Mammalogy Lecture 14 - Social Behavior

I. Social interactions are ubiquitous in mammalian biology. Even the most solitary species have bouts of social behavior at least twice throughout the course of the lifetime.

Once at nursing, because all mammals lactate.
Once at breeding, because all mammals reproduce sexually.

II. Although there is a continuum of social systems, we might envision **degrees of sociality**, can be demarked by complexity of interactions. We'll discuss 5.

A. **Asocial**: Minimal contact, usually **marked by aggression**

Males and females defend territories
Short-term pair-bonds may develop seasonally for breeding, usually with immediate separation after copulation
Females typically force young away after weaning

Puma concolor - Cougar
Lynx rufus – Bobcat (also *L. canadensis*)
Geomyids - Pocket gophers (*Thomomys*) – Their habitat is quite patchy, so they tend to be clustered, but are actually very asocial.

B. **Simple Aggregations** – Groups of individuals with no real cohesion, perhaps centered around a resource.

Short term and seasonal (e.g., dry vs. rainy season).
High turnover of individuals & group membership is fluid.

Many species of small antelope (e.g., *Aepyceros melampus*) aggregate around watering holes in the dry season, males are territorial in rainy breeding season.

C. **Reproductive Social Units** - Solely together for reproduction

Usually, there's not much turnover.
Pair bonds may last just the breeding season or may last for life.
Monogamous forms may be facultative (at low density individuals are only likely to find one mate) or may be obligate.

Peromyscus californicus – Obligate monogamy, long-term pair bonds & paternal care.
Madoqua kirki (Kirk's dik-dik) – Monogamy forms at low population density w/o paternal care; at high densities, they're not monogamous.

D. **Simple Social Systems**

- **Groups are persistent and stable.**

- An ordered hierarchy of dominance may form.
- **No division of labor.**
- Groups may be unisexual or of all the same age.

Examples - Bat nursery colonies. In *Myotis* and many other bats, females roost together while nursing in the summers. Males tend to roost in several smaller colonies near but separate from females.

- *Equus burchelli* - Male, often assisted by a sub-adult, defends a harem of females year-round and there may be age structure.

E. **Complex Social Systems** (of several types - we'll look at 3)

- Groups are stable & membership tends to **span generations**.
- Ordered dominance hierarchy.
- Complex within group communication.
- **Division of labor.**
- Pair bonds are persistent.

1. **Monogamous family groups** - a single reproductive pair + nonreproductive individuals (usually related).

   Examples include primates (e.g., *Homo*) and cetaceans.
   Also include canids, especially *Canis lupus* (cooperative hunting)
   and *Lycaon pictus* (cooperative feeding/nursing young).

2. **Polygamous family groups** (usually polygynous) – Include a single vigilant male with a harem of females plus offspring. (Polygamous systems include polygynous and polyandrous systems).

   Baboons - *Papio* (See "A Primate's Memoir" by Robert Sapolsky)
   Howler Monkeys - *Alouatta*

   Social status is often inherited.

3. **Eusocial systems** - queen (single reproductive female) and castes, including non-reproductive workers.

   Naked mole rat Bathyergid genus *Heterocephalus* is a hystricomorphous rodent in the family Bathyergidae. It's the only mammal, in fact the only vertebrate, known to exhibit eusocial behavior.

   Single breeding female (queen) and she actually suppresses the estrous cycles of other females pheromonally.

Non-reproductive workers.

Occur in colonies of 40 - 70 individuals.

Three castes defined by maximum adult body size.
Queen - Single reproductive femals.
Frequent workers – smallest, & range from 25 - 30g
– do the majority of the burrowing work & foraging,
Infrequent workers/soldiers – intermediate size 35 g.
– do a little of the burrowing work.
– defend the colony.

Non-workers – 40 - 45 grams
– Don't burrow at all.
– Don't forage but are fed by frequent workers.
– 1 - 5 males that take care of young.

All males are fertile (that is, produce sperm) but only the large non-workers mate.

If a queen dies, pheromonal suppression ceases and the 1st infrequent worker female to initiate estrus becomes the new queen, and she begins suppressing other females.

The new queen grows, but, since epiphyseal plates have closed, growth is accomplished solely by expansion of intervertebral disks.

Once again, **these categories are generalizations and there is a continuum of social behavior** in mammals from asocial, at one end, to eusocial at the other. Prox & Farine (2020. Ecol. Evol., 10:791) recognize 8 dimensions of social behavior in mammals.

III. Lots of hypotheses have been proposed to explain the origin of social behavior.

D. W. MacDonald (1983. Nature, 301:379) proposed the Resource Dispersion Hypothesis as providing a general initial catalyst.

Common set of starting conditions:
- Basic territoriality
- Individuals defend the smallest area that will support them in a bad year
- Size of the territory depends on dispersion of resources.
- Key is that it's usually not a bad year and resources are readily available -- each resource patch may support more than one individual
- Most of the time there is a very low cost to group formation --> benefits outweigh the costs.

Type of social system that will evolve then depends on the biology of the particular organism.

Reviewed by Johnson et al. (2002. TREE. 17:563); re-evaluated by Elbroch et al. (2016. J. Animal Ecol., 85:487-496.) in *Puma concolor*; and again by Peignier et al. (2019. Ecol. Evol. 9:5133) in *Rangifer tarandus*.

IV. Maintenance of Social Behavior - Social behavior often appears altruistic, and to benefit others at one's own expense.

Reciprocal altruism, is seen in (e.g.) *Desmodus rotundus* (Carter & Wilkinson 2013).

May fail to feed for several days. Individuals who have fed will sometimes share meals, and they're more likely to share with individuals who have shared with them recently.

Reciprocal altruism is rare (Silk 2013). It requires very low dispersal, and the ability to discern sharers from cheaters.

Kin selection is a much more common cause of apparently altruistic behavior.

A series of studies by Paul Sherman (e.g., Sherman 1981. Behav. Ecol. Sociobiol., 8:251) on alarm calls in *Urocitellus (Spermophilus) beldingi* addressed apparently altruistic behavior, behavior that enhances the fitness of other individuals at the expense of your own fitness

- These squirrels occur in grasslands in the inter mountain west and they form breeding colonies.

- As a predator approaches, a squirrel will emit alarm calls and the rest of the colony will flee into burrows.

- This really does appear to be altruistic behavior because Sherman has been able to show that there is a higher probability of predation on call givers. That is, the call attracts attention to the giver, who then suffers a higher risk of predation.

This should be maladaptive, but Sherman hypothesized that kin selection could explain it

In order to understand this, we need to understand a little about *kin selection* and *inclusive fitness* (Hamilton 1964. *J. Theoretical Biology*, 7:1-6.).

Our own offspring share on average 50% of our genes. Therefore, we share 25% of our genes with our grandchildren.

On average we share 50% of our genes with our siblings. Their offspring share 50% of their genes; thus, our nieces and nephews share 25% of our genes, the same as our grandchildren.

I'll illustrate this on the board with two pedigrees.

So, one way to optimize our genetic contribution to subsequent generations is to act in a manner that increases the success of our relatives.

Therefore, we need to focus on **inclusive fitness**, not just **direct fitness**. This is the sum of direct fitness accrued through direct descendants plus indirect fitness accrued through relatives: Inclusive Fitness = Direct Fitness + Indirect Fitness.

Another way to formalize this is through an equation known as Hamilