogeny (assumes that most change occurs from speciation, not from slow change over time).

Create cladogram (using molecular techniques, etc). Then create monophyletic groups (all species that share a common ancestor). Do NOT group animals just based on their features: paraphyletic groups. In the cladogram above, the groupings [D] [EFG] are paraphyletic. Also, avoid polyphyletic groups: [D][EF][G] in the cladogram above. (eg., grouping birds and bats)

Define an ingroup. Then define the sister group and the outgroups (sister group is just the closest outgroup).

Some Concepts in Cladistics

16.3 The Problem of Homology

Homology: a character of 2 or more taxa which is found in the common ancestor; a trait shared by common descent. Note that this can be tricky: bird wings and bat wings are homologous at the level of both deriving from forelimbs, but are not homologous as wings.

Homoplasy: similarity in form without common ancestor. Arises from convergent evolution, or because of parallelism.

Always begin by assuming that traits are homologous. If not, then we'll find out after our analysis.

16.4 Reconstruct History of Trait

Parsimony

If you're confronted by 2 competing theories, choose the simpler one. In particular, try to figure out how to get your traits with the fewest changes. Consider, in the cladogram above, A=X, B=X, C=-, D=X. Comparing C and D, look at outgroups, and come up with the hypothesis that the character was gained at [ABCD] or below, and was lost at C: this gives 2 transitions. Lets us infer that [CD]=C and [ABCD]=X. Note that if a trait is common to every animal in the group, this doesn't tell us anything.

Outgroups

Note that we cannot ignore any outgroups – doing so might give misleading results.

Example: Agression in Sticklebacks

Tinburgen hypothesized: the more agressive a species, the more likely to find ritualization: allows species to form hierarchies using ritual fighting instead of real fighting. Phylogenetic tests supported this hypothesis.

Example

Hypothesis: sexual selection can cause speciation. In many groups that speciate a lot, dimorphism is common. Test it with phylogeny.

17 Behavior and Evolution

Monday, September 27, 1999

18 Basic Concepts in Behavioral Ontogeny

Animals inherit more than just genes – they inheret a species- specific environment.

Originally, the study of ontogeny was regarded as the study of ”instincts.”

18.1 What is an Instinct?

Instincts are thought of as adaptive traits that an animal is born with; they are species-specific and don’t require learning. Usually it responds to a very narrow class of stimuli. It occurs the very first time you need it.

People often conflate ”genetic” with ”innate” or ”instinctive.” Often, people also think that instincts ... The idea of instinct also suggests that there is a strict genetic program that doesn’t get affected by the environment. People think calling something instinctive ”explains” it.

You can ask where variation comes from (genes or environment), but you can’t ask whether genes cause something or whether the environment does – they always work together..

We need to know how behaviors arise – we can’t just decide something is innate and then leave it at that.

18.2 Relationship between Genes and Behavior

The relationship between genes & behavior is moderated through many levels: genes, chromosome, nucleus, cytoplasm, tissue, organ, organism, environment.. All of these layers can interact with each other, and interact within the layers. ”Probablistic epigenesis” – we don’t develop in a lockstep, mechanical fashion. Instead, different layers interact in a nondeterministic way to give rise to animals.

All species-specific behaviors have developmental histories, and change over time. Furthermore, different factors can affect them at different points of development.

18.3 Ontogenetic Niche

Animals are formed and grow up in a specific environmental and social setting: breeding grounds, food, breeding grounds, parents, etc. This environmental information is ”inhereted” along with the genes. Thus, species-typical behaviors may depend (in part) on the fact that there is a species-typical environment.

18.4 Ontogenetic Adaptations

Animal must adapt and survive in its ontogenetic niche. Animals often need very specific adaptations for different points in development. Thus, some adaptations exist because they are necessary at one specific point in an animal’s development.

For example, in rats, we find that rats develop lactase early, but it drops at about 15 days of age. They develop other enzymes at about 15 days. Thus, presence of lactase is an ontogenetic adaptation – needed for nursing, not needed later.

At any point, an animal must develop both to survive its current conditions, and to prepare to be able to survive later conditions.

19 Egg & Uterus as Habitat

19.1 Features of Uterine Life

Tethered by an umbilical chord that provides nutrients and oxygen. Live in a fluid-filled environment. With growth, movement becomes restricted. For animals with multiple offspring, uterine is shared with other embryos. Stimuli available are mainly chemosensory and touch.

19.2 Embryonic Behavior

Embryos do have organized behavior – sequential organization, temporal organization, spacial organization.

n.b.: the way you asses a problem can affect the answers you get. E.g., if we study embryo behavior in utero, it increases and decreases. Might think this is a "genetic program," but is actually caused by constriction of movement – if we take the embryo out, it still shows behavior..

19.3 Antecedents of Post-Natal Behavior

Facial Wiping

If you insert small amounts of food into an embryo's mouth, it will wipe its mouth – antecedent of grooming. Wiping behavior seems to depend on amnionic fluid – thus it drops off at birth, once the animal is born. Also, it can depend on the animal's position (suppine vs. prone), since grooming can conflict with staying balanced.

19.4 Adaptations to Uterine Life

Some patterns of behavior we see in embryos don't seem to be antecedents of post-natal behavior: ontogenetic adaptations

Response to Umbilical Occlusion

If a fetus accidentally occludes the umbilical chord, it has a very particular response. First, suppression of fetal activity and depression of heart rate. Then increase of activity (head toss, flexing body), then drop in behavior. You don't find this behavior after the rat is born.

19.5 Sensory Stimulation and Future Behavior

While in the uterus, the embryo has sensory stimulation (mainly sounds and smells).

The Duck Assembly Call – Gottlieb

The assembly call is used by the mother to keep the flock together. Basically it means "come here kids." How do children recognize the call? If you put eggs in incubator (away from the mother), they'll still prefer their mother's call. Is the call hard-wired? Over development, the child starts vocalizing before birth. The children can hear both their own vocalizations and those of other eggs. These can prime a chick to follow assembly call.. If you put an egg alone, and don't allow the embryo to vocalize, then the chick won't have a preference for one call or another.

20 The Transition to Being a Neonate

20.1 How Rat Pups Find their Mother's Nipple

Behavior is determined mainly by experience with the mother's odors: if you wash the nipples, then the children won't attatch. Odor source comes from 2 things: mother's saliva, and amnyonic fluid. Effects very specific: e.g., the saliva of a virgin mother won't elicit attachment. After 4-5 days, pup saliva also causes attaching.

20.2 Learning about Odors In Utero

How does the pup know which odor cues to use? Hypothesis: exposure to amnyonic fluid causes this preference. Try injecting an odor into amnyonic fluid. Then stroke the animal (simulates mother licking its children) either in the presence of the odor or not. The animals will attach if the nipples smell like citrol. But this effect doesn't occur without the stroking. Thus, child is learning that stimulation (licking) in the presence of an odor means that the child should find that odor and attatch.

21 Mother as Habitat: The Consequences of Suckling

Young rats learn about who they should mate with in the future based on what their mother smells like. Rats which are capable of mating smell similar to rats which just gave birth. Rats smell their mother to learn what rats that are capable of mating smell like. Male rats mate more efficiently with rats that smell like their mother. To some extent, the rats imprint their mother's odor & use it to find rats for mating.

Wednesday, September 29, 1999

First Exam is Next Wednesday *Paper Topics Due Next Wednesday*

22 Basic Features of Bird Song

22.1 What is Bird Song?

Defined by a long, often complex sequence of vocalizations. Usually produced by males in breeding season. Different from "calls," which are short, simpler, produced by both sexes, and produced outside breeding season. Bird Song is a broadcast signal – not directed at a particular recipient. Used for teritory marking and mating calls. "Oscine"=song bird. Oscines make up about 1/2 the species of birds.

22.2 How do we study it?

Use sonogram. Fourier transform over time. Songs can be described in a hierarchy. Several song types make up a repetoire. Each song has distinct sections (=phrases) phrases broken into syllables, which are broken into elements (or notes).

23 Bird Song is Learned

Other bird vocalizations (calls) usually aren't learned, but bird song is.

23.1 Clues from the Field

Geographical variation of bird song within a species: "dialects."

23.2 Isolation Studies

If you acoustically isolate a bird from hearing bird song, they will develop a degraded version of bird song. Song is similar to adult song, but is "messy," and lacks complexity.

23.3 Hearing Adults is Critical for Song Learning

A bird will sing the dialect of the adults around it. In some instances, you can teach bird A to learn bird B's song.

23.4 Deafening Studies

If you deafen a bird before it hears song, it produces very messy song.

24 The Model of Song Learning

24.1 Acquisition of Song (Sensory Stage)

Auditory Template model of song development

Bird has template; it is matched to hearing its own species song. This allows the bird to create an exact template. The animal then starts singing, and tries to match its song to the exact template.

Evidence for a Template

1. There is substantial structure in isolated bird song.
2. Some structre is retained in deafened bird.
3. Very little exposure is needed to learn bird song (song sparrows can learn in about 30 exposures in 5 min; nightingale can learn to 75% in 10 presentations)
4. There are species-wide universal features (despite dialects)
5. If you give a child a choice between its own species' song and another species' song, it will preferentially learn its own.
6. Birds heart rate is higher when hearing their own song than when hearing another bird's song.

conspecific = a bird's own speceis' song; heterospecific = another bird's species' song..

What features do song birds use to learn?

Computer generate and manipulate syntax and syllables. Some species will mainly just learn syllables, and then put them into their own syntax. Others will learn both syllables and syntaxes..

Timing of Acquisition (Sensitive Period)

The song must be presented in the "sensitive period." Before or after that time, the bird will not learn the song (originally known as "critical period"). But if the bird is deprived of song past their normal song learning period, they can extend the sensitive period.. Some birds (close ended learners) learn songs as juveniles & then keep that song for the rest of their life. (to test, play different songs at different points in development, and then record which song they learn) Others change their songs from year to year (open ended learners). Usually change to match the songs of other animals near them. For open-ended learners, there is an annual sensitive period.

Social Effects

There are differences in learning between learning from a tape and from a live tutor. White crown sparrows will learn song sparrow songs from a live tutor, but not from a tape. Social stimulation also broadens the sensitive period. These effects vary based on species: some species can learn equally well from tapes & tutors; others seem to only be able to learn from live tutors.

Experiment: bird 1 can push 2 buttons to make 2 different songs play. Bird 2 listens to the same songs as bird 1, but has no control. Then bird 1 learns song much better than bird 2.

Birds tend to learn better from aggressive tutors – increased stimulation and salience.

How Accurate is song learning?

Animals can sometimes combine different phrases from different tutors.

24.2 Storage

Animals store information about songs that they learned for a long time before they actually produce the song (as much as 300 days).

24.3 Retrieval and Production

Birds seem to pay attention to their own feedback. If you deafen a bird after acquisition, but before production, it will only acquire a very degraded song. Timing of stages of production are usually species-typical.

Subsong

Initial bird vocalizations are fairly messy. Structure is present, but noisy. People believe that in this stage, the bird is learning to coordinate different systems (breathing, beak, tounge, syrinx, etc). There are species-specific differences in subsong. These differences may depend on auditory feedback. Very hard to recognize final song from sub song.

Plastic Song

Plastic song changes over time, and approaches the tutor's song. Characterized by overproduction of syllables. Then syllables are removed from the song: selective attrition. If a bird has heard conspecific and heterospecific songs, then it will loose the heterospecific syllables more readily than the conspecific syllables. Birds seem to get rid of songs that don't match their neighbor – keep the song that most closely matches their most active neighbor.

Crystallization

Eventually, song will stop changing. Deafening bird after crystallization doesn't have as much of an effect. Crystallization correlates well with increasing testosterone. Experiments suggest that testosterone is necessary for crystallization.

```
    subsong     plastic song   crystalized
                  ----
                 |C    \
                 |B  B   \
_______________|A__A__A___A__A__A__A__A
     x  x      |  |  |  |  |     |
A  B  C  D  E     A'
```

25 Distribution of Song Learning

26 Why Learn Songs?

We don't really know.. mating, territory marking?

Monday, October 4, 1999

27 Quantitative Genetics

27.1 Strain Studies

Inbred strains created through selective breeding – each strain is essentially genetically identical within the strain.

Inbred strains can tell us whether variation in a given trait is based on variation in genes – if animals from 2 strains raised in the same situation always develop differently, that difference must be genetically based...

Contextual fear – animal will condition to its environment as well as to the conditioned stimulus. Do tone → shock conditioning in setting A, then check whether association is stronger or the same in setting A or in some other unrelated setting. Contextual fear varies based on strains – thus, it's affected by variations in genes.

Marr's watermaze: there is a vat of water with a hidden platform. How quickly will mice learn to swim to the platform? Note that the vat is surrounded by consistant visual cues. Time to find platform, how long mice remember where the platform is, varies based on strains – thus, it's affected by variation in genes.

Environment also has an influence

Enriched environment vs. impovrished environment. Enriched environment improved performance of mice that are bad at maze learning, didn't affect mice that were good. Impovrished environment degraded performance of mice that were good, didn't affect mice that were bad.

Even if environment is -very- carefully controlled for, which site an experiment is run at makes a signifigant difference in the results.

In mice, which mother rears a mouse & which mother carries a mouse (when it's pregnant) doesn't seem to have much effect on the mouse's development.. (?)

27.2 Artificial Selection

If we do artificial selection on a trait whose variance is controlled by 1 gene, we should see a bimodal distribution very quickly (within the first few generations).

If we do artificial selection on a trait whose variance is controlled by several different genes, we should see a much more gradual divergence, and there should be lots of intermediates.

> $R=h^2(S)$
> R = difference in parents (?)
> S = difference in children (?)

28 Forward Genetics

Makes no assumptions (?) Develop a good behavioral profile, then randomly change the genes (induce mutations) See which changes cause deficits in behavior. Examine what changed in the genome, & find which genes are necessary for a behavior.

Forward genetics is more expensive, since you need a lot of subjects.

28.1 Bacteria

Bacteria will move towards certain chemicals (chemotaxis). Hill-climining, tumble & roll.

- Detecting the odor
- Movement generation

Induce random changes in genes, and see which changes cause deficits in behavior. About 20 genes involved in detection of the odor.

28.2 Flies

How do you make the changes?

Three primary ways to induce mutations:

- Chemical mutagens. Generally cause very small deletions. Single mis-pairings in base-pairs.
- Radiation. Causes rearangements, deletions, replications, etc. Causes a lot of different changes.
- P-element (transposable). P-elements can jump around in the genome. Animals with p-elements have repressors in cytoplasm. But if you cross them with an animal with no p-elements, then there will be no repressors in cytoplasm, so p-elements will jump around and cause mutations.

What are the results? Odor – shock association

You can train flies to associate odor with shock. Flies that associate odor with shock will tend to avoid that odor.

It's possible to dissociate different types of memory using this paradigm (9.03 whee). Flies have STM, LTM, MTM (for odor-shock association). You can selectively eliminate them. These experiments let us determine more about the biochemical pathways involved.

28.3 Mice

QTL: Quantitative Trait Loci

Find 2 strains that are particularly good and particularly bad at a particular trait/behavior.

E.g., pre-pulse inhibition: if you get a little shock before a big shock, you won't respond to the big shock as much as you would otherwise. One parent has high pre-pulse inhibition, the other has low pre-pulse inhibition. The F1 generation tends to have high pre-pulse inhibition. The F2 generation has bimodal distribution – examine the genotypes of animals on either end of the bimodal distribution, & compare. Somehow this can tell us about what genes are involved.

Spontaneous mutations

We can do Mendelian-type studies on spontaneous mutants to see if they're caused by 1 gene, or maybe 2 genes..

Induced mutant screen

Induce mutations in a strain, and look for changes in a particular behavior (esp. effective with robust behaviors). When you find a change (e.g., circadian rythm gets signifigantly longer), clone the animal & look at its genes to try to figure out what the mutation was that caused it...

29 Reverse Genetics

- Good way to target genes.
- Effects tend to be global.
- Can end up with compensation, etc.
- Expensive.
- Problems with multiple genes involved in behavior.

29.1 Flies

How do you do it?

- Directed mutagnesis Take a p-element, and use a targeted vector to insert it in a particular point.
- Conditional expression Use promotors (only activated in some contexts)
- Tissue-specific expression

What do you see? Courtship behavior

29.2 Mice

Knock-outs

Use a vector to insert a marker and something to disrupt the gene. Then inject these cells back into a blastocyst. This will create a mouse where part of it has the gene active and parts have the gene disabled. Furthermore, which part is which is marked. "chymera"

Transgenics

Same idea, but add new genes to an egg. That way we can create a new mouse with an added gene.

Variations on a theme

We want to know what the gene that we changed does on a global scale

- - therefore we want to do a whole battery of tests, to characterize

the change more completely. Example tests: water maze, contexutal fear, activity, rotorod, wire hang, footprint (=test gait), order discrimination, etc.

What do you see?

We see that we're out of time.

30 Conclusions

Not today.

Sexual Selection I: Intrasexual Competition

Wednesday, October 13, 1999

31 The Basics of Sexual Selection

31.1 Problems faced by Linnaeus and Darwin

Linnaeus thought that there were two "species" of duck which looked very different. Later it was realized that one was the males and the other was the females. Males and females can vary dramatically in both appearance and behavior.

Darwin noticed that there are certain traits (singing, bright displays) which appear to reduce the probability that the a particular animal will survive. How do such traits evolve? Make distinction between natural selection and sexual selection. Sexual selection depends, not on a struggle for existence, but on a struggle for access to females. The consequence of failure is not death, but very few offspring. Note that normal natural selection and sexual selection can push in opposite directions.

Divide sexual selection into 2 parts: intersexual selection and intrasexual selection. Intersexual selection = female choice; intrasexual selection = male-male competition. (in less common situations, intersexual=male choice, intrasexual=female-female competition).

31.2 Why does Sexual Selection exist?

Differences in Reproductive Potential

Difference in the size of gametes. Females produce few eggs and produce large ones. Thus, females invest more. Males produce more sperm than females produce eggs. Thus, males could potentially reproduce much faster than females. A male could increase his reproductive success by finding & fertalizing lots of females. Thus, females are a scarce resource. In contrast, a female can only increase her reproductive success by speeding up her production of young. Generally this means getting more food.

Differences in Parental Investment

Females tend to invest more energy in increasing the welfare of their offspring; males tend to invest more in trying to make more offspring. Where one sex invests signifigantly more than the other, the latter sex will compete for access to the former.

31.3 The Intensity of Sexual Selection

The intensity of sexual selection depends on how easily one sex can get access to the other sex.

Differential Effort between the Sexes

If males & females invest the same amount in young, sexual selection won't be as intense.

Operational Sex Ratio

Operational Sex Ratio = the ratio of # of males & # of females who come into breeding condition at any given time. If all females become available for breeding at the same time, then more males will have access.

If females become available in waves, one group of males can monopolize each wave. To the extent that the operational sex ratio is closer to 1, sexual selection is less intense.

31.4 Intrasexual vs. Intersexual Selection

Problems

It's hard to distinguish intrasexual from intersexual selection. For example, there are pretty birds in some birds. Seems at first that these are probably just for intrasexual selection. But they use them to fight. Thus, they're also intersexual selection. Another example: bird with spurs. The spurs look like they'd be use for male-male competition. But spur length doesn't correlate with dominance. It does, however, correlate with female choice. Thus, spur length is probably involved in intrasexual selection, not intersexual selection. Moral: you have to do experiments to tell if something's intersexual or intrasexual; you can't just tell by looking at the trait.

Within-species Variation

Within some species, there can be 1 population that uses more intrasexual selection, and another that uses more intersexual selection. For example, to the extent that there are fewer nesting sites available, we expect stronger intersexual selection, since males must compete for nest sights. This leads to populations that are more dimorphic where nests are less common, and populations that are less dimorphic where nests are more common. In summary: increase nests, and there's more room for intrasexual selection (females can be choosy about which male to mate with); decrease nests, and there's more room for intersexual selection.

32 Intrasexual Selection

32.1 Scramble Competition

When females are scattered in space, main intersexual selection involves finding the females to mate with them.

Traits Selected for

Intersexual selection will lead to persistance in searching, good spacial memory, good ability to percieve females, mobility.

Thirteen-lined Ground Squirrels

track ground squirrels before, during, and after breeding season. Area covered increases during mating season, drops off before & after it. The amount of area covered accounted for almost 1/2 the reproductive success in reproduction.

Common Toads

Explosive breeder (i.e., reproduces in a very short time frame). All reproduction must be done in a very short time period. Females come to pond to mate. Males can either intercept females before they get to the pond, or can displace other males once the females get to the pond. Larger males are not more successful at intercepting females, but they can interrupt other matings. The larger you are, the less likely you are to be displaced.

Thus, there are 2 mating phases: scramble phase, where you try to get to the female first, and other phase, where you try to use your size to displace other frogs & get mating.

32.2 Endurance Rivalry

The male who stays around longest (at breeding sites) is the most likely to get mates.

Traits Selected for

Intersexual selection will lead to male energetic effeciency, endurance. It should select for larger (fatter) animals, and for the ability of animals to fast.

Grey Seals

Copulations per day correlates with initial body mass (body mass at the beginning of the reproductive season). The larger they are, the longer they can spend at the mating site, & the less time they have to spend feeding.

Elephant Seals

One of the most sexually dimorphic species among mammals. Males are very very large. Females must give birth on land (they mate there too). Very few good spots on land. Thus, females cluster on these breeding areas. Males stay on the breeding area for the entire breeding season (3 months), and don't eat at all. But they must have enough energy to defend the females and to mate. The dominant males loose their mass at higher rate than less dominant males. Often the dominant male will loose 1/2 his mass by the end of the breeding season.

32.3 Contests or "The Law of Battle"

Males can compete with each other directly for access to females: either attack each other or have contests & let females choose. Males can either compete directly for males or can compete for some resource that females need (e.g., breeding sites)

Traits Selected for

Size, weaponry, threat signals, alternative mating strategies.

Red Deer of Rhum

Males and females differ signifigantly in size. Males have large antlers. Deer are polygenous. Breeding season is very short. In females, reproductive success is mainly dependant on how long a female lives. Male reproductive success is mainly dependant on ability to get access to females. Male reproductive success doesn't seem to be determined by female choice. Fighting success correlates very well with how long a harem can be held. Fights mainly occur when males are of similar size.

Assesment behavior: roaring, parallel walk. Animals holding territories tend to roar more. Animals that are in better condition are much better at roaring. Thus, it's an honest signal of your ability to fight.

Elephant Seals

Most successful holders are the largest. Big harems are formed first, smaller ones later. Fighthing increases directly after formation of harems.

Common Toads

Male toads assess the size of another toad before they attempt to dislodge them. Smaller males are unlikely to try to displace larger ones. How does assesment work? Frog croak becomes lower-pitched as the frog gets bigger. Thus, croak is a good signal to use to assess the size of frogs. If we silence frogs, and either play high-pitched croaks or small-pitched croaks, competitor males's attack rate will depend on the recorded croaks. It also depends on the size, though, so they must have some other ways of assessing size, too.

Something Different: female-female competition

If males are a scarce resource (esp. if males provide parental care), then females may compete with each other for access to males. E.g., in some hen, males incubate the eggs, & females compete for good males. What makes a good male? Fatter males – must incubate for a long time without eating much. Also short males. (unclear why they want short males)

32.4 Sperm Competition

Competition between the sperm of several males for the ability to fertalize a female's egg. Only present when females mate with multiple males. In general, there is a last-male-preference: the last male to copulate will have the most offspring.

EPC's: Extra Pair Copulations

Sperm competition selects for copulation outside of normal pairings. EPC's are quite common in nature.

Mate Guarding

Selects for guarding your mate from having any EPCs.

Retaliatory Copulation

Retaliatory copulation: if a male is guarding a female, and sees another male copulate with her, the guarding male will copulate with the female a lot to try to decrease the chances that the female will have the userper's children.

Cloacal Pecking in Dunnocks

Males force females to eject sperm from previous males.

33 Female choice

33.1 Examples

Peacocks

Peacocks have lots of eye spots.. Correlation between # of eye spots and # of matings.

Other birds

There seems to be female choice in a bird w/ long tails. Seems that males don't use tails except to display to females – no male/male aggression effects. Text experimentally: if we shorten their tail, they get less mates; if we lengthen their tail, they get more mates. Thus, females are choosing males on the basis of tails. Evidence that there are no male/male agression effeects: when tail lengths were modified, sizes of territories didn't change any.

Guppies

Where there's lots of predation, guppies are duller. When there's not as much, male guppies have bright spots. Hypothesis: females choose on the basis of male spots. Find proportion of male displays that elicit reactions. Test males both under normal light & under orange light – under orange light, their spots are hard to see. Also test under blue light – in blue light, the orange spot looks black, but the contrast is still present. Under blue filter, females as much as under normal light. So it's the presents of spots (regardless of color) that attracts the females.

Bower birds

Bower = pretty house thingy that birds make. Male makes elaborite bower which is basically just used for mating. Males with the most highly decorated bower gets the most mates. Experimentally try removing decorations from bowers – males get less matings.

34 Direct Selection

Direct selection = females gets direct gains by choosing certain types of mates.

34.1 Selecting on correlating traits

Males sometimes produce some sort of resource to the female. Sometimes the amount of resource depends on the trait that females select on.

In one species of bird, males that are more red are chosen over males that are less red. In nature, there's a correlation between how red a bird is, and how well it feeds its offspring. Thus, females select males that are redder because it means they'll feed her offspring better.

34.2 Nuptual Gifts

Sometimes a male gives a female a "nuptual gift," and the size of the gift determines how much the female will mate with the male.

34.3 Choosing a particular male can decrease costs

Choose a male that's close by – takes less energy, & might get eaten. Choose a male without parasites.

34.4 Complementary size/genetics

Choose a male with complementary size & complementary genetics. E.g., in one animal, females choose males that are about 70% of their size

- - if male/female size is too different, then matings won't be

successful.

Complementary genetics – in one bird, tested what animals they prefer: siblings, 1st cousins, 2nd cousins, 3rd cousins, etc.. They tend to spend the most time with 1st-2nd cousins. This may be an example of "optimal outbreeding." If you mate with people too closely related, you can bring out homozygous traits.. If you mate with people too distantly related, it's bad too.. ?

34.5 Sensory exploitation hypothesis

Sensory systems have evolved to suit a number of purposes. Males can evolve traits to explit biases in sensory systems. For example, water bugs use water vibrations to find prey. But males that can imitate these vibrations get more matings. This hypothesis makes a very specific prediction: female preferences evolve prior to males having the traits. How can we test? Look for female attraction to specific calls..

In a certain bird, females have optimal hearing at frequency f, but males produce a call at frequency f+k. Why the mismatch? Because males are trying to match, but haven't succeeded?? Female always prefers smaller k (even if other traits of the call are wrong). True across several species.

Take a phylogenetic tree, with 4 ancestors. One has a call with whine + chuck. Females prefer males with larger chucks. Others have calls with just whines. So the question is: in that one, did the males add the chuck after the female had the preference? Try playing whine+chuck to the species where males don't produce chuck. Then the females prefer these sounds! So the females had preference before males made call.

35 Indirect Selection

35.1 Leks

Females choose particualar mates on a lek. But the males don't provide anything. Why?

35.2 Runaway selection

One thesis – runaway selection. Assume that there is heritable variation both in trait and in trait selection. Self re-inforcing selection: males tend to mate with females that have selection, and females tend to mate with males with trait. No real support for this hypothesis – maybe treat it as a null hypothesis.

For example, sticklebacks. Differences in dull & bright males, and differences in preference. Found high correlation between father's & son's intensity of red. Also, found correlation between father's intensity & daughter's ..?

35.3 Judging male by traits that corellate w/ fitness

Another idea: Females can select healthy males by seeing how much of a handicap he can live with. If you have the trait, & are still alive, it shows that you can overcome selection against it – good genes. Or amount that you can invest in the trait depends on how healthy you are.

Offspring Survivability

Look at relationship between a male's trait & the offspring's survivability. At least in some cases, they're correlated. Not correlated with foster-fathers. Thus, genetic... Proportionately more offspring survive if their genetic father has bigger stripe. In peacocks, when father has more eyespots, the (male) children tend to grow more. Also, size of eyespots of father correlates well with offsprings' survivability (probably because of weight).

Parasite Loads

Look at whether females choose males on the basis of parasite load. Direct benefits: they won't get parasitized. Indirect benefits: their offspring may be less suceptible to parasites. Seems to be true in at least some species. For example, in a bird with tail streamers, the males with larger tail streamers do much better w/ female selection. Also produce more offspring. Found that, by changing parasite load, the tail streamer length can change. Males that find mates tend to have lower parasite load than males that don't. In extra-pair copulations, males usually have very low parasite load. Tail length says something about how well the male can protect vs. parasites? Correlation beteen father's tail length and offsprings' parasite load.. even if offspring is raised away from father. No correlation between adopted father's tail length & offsprings' parasite load.

Fluctuating Asymmetry

Look at why asymmetrical males are less preferred than symmetric ones. Some males are more symmetric than others. Symmetry seems to show that you can develop well, even when there is envrionmental stress during development. Adding mites give asymmetric tails. Removing mites gives more symmetric tails. So symmetry may be a "fair measure" of male fitness..

Mating Systems

Wednesday, October 20, 1999

36 Basic Aspects of Mating Systems

36.1 Definition

36.2 Modern conceptualization

36.3 Types of Mating Systems

- monogomy
- polygamy
  - polygany
  - polyandry
  - promiscuity

37 Determinants of Mating Systems

37.1 Physiological constraints: birds vs. mammals

What factors effect which mating system an animal uses:

- physiological constraints / phylogenetic constraints. For example, in birds, parental care can be done by either sex. Male can increase reproductive success by providing parental care.. Thus, about 90% of birds are (nominally) monogamous. In contrast, in mammals, the mother puts in signifigantly more energy into the wellbeing of their offspring: mother carries child for a long time, and then provides milk. Thus, a male doesn't loose as much if he deserts. About 90% of mammals are polygenous.
- ecological factors: how are males & females dispersed in space.

37.2 Ecological Factors

Dispersal of males and females

Females tend to disperse according to where the resources that they need are. Males tend to disperse according to where the females are.

Example of the Grey-Sided Vole

Both males & females form territories. Experimenter found small island, removed all rodents, and experimentally introduced voles to the island. Females' territories were spread-out and were non-overlapping. Then add clumped food sites. Females change their territories to be around the food sources & to be small. Males follow the females. If you artificially force females to have certain ranges, males will go to ranges with greatest female density. If you artificially force males to have certain ranges, females will ignore them.

Economics of female defence

It's easier for a male to monopolize females if they're clumped (vs. evenly distributed). Also, operational sex ratio is important. Synchronous breeding gives low operational sex ratio; asynchronous breeding gives higher operational sex ratio.

38 Mammalian mating systems: Male care?

38.1 Monogomy: Obligate vs. Facultative

In males, monogomy is odd, since females invest so much more. Obligate monogomy = children will only survive if both of their parents provide them with care. Facultative = a male isn't really necessary for parental care, but it's mainly because the male can't find other mates for some reason. For example, females widely dispersed, high predation pressure..

Djungarian hamsters (Obligate)

In Djungarian hamsters, signifigantly fewer offspring live with 1 parent, even given all the food etc. that they need (raise them in the lab). Another experiment: put them in cold room (similar to the environment they would normally be in). Then children can't survive without the thermal regulation provided by the father.

Kirk's Dik-Dik (Facultative)

Small animals, widely dispersed, high predation pressure. Monogamous. Facultative monogomy? Other things we can rule out (at least in this case): males are defending food resources; ability to detect preditors; protection against infanticide).

38.2 Polygyny

Female solitary and defensible (˜60% mammals)

Males can defend more than one female. Males can form territories which let them monopolize several females

Female solitary and not defensible

Female ranges are too wide for males to defend them. Males & females mainly associate with each other during reproduction.

Females social and defensible

Male can monopolize a single group of female.

Females social and defensible: predictable vs. unpredictable mvmt.

Males can't defend the whole region. But they can anticipate places where females will go, e.g., watering holes. Males can follow the group of females → harems.

39 Leks

39.1 Features

Males have tiny territories with no apparent value. Males are very aggressive and very bright. Females visit lek, look through the leks, mate with one, and leave. Huge reproductive skew: dominant male gets almost 1/2 of all matings on the lek. (Leks are fairly rare)

39.2 Why do leks occur?

When males can't defend a female, or defend her resources. Species that lek tend to have much larger ranges, lower density. There is an inverse correlation between female range size & male range size, esp. for very large female range sizes.

39.3 Why do males aggregate onto leks?

Hotspots

Males might aggregate at places like watering holes, where females will come to them. In some species, leks tend to form in places where female ranges overlap.

Avoid Predators: tundra frogs

Leks reduce predator pressure. If you're in a crowd, you're less likely to be picked off by a particular preditor. For example, tundra frogs are eaten by bats. As the lek size increases, the predation per individual animal decreases.

Hotshots

Males tend to aggregate around a very good male. Other males parasatize his ability to attract females. "Satellites." Then they may be able to get matings with the females attracted by the hotshot.

- Natterjack toad: small males can't produce loud vocalizations. So they hang around bigger males. In these toads, if a toad is 1/2 as loud as another male, he tends to become a satellite.
- Sharp-tailed grouse: males seem to want to be in the middle spot. Females seem to be attracted to the male in the middle spot. The males are competing to get to the middle spot. So is it really hotshot or is it hotspot?
- Fallow deer leks: if you force successful males to move (even to periphery), they still remain successful. This is evidence for hotshot.

40 Avian Mating Systems: Role of Male Care

Birds are primarily monogamous. Males provide care.

40.1 Monogamy: Causes?

Obligate?

In some sea birds & other species, it takes both parents to produce any offspring at all. If you lose your mate, you may lose your entire clutch.

Male care important?

But in many bird species, single mothers still have a fair amount of success (although it's almost always less than a couple). Often females will compensate for male not being there by getting more food (as much as the male would have), but time spent defending the nest & caring for the young goes down. In a few monogamous species, removing the father doesn't decrease the success of the children.

Why are males monogamous?

Often, even though a species is monogamous in its normal environment, it will be different in other environments: if you decrease the # of males enough, males become polygynous.

Sperm competition and egg dumping

- Mixed strategies. There are a lot of EPCs in some species. Amount of EPC varies a lot from species to species (0%-35%).
- EPC's: Zebra finches. Figure out who's the most attractive male. Randomly pair females with random males. Females will have more EPCs with males that are more attractive than their own males. Suggests that they're looking for good genes.
- Cliff Swallows as brood parasistes. Females can dump eggs in other animals' nests, and also raise your own, you can have more offspring. Egg dropping especially prevalant in large colonies.

40.2 Polygyny: Causes?

Males can monopolize resources that females need.

Costs or no costs?

Often males don't provide any parental care, so they don't care who they mate with. But sharing a male means sharing a male's parental care and monopolized resources.

In some species, females will only mate with already-paired males if all the males with resources are already paired.

Polygyny threshold model: evidence and problems

Sometimes there's a choice: second female on a good territory, or an only female on a bad territory. Basically, predict that there will basically be a theshold where polygyny with a good territory becomes more profitable than monogomy with a bad territory.

Problems: if you remove the first female, it doesn't result in increased female settling. So size of group is decreased. But the females' success doesn't seem to decrease.

Sometimes males set up 2 territories, far apart, and decieve females into thinking that the male has no mate.

Mechanisms of Mating Behavior

Monday, October 25, 1999

OUTLINE DUE NEXT WEEK EXAM ON THE 10th

41 Neurological/Physiological Mechanisms of Mating Systems

Why, among closely related species, do some pair-bond, and others don't?

41.1 Voles as a model system

A small rodent. Some voles are polygamous, others are monogamous.

- The parie Vole is monogamous
- The montane vole is polygamous

Evidence for monogamy

- Set up traps, and see how many times you catch males and females together. If you catch males & females together, then that's evidence that they form pair bonds.
- Fathers show more paternal behavior in prarie vole: evidence for pair bonds.
- If you raise them in a large enclosure, prarie voles spend lots of time in male/female pairs.
- Put a male with a female for a while. Then give the female the choice of two males: her old partner, and a new animal. Monogamous animals will prefer the old partner over the novel animal.
- Males can become very agressive (to intruders) after mating. Agression applies to any vole except the vole that was mated with.

41.2 Differences in the brains of these two species

Oxytocin and vasopressin affects pair-bonding in prarie voles

Prior evidence suggests that increasing oxytocin increases how much animals associate with each other. Look at oxytocin receptors in prarie voles and montane voles. Monogamous voles tend to have similar oxytocin receptor distributions, and polyganous voles tend to have similar receptor distributions.

Another peptide: vasopressin. Difference between vasopressin receptor distribution between prarie and montane voles. These differences appear fairly early in development.

Peptide and antagonist infusions affect pair-bonding in voles

Inject female with oxytocin. Expose a montane vole to a male for 6 hours. (Normally this won't lead to pair-bond formation) Then later (after oxytocin is gone), test preference of female. Then the female will show a strong preference for the male she was exposed to. Thus, oxytocin release during time of mating seems to be important to the formation of female pair-bonds.

With males, vasopressin seems to cause pair-bond formation. Inject males with vasopressin-blockers, then males won't show post-mating aggression formation. Also, they won't show preference for the female they mated with.

Also, try putting males & females together for a short time (not long enough for them to normally form a pair-bond), & inject then with oxytocin(female) or vasopressin(male). Then they'll form a pair-bond.

Manipulations have little effect in monotane voles

Try these experiments with the montane vole (polyganous). They show no signifigant effect. Probably because the montane voles don't have the right receptor distribution.

Genetic manipulations and affiliative behavior

Cloned the genes for oxytocin/vasopressin receptors. There are differences in the genes. Try transplanting the monogamous form of this gene into mice. Then we get mice with similar receptor distributions. Now, inject vasopressin. Then mice get higher affiliative behavior.

42 Basics of Sexual Selection and Gonadal Hormones

42.1 General Issues

Normal course of mating:

- Females engage in "Proceptive behavior": behavior that makes mating more likely to happen (indicates her willingness to mate; i.e., indicates that she is receptive).
- Males examine females, determine whether they're receptive
- Mounting
- Intromission (inserting penis into vagina)
- Ejaculation

After mating, the female often becomes agressive (esp. in polyganous species).

42.2 Description of Male Rodent Copulatory Behavior: Variations

Variations:

- copulatory lock?
- thrusting?
- multiple intromission?
- multiple ejaculation?

42.3 Description of Female Rodent Copulatory Behavior: Lordosis

Curvature of the spine, to allow males to mate.

42.4 Role of Gonadal Steriods in the Regulation of Sexual Behavior

Types of Gonadal Steroids

- Androgens: testosterone, etc. In general, stimulate male characteristics.
- Estrogens: estrodyle, etc. In general, have femanizing effects.
- Progestons: progesterone, etc. Acts in uterus to allow for successful fertilization or birth or something.

Properties

All of these hormones come from cholesterol. The steroids can be transformed into each other fairly easily. E.g., there are enzymes that transform testosterone to estrodyle. Hormones are fat soluble, so they spread everywhere in the body.

Steroids attatch to DNA, and stimulate certain types of protein production.

Regulation of Steroid Release

Production of gonadal steroids is regulated by lutenizing hormone (LH). LH is regulated by LHRH (LH releasing hormone, AKA GNRH). This happens in the pituitary, in the brain.

The gonadal steroids act as a general overall signal which controls mating behavior.

”male” vs. ”female” hormones

Hormones aren't really ”male” or ”female.” They just do different things in each sex.

42.5 Why do Hormones Regulate Reproductive Behavior?

43 Male Sexual Behavior: Hormonal Mechanisms

43.1 Berthold's classic example on roosters

43.2 Remove and Replace Experiments

Findings

If you remove testes, & replace them, then sexual behavior develops normally (thus, not caused by neural mechanisms, because neurons were cut). If you remove them & don't replace them, sexual behavior goes down. Inject testosterone after castration, and sexual behavior appears again.

Caveats

Some animals show sexual behavior without gonads, esp. if they have mated prior to castration. Also, there are individual differences in sexual behavior that are independant of testosterone. Only a little bit of testosterone is needed, and providing more doesn't have much of an effect.

43.3 Testosterone and Estrogens

43.4 Variations: the Red-Sided Garter Snake

Canadian snake that hibernates for up to 9 months. Males store sperm from the previous year. Mate at the beginning of the season, when testosterone levels are low. Then as the season goes on, testosterone increases, & gonads enlarge, so that at the end of the season the male will have sperm to store for the next year.

44 Female Sexual Behavior: Hormonal Mechanisms

44.1 Cyclicity

Unlike males, females tend to have cyclic periods of receptivity (not all – reflex ovulation = ovulate just when you get male stimulation).

44.2 Estrogens and Progestins in the Regulation of Sexual Behavior

Increasing estrogen tends to increase receptivity. In general, in order to cause receptivity, you have to simulate the normal cycle of hormones. Normally, estrogen for some time, then progesterones.

44.3 Female Rats Control the Pace of Mating

At first, it seemed that males controlled the pace of mating. But if you put them in a more natural environment – i.e., a large, social environment – then the females will control the pace of mating. If mating occurs at the pace of the female, pregnancy is much higher.

45 How do Hormones Affect Sexual Behavior?

45.1 Act Directly on Brain and Spinal Cord

Steroids and the CNS

Steroids are fat-soluble, so they can go through the blood/brain barrier. Receptors in hypothalamus and other brain areas.

The hypothalamus: AH-POA and the VMN.

The anterior hypothalamus/pre-optic area (AH-POA) seems to be related to male mating – ablate it and mating behavior goes away. (but they're still interrested in females)

ventro-medial nucleus (VMN) seems to be related to female mating – ablate it and mating behavior goes away.

Neurons in these areas seem to be activated during copulation.

Steroids are important for the behaviors of these areas.

The amygdala seems to be related in making males want females. Get rid of amygdala, and the male will mate with females that are present, but won't try to find females (c.f. AH-POA, where males will try to find females, but won't mate).

Stimulation Studies

Neuronal Activation: c-fos studies

Intracranial Implants of Steroids

45.2 Act on the periphery

Increased somatosensory input

Hormones can increase the receptivity to certain types of somatosensory input. E.g., female rats will have increased input from stimulation on the back.

The muscles Involved in Penil Function

45.3 Beach's Model of Copulatory Behavior

1. Motor components are coded in the spinal chord – if you cut the brain from the spinal chord, then mating behaviors persist.
2. Brain inhibits the spinal reflexes.
3. Sex steroids act do dis-inhibit (i.e., to inhibit the inhibition).

46 How Do These Sex Differences in Copulatory Behavior Arise?

46.1 Basics of Sexual Differentiation

Sexes have some sort of differences. In mammals, XY vs. XX. In many reptiles, the temperature in which the egg was incubated leads to male/female. Either way, the gonads produce a signal to tell the rest of the body what sex to become. Default sex (sex if gonads are removed) is usually female.

46.2 The Organizational Effects of Hormones: Phoenix et al.

Exposure to hormones early in development causes different organizations to form.

Females exposted to high levels of testosterone as embryos/neonates will show decreased lordosis as an adult, and will sometimes mount other females.

If you remove gonads from neonatal males, then they will show female sexual behavior, and no male sexual behavior. Give them a single injection of testosterone, and they will show normal sexual behavior.

Females that are between males in the uterus develop more masculine characteristics, are more aggressive, develop larger territories, and are less attractive to males. Females that are between males give birth to more males, and females that are between females tend to give birth to more females.

Similar effects for males.

46.3 Trans-Generational Effects

The 2m-stuff and 0-m stuff can go across generations.

Evolution and Mechanisms of Parental Behavior

Wednesday, October 27, 1999

47 Differential Investments in Sons and Daughters

Parental investment is often necessary for the successful production of offspring.

47.1 Why should animals treat sons & daughters differently?

Animals often give more support for one sex than for other. In particular, if supporting one successor will increase your overall success than supporting another, then support the former.

The Red Deer of Rhum: males favored

Variation in male success is greater than variation in female success. Strong males can have many children. Adult size of male has a strong effect on their success. Therefore, feed male offspring more.

Breeding success of a female's son increases with her status ($\rightarrow$ the amount of investment she can put in children), but her daughter's success doesn't vary much.

Bonnet macaques: females favored

Breeding success of a female's daughter increases with her status ($\rightarrow$ the amount of investment she can put in children), but her son's success doesn't vary much.

47.2 Evidence for Differential Investment?

Sex differences in juvenile size and growth

Sexual dimorphism is present from birth.

Sex differences in energetic costs of rearing

In sexually dimorphic species, the energy intake of males is often greater than the energy intake of females. Males spend more time suckling, etc.

Differences in reproductive costs of rearing males or females

If a female has given birth to a male the preceeding season, then she is less likely to have a child in the next season. Also, it takes her longer to conceive. Also, more females die if they reared a male the previous year.

47.3 Sex ratio variation

If resources are plentiful, invest in males; if resources are scarce, invest in female.

Why vary sex ratio?

If it's more costly to produce one sex than another, then it might make sense to vary your sex ratio. There is often a trade-off between the number of each sex you produce and how expensive each is. For example, if you're in bad shape, produce 1 daughter. Slightly better shape, 1 male. Slightly better sex, 2 females. Slightly better shape, 1 of each. Etc..

Does this happen? Red Deer, Bonnet macaques, and Baboons

In low-dominant animals, males are much less likely to survive than females. In high-dominant animals, it's about the same. Dominant females seem to produce more males than females; subordinate females seem to produce fewer males.

In species with matrolines, dominant females will produce more females, and subordinates will produce more males.

Scarce resources and investment

Amount of resources available affects the sex ratio. Reduced food intake → smaller litter, and fewer males. This effect holds if the female was food-restricted during development but not during breeding. It also holds across generations: the daughters will have fewer females..

Mechanisms

This seems to occur because there are many more male spontaneous abortions when food is scarce etc. Also, if food is low, then males have a higher mortality rate.

48 Maternal Effects on Offspring

48.1 Maternal Anogenital licking (AGL) in rats

description and function

Mothers lick their offspring to clean them off. Females lick the anogenital region of offspring to reclaim water, since lactating females need a lot of water: reclaim it from offspring's urine.

Sex-bias in AGL

Males are licked more than females. If you put male urine on a female, then the female gets licked more. If you mask odors, preference goes away. Thus, it seems to be smell cues in male juvenile urine that causes males to be differentially licked. This is a testosterone-dependant effect.

Consequences

You can manipulate the amount of licking a mother does, either by giving her dilute saline, or by eliminating her ability to smell urine. The males that recieve less AGL have poorer copulatory efficiency. This is due to a decrease in the number of motor neurons.

Take 2 strains of rats with different salt tolerances. One does less AGL than the other. The ones that are licked more succeed better in producing offspring.

48.2 Differential effects on sons depending on who the father is

You can make zebra-finches more or less attractive by giving them leg-bands. If they're mated to a more attractive male, they'll produce more male offspring. They can also bias clutches in another way: if they mate with an attractive male, then they'll add more testosterone to their eggs. More testosterone: grow faster, beg for food more intensely, and are more likely to be dominant.

48.3 Effects of maternal care on adult "personality"

More AGL can change a rat's response to stressful situations. Children with more AGL will have lower level of stress when put in stressful situations. Also, rats that have recieved more AGL explore their environment more. Rats that recieved more AGL will be more likely to eat food in a novel environmnet.

49 Experiential and Hormonal Mechanisms of Rat Parental Care

49.1 Basic types of maternal care in mammals

All mammals lactate (the only food that their offspring can consume).

Three categories

- Female gives birth to altricial young: highly undeveloped young that are left in a nest. Female provides milk, warmth, protection from predators.
- Females give birth to procotial young: children are fairly well developed, have independant mobility. Usually have a nest. Either (1) the offspring hides in the nest & the mother comes back with food etc; or (2) the offspring follows around the parent.
- Females give birth to semiprecotial young: in between. Like humans.

49.2 Effects of experience on rat parental behavior: concaveation

concaveation: if you put a pup with an animal long enough, it will eventually show parental behavior. Not hormonally caused: still occurs if you reduce gonads, etc.

Present pups to an animal, and see how long it takes for them to show any parental behavior. If a mother has just given birth, she will show parental behavior almost immediately. This is caused hormonally. If you've never given birth, then it will take you a while to show parental behavior.

49.3 Effects of hormones on induction of rat parental behavior

Clues from natural fluctuations

Over pregnancy, estradiol increases right before birth; progesterone drops right before birth. Check to see if these changes cause the behavior?

Parabiotic evidence

Connect the blood supplies of maternal and non-maternal females (thus all signals must travel via blood $\rightarrow$ hormones). Then the non-maternal female will be paternal more quickly.

Hormonal manipulation and hysterectomy

See if pregnancy termination causes female to act parentally. Remove placenta → progesterone drops quickly. Conditions seem to be an increase in E followed by a drop of P.

49.4 What maintains parental behavior?

Non-hormonal mediation

Even though the rapid induction of parental behavior by mothers who just gave birth is hormonal, the maintanance of that behavior isn't. Test with parabiotic experiments. Remove hormonal organs of a rat w/ maternal behavior, & parental behavior persists.

Pups control duration of parental behavior

The pup's behavior seems to be what causes parental behavior to be maintianed: if you rotate through young pups, so the mother has the illusion that her pups are staying the same age, then the mother will stay maternal.

Suckling and temperature

Cut the sensory nerves around the mouth, or give litocane injections, then mothers will become less maternal: she tells how old her pups are by sensory stimulation (nuzzling, suckling)

If you cool down pups, they stop moving, and the mother will stop showing maternal behavior. Also occurs if you anesthatize the pups.

Inject litocane into pups' mouth, so they stop suckling. Then the mother will stop showing maternal behavior.

49.5 What terminates parental behavior?

If you increase stress hormone, it decreases the amount of time spent breeding. Stress hormone increases mother's temperature. This increases her temp. So she can't stay on pups as long, because she'll overheat. When her brain temp is lower, she shows less maternal behavior. As pups get older, they start regulating their own temperature → they become heat sources. So the mother spends less time being maternal because mother's brain temp gets higher.

50 Neural Mechanisms of Rat Parental Care

50.1 The preoptic area of the hypothalamus

Lesions

If you lesion this area, then some parental behaviors are greatly reduced (e.g., nest-building, retrieval).

C-fos experiments

Use C-fos to map out activity in the brain. A female that becomes maternal in response to pups have more activity in pre-optic area than females that don't become maternal.

estrogen receptors

Estrogen will trigger early onset of maternal behavior.

50.2 Sensory mechanisms for induction of parental behavior

Certain sensory mechanisms affect how long it takes animals to show parental behaviors. E.g., ablate olfactory bulb → rats become maternal faster.

51 The Sheep: formation of selective bond with offspring

Sheep are herd animals, and young must follow their mother around from pasture to pasture. Sheep form selective bonds between young and mother. Sheep will not become maternal unless they go through the physical act of giving birth.

51.1 Hormonal effects on maternal behavior

You can use estrogen/progesterone to mimick the effect.

51.2 Vaginocervical stimulation and maternal behavior

Stimulation in the vaginocervical area is critical to showing maternal behavior. If you give stimulation to non-pregnant sheep, you can induce maternal behavior. Also, if you give additional genital stimulation to a pregnant sheep, she'll show more maternal behavior.

But they don't require as much vaginal stimulation if they've given birth before.

51.3 Olfaction, amniotic fluid and the selective bond

It's the olfactory cues that are responsible for forming selective bonds. Reject sheep on the basis of their smell in close proximity. This depends on the amniotic fluid. Dry amniotic fluid off a newborn, then they won't be accepted as well.

51.4 Vaginocervical stimulation and olfactory processing

Vaginocervical stimulation increases the chance that she'll accept alien lambs etc.

51.5 Natural mechanism of the selective bond

vaginocervical stimulation increases hormones that increase plasticity in the olfactory bulb. coop 3rd floor

Communication II: Birdsong

Monday, November 1, 1999

Exam next Wed

52 Mechanisms of Song Production and Perception

52.1 Song Production

The Syrinx: 2 songs - one throat

The syrinx is a structure that only appears in song-birds. It's located at the junction of the broncheal tubes. There are two MTM's, which are stretched membranes. As air passes over the MTMs, they vibrate. Thus, there are 2 potential sources of sound – two songs are produced and combined by songbirds.

Are the two MTMs ever used seperately? Yes. Airflow through each broncheal passageway is controlled independantly, as is tightness to MTM. Evidence: cutting nerves innervating each side of the broncheal tube gives different effects.

The rest of the vocal tract filters the sound.

CNS mechanisms of song production

There is a system that seems fairly dedicated to song production. HVC sits at the top of the system (high vocal center). Basic motor circuit is:

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HVC → RA → crainal nerve nucleus nXII in the hindbrain
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How do we know this is important for song production? Destroy HVC, RA, or nXII, and the animal will stop singing. He gets in the posture for singing, and open their mouth to sing, but don't sing.

Birds can still produce vocalizations without (some of) these structures – for example, calls. In fact, for calls that are partially learned, lesioning this pathway will selectively remove the learned components. Thus, this structure is probably involved in learned songs.

Also, tight correlations between neurons and song. In HVC, correlation between neurons and syllables. In RA, correlation between neurons and notes.

If the animal is singing, then production of Zenk (some random protein) increases in HVC (and RA?)

If we stimulate HVC or RA electronically, you can elicit a song. Songs are fairly close to their normal songs. In contrast, in midbrain stimulation elicits calls.

Structures that are important for learning songs:

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HVC → X → DLM → LMAN → RA
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If you lesion this pathway, it doesn't impair production in adults. But in juveniles who are still learning their song, it degrades learning. Seems that the song crystallizes too fast.

Structural features of song system

The HVC→ RA→ nXII structures seem to be specific to song-birds. Other birds that learn sounds (parrots, etc.) use different structures. Males have more primarily developed HVCs etc. (since primarily males produce song, we would expect this). The differences are formed early. Look across species to see if sexual dimorphism in volumes of HVC etc tracks dimorphism in song production. Indeed, in species where both sexes sing, the HVCs etc are similar size, and when only males sing, HVCs are larger in males.

There is a correlation between how many song syllables you produce and how big your production pathway (HVC, RA, etc) is. (note correlation

- - we don't know which way it goes yet).

There is a correlation between ?? and how big your learning pathway (X, DLM, etc) is. (note correlation – we don't know which way it goes yet).

There is a correlation between how many song types of song you produce and how big your production pathway (HVC, RA, etc) is. (note correlation

- - we don't know which way it goes yet).

Examine which way the causation goes for these correlatoins: is the size of the structures the consequence of singing?

We can experimentally produce birds where some are only taught 5 songs, others are taught about 45. Then compare voulmes – they don't differ. This suggests that it's not that sining more makes your HVC bigger, but rather that bigger HVCs allow you to learn more.

Sizes of HVCs etc change over time, and over seasons. You can manipulate this in the lab by manipulating photoperiod – expose animals to short days, and their HVC & RA will get smaller. HVC kills neurons when it doesn't need them, and then makes new ones when it needs them (neurogenesis).

HVC size changes also correlate well with testosterone levels. HVC etc are affected by testosterone etc. Singing is experinmentally dependant on testosterone. Castration decreases singing, then testosterone injection restores it.

52.2 Song Perception

Perception of Song and Field L

How do birds percieve songs? Field L is a part of the brain that projects near HVC. Field L seems to be involved in the perception of song. Field L seems to be interrested in any song.

Perception in the Song Production System?

Structures that produce vocalizations are also sensitive to their own vocalizations. HVC seems to be interested only in the animal's own song – feedback for learning.

Females use HVC to recognize songs. If you lesion HVC in females, then they'll respond to other species' songs.

Song perception and gene expression

NCM is innervated by Field L. Zenk production is increased in NCM by conspecific song. MCM projects to HVC. NCM may be involved in recognizing conspecific song.

53 Getting The Message Across

53.1 Attenuation

Sound gets weaker the farther you go. High frequencies attenuate more

- - atmospheric turbulance, etc. But low frequencies interact in bad ways with the ground. Thus, birds sould try to produce low-freq songs and get high off the ground to sing. But birds have small vocal tracts, so it's hard to make low frequency songs. Also, low freq songs are more expensive.

53.2 Degradation

Sound gets degraded (the environment acs as a filter). It's mostly high-frequency sounds that get degraded. Reverberation causes signals to blur.

53.3 Adaptations to noisy environments

Singing position

Birds try to sing from high positions. Males compete for good positions from which to sing.

Correlation with habitat

In open country, birds tend to produce rapid frequency modulations. In dense forests, birds use low frequencies. Some songs have different types of songs that are suited to different environments.

Using degradation of song as a cue

Animals use the degredation of a song to judge whether the producer is nearby. Males will respond more agressively to undegraded song than to degraded song. (??)

Predation pressure

Calls can be affected by predation pressure. For example, alarm calls are similar in most species. The features of these common calls may make it difficult for the predator to find the prey that's making the alarm call.

54 What are the Functions of Song?

54.1 Territorial Devence

Effects of muting male songbirds

If you mute a male, it gets challenged more, and it usually loses his territory. Also, muted males take longer to get territories. Muted males need to engage in much more direct agressive behavior, since they don't have a way of anouncing their status.

Speaker exeriments: Removing the male

Replace the male with a speaker that makes the male's song. Then territory shrinks much slower than if you just remove the male.

One idea about why a bird sings multiple songs: it's pretending to be multiple males ("Beau Geste" hypothesis – guy left alone at a castle propped up his dead comrades against the walls to make it look like the castle was manned & so he could scare off the intruders). Areas where speakers play bigger repetoires get filled up slower.

54.2 Recognition

Species

Recognize whether birds are conspecific or heterospecific. Important for competition and for finding mates. Sometimes invariant features are the important features in species recognition.

Parent-offspring recognition

Birds show preference for their parents' calls and their offsprings' calls, especially in social birds.

Mate recognition

Monogamous birds show preference for their mates' calls.

Neighbors and Strangers

Males have territorial neighbors. Males distinguish neighbors from strangers. You've already settled on boundries with neighbors, but strangers generally don't have territories yet, so respond more strongly to strangers' calls. Birds keep track of where neighbors are

- - if you present a neighbor's call from a new area, then respond

agressively (that neighbor is expanding?). Birds even remember their neighbors from previous years.

54.3 Attraction of Females

Muted males don't attract females. Speakers producing male calls attract females. Females aren't fooled by mimick birds (even though males are). Hearing songs to femalse increases females' reproductive behaviors. Fast singers selected over slow ones. Ability to feed young increases with increasing song rate. How quickly you pair increases with repetoire size.

Muted Males

Attraction

Reproductive Activity

Female Choice: Output and Repertoires

Communication II: Chemosignals in Vertebrates

Wednesday, November 3, 1999

55 Production of Chemical Signals

Many animals learn about other animals through chemical signals. This method of communication is very phylogenetically old. It's present in most animals. True of almost all nocturnal mammals (and most mammals are nocturnal).

Olfaction/chemical communication harder to study because we can't detect it as directly.

Some lemurs that rub their tail with their arms – puts their scent on their tail. Then they wave their tail at competitors.

Chemical signals are different than most signals because they persist in the environment – you can leave a signal and go away. Also, they can provide information about how long that scent can be there. c.f. visual signals.

55.1 Sources of Odor

Glands

Many odors are produced by specialized scent glands.

- Location: glands can be found just about anywhere on an animal's skin. Heads/body/arms/legs/tail/etc. Can be big or small. Often found in andogenital area. Also can be located inside the animal.
- Structure: usually modified hair folicles (sebatious). Produce sebum, which is a type of oil.
- Sexual Dimorphism: many scent glands are sexually dimorphic in size. Sometimes glands are bigger or only present in males, sometimes in females.
- Regulation by Gonadal steroids and seasons: The glands are regulated by hormones (males' usu. regulated by testosterone, females' usu. regulated by ovarian hormones). There are also seasonal differences. Often become bigger when animals are competing for territories.
- Social Status: Glands are larger in dominant glands.
- Bacteria: bacteria proliferate in warm wet places. Often it's the bacteria working on the products of the odor glands that produces the actual scent. Often it's harder for animals to discriminate odors that come from animals w/o bacteria – maybe different bacteria produce different scents?

Excreted "By-Products": Urine, feces, and saliva

Urine is a very common scent-marking device. It's cheap to make, since animals urinate anyway. Ungulates (antelopes etc) often use feces. Urine can allow animals to learn about the reproductive state of the urinating animal – animals with more progestine in blood stream (i.e., ready to mate) will often have more progestine in their urine. Same with other hormones. Males can pick up on these scents in the urine to determine how receptive females will be. In pigs etc, saliva is used to scent mark. Saliva contains sex hormones that increase female receptivity.

Different glands – same/different information

Many species have multiple sources of odor. Often the different sources of odor contain different information and serve different purposes. Can tell whether an odor is used by testing whether animals can distinguish odor from different animals and whether they respond differently to male & female odors.

55.2 The odors themselves

Complex Mixtures

In vertebrates, the odors are huge mixtures of molecules – there is usually no single phermone molecule that accounts for the effect. Use gas chromatogram to seperate out different molecules – allows us to compare odors produced by different animals, and differences in male vs. female. Often there are compounds that only one sex has.

Changes with sex and reproductive status

The scents put out by females changes depending on how receptive they are. Often females have new chemicals appear in their odors when they are receptive. Also, dominant animals often have different odor compositions than subordinate animals. We can use gas chromatograph to figure out which odors might designate dominance or receptivity.

Changes with social status and testosterone levels

- Tree Shrews: castate males, and they no longer have a compound in their scent that males normally have. Give them testosterone and they'll start having that compound. Experiment: first, males scent mark more if they smell normal scent than if they smell castate scent. But if we put the compound there, then they will scent mark more.
- House Mice: castrate male urine doesn't elicit the responses that normal male urine does (agression from males, female attraction, induce estrus, etc.). Examine urine of castates and normals. There are 2 chemicals missing from castrate urine. If we add those chemicals, then agression increases. Also, if we add those chemicals, females are attracted & estrus is induced.

Peptides as social odors in newts

Males produce a peptide odor attractive to females. Female has to be in reproductive condition to be responsive. Odor production dependant on testosterone. Detected via olfaction. Peptides can function to distinguish species (a fairly similar peptide is attractive to females of a closely related species).

55.3 Deposition of Odors

Injection, the direct approach

Directly inject the odor into the females' bloodstream.

Direct release into the environment

Release odors into the environment in an uncontrolled fashion (fish).

Secent Marking

Put scents in specific places. scent mark places or yourself or other animals.

- Motor Structure: basic mechanism differs among animals, and is strongly affected by where the odor glands are.
- Sexual Dimorphism: often males mark more than females. sometimes they mark in different ways.
- Regulation by gonadal steroids and seasons: scent marking is often seasonal (manipulate photoperiod). Marking is regulated by hormones (usu. sex hormones).

- Odors and social status: scent marking is regulated by odors – try to cover up other animals' odors with your own. scent marking is also regulated by dominance – dominant animals tend to scent mark more than subordinates.
- Neural mechanisms of scent marking: in mongolian gerbils, there are specific places in the brain where you can inject hormones to cause scent marking. Lesioning these areas reduces scent marking. In hamsters, vasopressin injected in a particular area will elicit a lot of scent marking. A vasopressin-blocker will reduce scent marking. Dominant animals have more vasopressin fibers in this area of the brain.

56 Getting the Message Across

Substrate

Where you put the odor affects how long odors will last. Sebum may cause odors to evaporate more slowly.

Conspicuousness: scratching and UV

Animals can make their marks more conspicuous – pair visual cues like scratched trees with the mark etc. Sometimes odors might be colored (e.g., iguanas' odors are colored in the UV spectrum).

Correlation with environmental context

Sex attractant components of scent tend to evaporate quickly. Territory marking components evaporate less quickly.

Where humidity is higher, animals produce heavier chemicals (to slow down evaporation, since humidity increases evaporation rate).

57 Perception and Function

57.1 Information in the Scent

Species

Animals prefer the odors of their own species.

Sex and Reproductive Condition

Males are attracted to female odors, & females are attracted to male odors. Also, odors contain info about reproductive condition. Odors of reproductive animals are much more attractive.

Social Status

Females prefer the odors of dominant males. But if a female isn't in reproductive condition, this preference disappears.

Mate recognition

Prefer to interact with familiar mates rather than unfamiliar mates. Prefer to investigate your mate's odor.

Individual discrimination and recognition

Animals can learn to discriminate individuals' odors (via skinner box) very easily. Animals recognize which odors from different glands go to the same animal.

57.2 Mate Choice

Odors are usually involved in female mate choice. Females tend to prefer dominant males with high testosterone.

Overmarking and resource holding

Males mark over other males' cues. The better a male does this, the more a female will prefer them. If there is lots of M1's scent, but it's marked over by a small amount of M2's scent, the female will still prefer M2.

Parasitism

Females avoid the urine of infected males.

Diet and choice

Females prefer the scents of males that eat more protein.

Costs of scent marking/odor cues

Urine is detected by predators.

57.3 Territorial Interactions: the scent-matching hypothesis

Dominant animals will expand their territory to subordinate animals' territories. Most marking happens at territory borders. If males detect that the odors of an animal don't match the odor of the territory they're on, then they'll be more agressive.

57.4 Neural Mechanisms of Social Odor Recognition

The Olfactory and Vomeronasal chemosensory systems

Petrulis' Work

Socail Living and Altruism I: Kin

Monday, November 8, 1999

58 Why live in a group?

- Predation pressure
- Food is difficult to find

In some guppies, sociality increases as predation pressure increases.

58.1 Predation Pressure

Vigilance

The more animals in your group, the more animals can look out for predators.

Goshawks eat pigeons. In an experiment, the more pigeons, the less effective the goshawk was at getting any prey. Also, the earlier the pigeon sees the hawk, the more likely it will survive. And as you increase group size, the distance at which you see the hawk increases. The time spent looking for predators also decreases as group size increases (presumably giving more time for foraging). Also, scanning of a single pigeon is fairly predictable – they just scan every 10 seconds or so; but much harder to predict scanning times of a group of animals.

Alarm Calls

Often, groups of animals have "sentinals" whose job is to look out for predators.

Certain type of squirrel has 3 alarm calls – snake, leopard, bird. Other monkeys respond differently to each call.

When an arial predator is spotted, everyone makes call and everyone runs. In this context, the animal that gives the alarm call decreases their chances of getting caught. This type of call is not sensitive to who's around you. Explanation: make the call to create confusion and confuse the predator.

Dilution Effect

The more animals that are around, the less likely it is that you'll be attacked – there are many other targets for predators to choose from.

Scanning as group size increases. If group size gets big enough (>60 or so), the amount of total scanning becomes less than an individual would scan (everyone assumes that everyone else is scanning). But even though there's less scanning, the dilution effect makes it beneficial – it's unlikely that you'll be killed even if a predator does come.

Dilution effect is seen in groups of monarch butterflies, too.

Horses in a swampy area are assulted by blood-sucking insects. The larger the group the horse is in, the fewer insects are sucking their blood – if there are enough horses around, then there are fewer insects/horse.

"Selfish Herd" effect: Bluegill Sunfish

Groups band together to try to avoid predation. It's the animals on the outside of the group that get eaten, so you should try to stay in the middle of the group.

In sunfish, predators tend to attack single nests instead of colonies. Solitary nests can be attacked from any side, but peripheral colony nests can only be attacked from one side.

Group Defence: Cultural Transmission of Mobbing

Groups can get together for defence. When a predator comes, they will all attack & drive off predators.

Mobbing can also be culturally transmitted: let an observer bird see a bird attack another bird. Then test the observer's response to the bird they saw attacked. They will react much more agressively. This could allow transmission of information (which animals should be mobbed) across generations.

58.2 Obtaining Food

Finding Good Food Sites: "Information center" Hypothesis

In weaverbirds, there are very sparce sites, each of which has lots of food. A colony is an "information center:" you can follow fellow animals to food sources & eat there. There is experimental evidence that weaverbirds can tell what other weaverbirds have been eating well, and will follow those birds.

Cliff swallows live in colonies. Individuals seem to follow successful foragers.

Foraging Together

Often foraging together is better than foraging alone. Jacks hunt anchovies in groups. The group of jacks tries to break up the anchovie group so they can attack individual anchovies. Jacks can get food faster and can get more food when they're in a group. The first animal to attack usually gets the most food. But the first animal to attack is the first animal to see the anchovies, so it evens out in the long run..

Harris' Hawks attack rabbits in groups (rabbit is 2-3 times heavier than the hawk). The groups tend to be of related animals. A variety of group tactics. E.g., take turns attacking, or having one chase the rabbit into the others. Larger group sizes signifigantly increase the number of rabbits killed.

Gulls feed on fish. Gulls in flocks of six each get more food than a single gull would. If there's one gull, the fish all run from it. But if there are 6 gulls to run from, then one gull can catch a fish as it's running away from another gull.

Foraging/Predation Tradeoffs: House Sparrow Chirrups

?

58.3 Costs of Sociality

Competition for food resources: starvation in fieldfares

If you're living in a group, then everyone in the group is competing for the same food sources. Children can starve.

Effort parasitized by other group members: male lions

Others in the group might not share. In lions, females tend to do the killing; but once the prey is dead, the males tend to displace the females.

Parasites: cliff swallows

The closer-packed a population, the more disease and parasites can spread.

59 Does "Altruism" Exist in the Animal World - Kinship

59.1 Indirect selection and inclusive fitness: Hamilton's Rule

Often, if you're living socially, you're living with relatives.

Sometimes, you forgo reproducing to help your relatives reproduce. We can explain this with "indirect selection." Direct selection is normal selection; i.e., you're more fit if you produce more viable offspring. Indirect selection is selection because of shared genes with relatives. You share 25% of your genes with a neice, so helping your sister have 2 more children will increase your genome representation in the population as much as having 1 child will. Inclusive fitness = how much you increase your genome's representation in the population.

Hamilton's rule: kin selection iff rB-C > 0b

Where r is the degree of relatedness to non-kin that you help. B is the benefit (the additional number of offspring you caused). C is the cost (the number of children you didn't have yourself because you were helping kin).

Animals take how related they are into account in interacting. Animals are less agressive to their relatives, more likely to cooperate, less likely to trespass on relatives' territory.

59.2 Eusocial insects (see Alcock text)

59.3 Alarm Calling and Social Interactions in Belding's ground squirrels

Belding's squirrels produce calls in response to ground calls. These ground calls have a cost: a calling squirrel increases their chances of getting eaten. Primarily females give calls (females are the ones who interact with their own relatives; males disperse from their homes).

59.4 Cannibalism and kin: Arizona Tiger Salamanders

Larvae can be either normal animals or cannibals. The cannibals prefer to eat less closely related animals over more closely related animals.

59.5 Kinship and Schooling: Toad Tadpoles

Toad tadpoles aggregate with their relatives – help their relatives.

59.6 Kinship and outbreeding

Toads

Golden Hamsters

Female seem to be less sexually attracted to closely related animals.

59.7 Kinship and Breeding: Male Lions

A coalition or males holds a pride. In small coalitions, males tend to be unrelated: they share the mating equally. In large coalitions, males tend to be brothers/kin: most males can't reproduce. These males get fitness benefit indirectly via their brothers.

Social Living and Altruism II: Kin & Non-Kin

Monday, November 15, 1999

60 Cooperative Breeding and Kinship

Cooperative breeding is fairly common (hundreds of mammal species & bird species). Help your kin breed. Usually decreases your ability to breed.

60.1 Florida Scrub Jay

Live in very harsh environment. Resources are patchy etc. About half of the nests have helpers. Helpers are often the youngest jays (1-2 yrs old).

Breeders benefit from helpers

Helpers assist in countering predation and in getting food. 64% of helpers help both of their parents. Most of the rest help one of their parents. A couple (~1%) help non-parents.

Helpers do help. Usually a nest w/o helpers generates 1 offspring/year, and a nest w/ helpers generates 2 offspring/year.

Helpers bring in food, but total food brought to chick doesn't increase – the parents bring less. This alleviates strain on parents, and helps the parents survive. Also, helpers do alarm calls to protect vs. predators.

To breed or to help?

On average, each helper produces 0.33 offspring/year. In contrast, a new breeding pair can produce 1.4 offspring/year. So why not breed? One reason is that leaving the nest early increases bird mortality. Chance of successfully finding a nesting site is low. Also, helping might make scrub-jays better parents.

Why stay and help: saturated habitat

Since the environment is so patchy and scarce, the jays have saturated all nest sites. Thus, it's very hard to start a new nest. If we give the jays lots of nesting sites, then there won't be any helpers.

Helpers expand and inherit territories

Males can inheret their parents' breeding territory. This is the normal way of acquiring a territory. Nests with larger groups of helpers will increase the size of that territory. If they increase the size of the territory enough, then they can bud off. So by helping, you are increasing the size of the territory you might get, and you're carving out your own territory.

As long as you're staying at home (to get territory), you might as well help your siblings.

60.2 Black-Backed Jackals

Form long-term pair bonds with helpers. Helpers are usually the parents' offspring from previous years. Helpers feed, groom, defend vs. predators, and protect vs. other breeding groups. Presence of helpers increases number of pups surviving. In general, each helper adds about 1.5 pups/yr.

60.3 White-Fronted Bee-Eaters

Clans, Relatives, and Helpers

Live in clans – groups of extended relatives. Several pair-bonds can be formed within a single clan. Each helper will help exactly one breeding pair. Helpers are more likely to help close kin. Give them the choice between helping a more or less closely related pair, & they will almost always help more closely related pair.

In-laws

If you join the clan from the outside as a spouse of a member, you very rarely help. This makes sense, since there's no one around who's related to you.

Disruption of Breeding Attempts

Often fathers will disrupt the breeding attempts of their sons, to make them into helpers. They can do this by disrupting courtship, blocking nest sites, etc. The younger the animal, the more likely it is to be recruited.

60.4 Do helpers really help? Experimental Evidence

Experimentally remove helpers from the nest. Then the number of offspring goes down.

60.5 Do Breeding Constraints Really Exist?

Superb Fairy-Wren: A female! My kingdom for a female!

Cooperative breeder, breeding pair + male helpers. Remove the breeding males from nearby territories. Then most of the helpers will disperse. But if you remove both male & female (so there's an empty territory, but it has no females), then they won't dispurse.

Seychelles Warbler: Discriminating tests

Very small species (˜300 members). Cooperative breeders appear once they start saturating their territories. There are some good territories and some bad territories. If you remove breeding pair from a bad territory, then helpers from good territories won't grab them. But helpers from a bad territory will. Part of this comes from the fact that helpers on good territories will live much longer, so they can afford to wait for good breeding sites.

61 Mechanisms of Kin Recognition

61.1 Spatial Proximity

Anyone in your nest is probably either your sibling or your offspring. Parents will often reject offspring if they are outside the nest, and will accept unrelated animals if they're in the nest.

61.2 Association in the Nest

Learn who your kin are because you grow up with them. Remember who you grew up with. Put unrelated animals in nest. Then everyone that grows up with them will treat them as kin. As soon as animals leave the burrow, associating with someone doesn't make you treat them as kin.

61.3 Phenotype matching

Belding's ground squirrels

You can recognize close relatives even if you didn't grow up with them. 1 theory: animals share common uterine environment. But in B's ground squirrels, they can tell full-sisters apart from half-sisters. Another theory: match your own scent to other animals'. Treat animals with similar scents as kin.

Golden hamsters

If you're raised with non-relative A, then how will you treat A's siblings? If you treat A's siblings more like kin than random people, then you must be doing some type of phoenotype matching, since you've never seen A's siblings before. You do treat A's siblings more like kin.

62 "Altruism" without relatedness – Mutualism

Sometimes it pays for animals to cooperate, since they both gain fitness from it.

62.1 Male Lion coalitions

In small coalitions, the males are unrelated. But they both get more reproductive success then they would alone.

62.2 The Dwarf Mongoose and the Hornbill

Mutualism exists between species. Dwarf mongoose and hornbill forage together. Both eat insects. Mongoose will go into anthills to eat, and hornbills will eat the insects that scatter. So hornbills get more food. Mongooses gain predator protection – hornbills make alarm calls. Mongooses do less alarm calling when hornbills are around.

62.3 Cooperative breeding and non-kin: Pied Kingfisher

You can sometimes find non-related helpers. Primary helpers (offspring from previous years) and secondary helpers (unrelated). Primary helpers will chase off secondary helpers unless they're having trouble feeding their young. Why do secondary helpers help? Well, first, they help less than primary helpers. Second, if a female looses their mate, it's easier for you to pair up with her. Also, secondary helpers survive longer than birds that just hang out.

63 "Altruism" without relatedness – Reciprocity

Very rare form of cooperation. If cost to you is much less than benefit to other guy, and other guy is likely to reciprecate, then reciprocity can happen. The problem is that this system is open to cheating: you can get helped by someone else and not recipricate.

In order for reciprocity to be evalutionarily stable:

1. Animals can't get away with cheating
2. Probability of encountering the animal you're being reciprical with again must be high.

63.1 Impala grooming

Animals groom each other. The amount of grooming you do to them is almost identical to the amount of grooming that they do to you. Grooming helps control parasites – animals can't sufficiently protect themselves against it.

63.2 Coalition Grooming in Vervet Monkeys

63.3 Vampire Bats and Blood Regurgitation

Vampire bats suck blood from large animals. Individuals often fail to get any food in a given night. When they do, they will beg for food from their neighbors, and their neighbors will give them food.

Must recognize cheats

Bats that receive blood tend to be more likely to give blood in the future.

Long-term interactions

Bats interact with each other for years.

Benefits of receiving aid must outweigh costs of donating

1 or 2 days without feeding can cause mortality. But if you have a lot of blood, and donate a little, it doesn't cost you much. But it helps them a lot.

Sacpe and Navigation I: The Why of Space

Wednesday, November 17, 1999

(lecture by Seth Ramus)

64 Deciding Where to Live

What factors might animals take into account to choose their habitats?

- Resources
  - Food
  - Water
  - Shelter
  - Mate Availability
  - Low Predation

Animals are optimizers: they choose where to live based on factors that maximize their potential reproductive success.

64.1 Ideal Free Distribution (Fretwell)

Dictates that animals will choose the best environment for their fitness. But this model makes some assumptions:

- Animals are "free" to go where they will do best – no exclusion.
- the animals have complete information about the availability of resources.
- Every animal ends up with about the same fitness

Asserts that each animal will move into the environment that maximizes its fitness, taking into account how the animals currently in an environment effect how good it is. E.g., if E1 has 10 food units, and E2 has 4 food units, the first 2 animals to arrive will move into E1. The next animal will move into E2. The next will move into E1.. Etc. An example of ideal free distribution is people choosing the shortest line in a grocery store. Milinksi did an experiment to test this with fish.

64.2 Despotic Distribution

Dictates that the first ("best") animal to claim a resource patch defends it to the exclusion of all others. The next animal takes the next best resource and defends it, etc., until all resources are used up. The remaining animals are "floaters."

Krebs studies great tits, which show despotic distribution.

64.3 Ideal Free Distribution with Unequal Competitors

This is closer to reality. Some animals are better competitors than others, and they chose the best places to live.

One way to account for differences in how well animals compete is to rate each animal with "competitive units" – better competitors will have more competitive units. Then use competitive units to do ideal free distribution, assuming that each animal will take up an amount of resource proportional to the number of competitive units they have. For example, consider a super market. Just counting up the number of people in each line isn't a good indicator of how long the line will take – you need to take into account how much resources each person will take (i.e., how much they're buying). People with lots of items have more competitive units than people with just a few. In the fish example, a fish that eats twice as much as another fish will have twice the number of competitive units.

Unfortunately, this makes the same basic predictions as ideal free distributions – since the big and little animals are usually distributed randomly anyway, it's most likely that we'll just get the same result as ideal free distribution. The chance that we'll get something signifigantly different from ideal free distribution (i.e., have lots of big fish in one region and lots of little ones in another) is low.

64.4 Ideal Free Distribution with Resource Defence

In reality, most examples include elements of both resource defence and ideal free distribution, resulting in unequal distribution of resources.

The example of aphids. Aphids try to find places to reproduce and to induce a gall. The best places are (1) the base of leaves, and (2) big leaves. The first aphids go for the largest unoccupied leaves. When all leaves are full, aphids will take places further out on already-inhabited leaves. Look at how well 1st stem mothers, 2nd stem mothers, and 3rd stem mothers, do on average. They all do about the same. This makes sense, because if 1st stem mothers did better on average, we'd expect some 2nd stem mothers to move to unoccupied small leaves… But also, aphids will fight for the position at the base of the leaves.

64.5 Economic Defendibility (Brown)

When the benefits of defending a territory outweigh the costs, then you should defend the territory.

Golden-Winged Sunbird (Gill & Wolf)

Sunbirds defend patches of flowers, and exclude other sunbirds from the patch. Can we show that defending the patch benefits the sunbirds more than it hurts them? If you defend a patch, the amount of nectar in each flower increases, since no one else is eating it. Observe the animals in the wild, and figure out how much time they spend defending, eating, foraging, etc. Then figure out how expensive each activity is, in terms of energy.

- Foraging: 1000 cal/h
- Resting: 400 cal/h
- Defense: 3000 cal/h

In undefended territory, foraging takes about 4 hours. In defended territory, foraging takes about 2.7 hours. This saves the bird (1000 cal/h)(1.3 h) - (400 cal/h)(1.3h) (since it's resting instead of foraging). So the bird saves 780 calories. But how much time needs to be spent for territorial defence? The average sunbird spends about (.28 hours) defending, so defence costs 728 calories. Since 780>728, the bird is gaining more than it's losing, so it makes sense to defend the region.

65 Deciding When to Move

Territories can have costs. Defending a territory can decrease your time available to mate, to find food, etc. Also, you can get hurt defending a territory. So sometimes it is / becomes a bad idea to defend a territory. And sometimes it makes sense to move on and try to find a new territory. Three examples of times when animals choose to dispurse or migrate:

- Natal Dispersal. When animals are first born, they choose to dispurse. This may have a lot to do with mates. If you don't dispurse, you'll probably mate with your siblings (inbreeding).

- If a territory turns out not to be good, then dispurse. E.g., redwing blackbirds will usually set up in the same territories after migration. But if a blackbird fails to mate well one year, they will tend to choose a new territory the next year.
- Migration, to maintain resources due to expected changes in the environment (e.g., seasonal changes). Cost of changing environment must be lower than benefit of moving. Some animals conditionally migrate.

66 Identifying Places in an Environment

An animal must be able to identify specific places in their environment – use local cues and other information. You have to know where the food, shelter, etc., of your territory are. Also, you have to know where the borders are, etc. It's important for defence and for locating resources.

Space and Navigation II: The HOW of space.

Monday, November 15, 1999

(lecture by Seth Ramus)

The problem of spacial perception is extremely compelex, and animals perceive space in every sensory modality possible. By contrast, spacial representation is more likely to be independant of sensory modality. It would be inefficient to have one visual map and a separate olfactory map.

All navigation basically requires:

- a map (a representation of the relationship between places stored in an animals brain)
- a compass (external cues as to the direction or position of the animal in external space)

67 Large Scale Navigation

navigation over large spaces (e.g., migration) doesn't require learning. Doesn't rely on landmarks, but usually on celestial and magnetic compasses.

Sun timer: watch where the sun is at different times of day, to figure out what direction you're going.

Magnetic compass.

Use the polarization of sunlight to figure out directions, since sunlight polarization changes over the day. Especially true of insects. E.g., some ants will wander around looking for food, and then will go streight home. How does it tell where home is? It figures it out from its path so far. If we pick up an ant and move it over by 10 feet, then it will search for its home at a 10-foot displacement from where its real home is. If we use a polarizing filter, we can fool the ants.

Bees also use the sun as a compass. See alcock

Ants do path integration. Path integration is one solution to navigation without landmarks: simply keep track of your "coordinates" relative to your home, so that when you want to go home, you know what direction and how far to go.

Large scale navigation is succeptible to errors: if you make a miscalculation, or something unexpected happens (you get picked up), you can get very confused. Usually use landmarks to refine navigation.

68 Small Scale Navigation (Local/Landmark)

Use landmark-based navigation for smaller scale navigation. One hypothesis is that we make a cognitive map. This is a representation of the world around you that has landmarks and their relation to each other (direction, distance, etc). This means: (1) that you always know where you are; and (2) if someone moves you, you'll still know where you are..

Landmark system must be plastic, since landmarks change over time.

Animals can take advantage of landmarks: place nests near large landmarks. An experiment to see if animals use landmarks: place distinctive landmarks around a wasps nest, let them get used to it, and then offset all of the landmarks by a fixed distance. Then the wasp will look for the nest where it should be relative to the landmarks.

An experiment for cognitive maps: let a rat learn a maze. Then teach it to go to a goal. Then see if, when we block off passages, it knows enough about the maze to take the most efficient path.

Bees maintain a cognitive map. Do bees have an understanding of the space around them? Expose a bee to a waggle dance, then put them somewhere random, and they'll still go to the food.. So they're not just going in the direction they're told. Another experiment: artificially make bees signal that there's food in the middle of a lake.. Stick bees on a feeder in the middle of the lake, and see if they can recruit other bees to come eat. They can't: other bees don't believe them.

69 Representations of Space

An oversimplification:

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Receptor → processor1 → processor2 → ... → high-order rep.
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The later processors combine modalities. 2 separate pathways for vision: the what pathway and the where pathway.

Cognitive map probably resides in the hippocampus. Hippocampus involved in memory. It's an association cortex that stores relationships between landmarks. Lesions of hippocampus cause navigation deficits.

2 interrsting cells that have been found in the hippocampus: head direction cells fire when the animal faces a certain direction (direction depends on environment). place cells fire when the animal is in a specific part of space.

Tape: place cells of a rat running around a maze.

Agression and Territoriality

Monday, November 29, 1999

70 Territoriality

70.1 Territory vs. Range

A territory is a fixed patch of resources that an animal defends. Ranges aren't defended.

Animals must "decide" how large of a territory to have, whether or not to even have a territory, etc.

70.2 Economics of Territory Defence

It takes energy to maintain & defend a territory. Animals use the costs/benefits to "decide" what to do about territoriality.

Costs of testosterone and aggression

- spiny lizards: males defend territories. try experimentally increasing the testosterone levels of some lizards. those lizards have a substantial increase in mortality. (thus, there's a direct cost associated with testosterone). testosterone-increased lizards are more agressive, and more active. this gives less time to forage for food: these animals tend to starve. also, they run about more, so are more conspicuous to predators. So there is a TRADE-OFF with testosterone: agression/activity for chance to live. (Experiments show that it's probably starving that kills them, not predation.)
- red grouse: males form large territories containing several female nests. Implant testosterone in some males, and their territories grow. Reproductive success is very high (almost tripple), but they all died over the winter, because they had spent less time feeding.
- dark-eyed juncos: monogomous species. Try implanting testosterone. Then they sing a lot more. But they spend less time feeding their young.

Defence and resources

Sometimes it makes sense to decide whether to have a territory depending on the value of the territory and the cost of defending it. So if costs are high, or territory value is low, don't defend it. If territory is too big to be useful, defend a smaller territory. Larger territories are harder to defend, expose you to more predators.

- Maximizing gain (Rufous hummingbird): defend an optimal territory size. Animal figures out over the course of about a week how large of a territory to defend to maximize net gain from territory.
- To defend or not to defend (Pied wigtails): defend patches of land that border rivers, to eat bugs that wash up. After you eat bugs from the river bank, it takes about 40 min for the bugs to come back. Intruders can come eat food before you can get to it. So it's good to defend a territory. Occasionally, a wigtail will allow a satellite male on the territory. They eat out of sync, so they each get 1/2 the food. But satellite male helps to defend the territory. Especially like to have satellite when there's lots of food, or when there's lots of intruders.

71 Mechanisms of Agression and Dominance: Hormones

Agression often correlates very well with hormones (e.g., testosterone).

71.1 Seasonal variation in testosterone secretion and agression

Seasonal variation in hormones correlate well with agression.

Red Deer of Rhum

Breeds during a short period of time. Levels of testosterone are maximum around breeding time. This is also the time when the deer are most agressive. Castrated males have smaller antlers, etc. Also, castrating an animal drops their dominance status. Testosterone shots increse an animal's dominance. (Part of this comes from antlers – remove a deer's antlers, and its dominance drops)

Badges of status: Harris's sparrow

Sets up territories in breeding area and dominance territory in wintering flocks. You can tell who's dominant by how many black feathers are on the chest: the more black feathers, the more dominant. Testosterone correlates well with black-feather-area during the summer. But not during the winter. Try dying a dominant white. Then other animals will think he's subordinate, but he'll keep responding agressively. Or try dyiing a subordinate black. Then they can't respond to challenges.

Not always correlated: Dusky wood rat

Defend fairly stable breeding areas. Castrated animals aren't less agressive. Even though there's a correlation between agression and testosterone, it doesn't seem to be causal.

71.2 Puberty, testosterone and agression

Testosterone increases and agression appears at the same time: puberty. Inject pre-puberty animals with testosterone, and they'll become agressive.

Why increase testosterone at puberty?

Animals disperse at puberty. You need to go find a territory, etc., and fight more. Giving testosterone early can cause early dispersal.

Dispersal in Belding's ground squirrels

Dispersal is sexually dimorphic: females tend to stay at home. Also, males explore more. Provisioned males (males with more food) will disperse earlier. But there's no correlation between testosterone levels and dispersal (males and females have the same testosterone levels when they disperse). But it's possible that, even though there's no activational difference from testosterone, there might be an organizational difference.. Provide testosterone to mothers, and their daughters will disperse much further.

Dispersal in primates: effects of status

Primarily the males disperse. Pubescent males are forced out of the group by the dominant male. Dispersing males can either try to directly take over a new group, or to slowly edge their way into groups. Sons of high status females show more play, less stress, less fight-or-flight, more exploration, etc.. They tend to be the ones to directly take over a group. The sons of low status females tend to try to sneak into a group. This has something to do with hormones, although I'm not sure what – maybe the sons of high status females have more testosterone?

71.3 Agressive behavior is often sexually-dimorphic

Male mouse agression: activational vs. organizational effects

Mice use odor cues to decide whether to attack mice. Male mice will only attack mice whose urine has testosterone (they won't attack females or castrated males). Being exposed to a female can increase agressive behavior. Where do these male/female differences come from? Agression comes from the organizational effects of testosterone: if there is testosterone circulating early, they will become agressive; otherwise, they won't. You're more agressive if you grow up between 2 males than if you grow up between 2 females.

Social dominance in beagles

These dogs form linear dominance hierarchies. You can masculinize females by giving them testosterone early. Between a male and a masculinized female, they'll fight for the bone; but females will always let males take the bone…

Rough-and-tumble play in rhesus macaques

Males prefer agressive, rambunctios play. If you masculinize females, they will engage in more rough-and-tumble play. Thus, this seems to be an organizational effect, not an activational one.

Female can be more agressive - the spotted hyeana

Social animal. Females are socially dominant to males. They're more agressive. Females have pseudopenises. Fairly small differences $\between$ males and females in testosterone. But there's another androgen, that females have more of. Inject animals with that androgen, and they get more agressive, etc.

71.4 Agression can increase testosterone levels

The "challenge hypothesis:"

Male red-wing blackbirds: T and LH

Seasonal correlation between agression and T

T important for initial interactions only

Increased T: Having a territory or acting agressive?

Simulated intrusions and T levels

T-implants: effects on nearby males

Non-T factors important in some species

Correlation between challenge response and mating system

Costs related to chronic T levels?

Animal Intelligence and Cognition

Wednesday, December 1, 1999

You can turn in papers on monday (in class)

Problems with trying to judge "intelligence:"

- what is it?
- how do we measure it?

72 Scala Naturae

Aristotle proposed a Scala Naturae: a hierarchical classification of living organisms. Scala Naturae assumes:

- "intelligence" varies along a linear scale

But evolution gave us an evolutionary tree..

Differences between S.N. and tree view:

```
Phylogenetic Scale       Phylogenetic Tree
------------------       -----------------
 hierarchical(?)           non-ranked
 unilinear                 linear
 less complexity           sequence indep. of complexity
     → more complexity
 complexity ↑ with time    complexity independant of time
```

72.1 Silly Ideas to Try to Preserve Scala Natura

One proposal: see how far back they split off (from our heritage): the more like us they are, the more intelligent.

Another proposal: Try ranking intelligence based on the size of brain. Or on ratio of brain size to body volume. Or on ratio of brain size to skin surface area.

73 Measuring Intelligence

73.1 Ability to Adapt

Barnett proposed that intelligence is the ability to adapt (i.e., change behavior adaptively in response to a chaning environment). So measure intelligence through learning experiments. But different animals can adapt in different ways.. A variety of studies based on this view gave confusing results.

(spider joke: take off all its legs & its deaf)

How do you decide which questions to ask? The questions asked have a large effect on what answers you get. The garcia effect (bait shyness): radiation can cause you to develop a food aversion. Bait shyness is single-trial learning, and can last a lifetime. But other types of negative feedback will need many more trials to learn association.. There are some types of learning that brains are specialized to do.. Can teach rats to rear up on hind legs to avoid shock, or to press bar to get food, but can't teach them to rear to get food.

It's very hard to find experiments that are eqivalant between species.

73.2 Information Processing

Intelligence = ability to take info in, process it, and use it. This model has turned into the modern field of compartive cognition. Learning set: learning non-specific facts through a series of trials (e.g., learning what the basic task is).

74 Intelligence as a Justification

If someone is more intelligent, we shouldn't use that as a justification for subjugation, etc..

Problems with standard iq test: correlates well with socio-economic status; cultural biases; test conditions; etc.

If we -could- find a good metric, then there's no reason to believe that different populations would score the same.

But at any rate, between-group variances are much smaller than within-group variances.

75 Why Study Intelligence?

Try to learn more about how we deal with our environment, and about how our intelligent behavior works. Comparitive cognition: try to figure out how cognition works in a variety of animals, so we can understand cognition better.

H.M.: lost declarative memory, preserved skill memory etc.

Monday, December 6, 1999

76 Caveats about Evolutionary Study of Human Behavior

Our psychological traits have evolved. blah...

76.1 Evolutionary does not = "genetic"

You can never ascribe a purely genetic cause for a behavior. The fact that you can't find genes for something doesn't mean its not evolutionary. Also, evolution can occur through non-genetic pathways..

76.2 Evolutionary does not = unmodifiable

Evolved behaviors tend to be very flexible.. Don't expect anything less flexible for humans.

76.3 Evolutionary does not = optimally designed

Human evolved behavior need not be completely optimal. In fact, we're in such a new environment that many of our traits are probably maladaptive. E.g., people like to eat fatty foods. There's often costs associated with different adaptations. Have to balance costs and benefits. Adaptations should be seen as "good enough."

76.4 Evolutionary does not = conscious strategies

There's no reason to think our adaptive choices should be controled by conscious mechanisms. When we talk about strategies, we mean that a particular adaptation has had strong selection pressure on it to make it more prevalant...

77 What is Evolutionary Psych? What are its Premises

The study of evolved psychological mechanisms for behavior in humans.

77.1 Adaptations for the problem of survival & reproduction

Almost all adaptations are specifically designed to (eventually) help us survive and reproduce.

77.2 Domain-specific psychological adaptatoins

Each adaptation seems to depend on a fairly small range of information. Posit a number of domain-specific strategies, that get used in the appropriate contexts..

77.3 Variable output of evolved psychological strategies

When there are strategies/mechanisms, there are a number of ways that humans can responds.. E.g., there may be some module that causes jealousy. It might cause a number of different behaviors, changes in state, etc., such as hitting someone, feeling angry, etc.

78 Human Sexual Strategies and Behavior: Females

78.1 Long-term mating strategies

The return of sexual selection

First, consider long-term bonds (marriage, etc). Females can produce children much slower than males.. Makes them a scarce commodity, so they can be choosy. (operational sex ratio is relatively high?)

Preferences for males with resources

Since females can be choosy, they should pick males with high resources (more children). They tend to prefer men with more resources:

- women prefer mates with good financial prospects (more than men)
- women prefer mates with high social status (more than men)
- women prefer older men: status and income tend to increase with age.
- structural powerlessness claims that, through social conditioning, and sex differencess in access to power, the only way that women can get power is through men. So they try to mate with more powerful males, to get access to power. It's emperically refutted to some degree. E.g., it predicts that women with access to power should act like men, but they don't. Also, it gives us no explanation for the power differences.. Other experiments help discredit structural powerlessness.
- women prefer physical features of dominance: height. Taller men are more likely to be hired, more likely to be promoted, etc. Also, more likely to be good leaders, etc.

Preferences for males with good health & "genes"

Mating with healthy males has direct benefits (you won't get sick) and indirect benefits (your children will have better genes). Healthiness indicates a (potentially heritable) ability to defend vs parasites. Try to pick symmetric mates.. Fluctuating asymmetry = absolute amount of asymmetry. Maintaining symmetry indicates that you are resiliant to environmental difficulties. Facial symmetry correlates well with both physical and emotional health. Females tend to pick symmetric males.

Actual behavioral choice of males?

Most of this is self-reported. Look at actual behavior.

- Female response to male personal ads. Females respond more to older, wealthier, taller men.
- Who do you marry? Usually older men. Also, prettier women tend to marry higher-status men.
- Male resources matter: Kipsigis are a tribe. Males own cattle. Females must marry to get access to resources. Often arranged marriages. The more land a woman has, the higher her lifetime reproductive success will be.

78.2 Short-Term Mating Strategies

Women do have short-term mating strategies. Extra-marital affairs exist in every culture studied.

EPC's and copulatory orgasms

Copulatory orgasm may be involved in human sperm competition. After copulation, females discharge some portion of the sperm (about 35%). Female copulatory orgasm decreases the amount of sperm discharged (by a small abount – about 5%). Also, most EPCs occur during ovulation. Women may be timing EPCs to maximize the chance of reproductive success.

Costs and beneffits of short-term mating

Males show a strong dis-preference for long-term-relatoinships with females with a large sexual history or a large number of EPCs.

Females may use EPCs for:

- mate switching (try to get a new mate, but don't throw away your old one until you're sure)
- gene selection

78.3 Physiological mechanisms of female sexual behavior

Lack of stereotyped postures

Hidden ovulation

No obvious indicators to males about when females are ovulating.

Sex and the menstrual cycle

Sexual behavior doesn't seem to change much over menstrual cycle.

Direct manipulations of steroid hormones and sexual behavior

Direct manipulations of some steroids (esp. androgens) increase sexual desire and sexual behavior. (Inject historectomized females with hormones.)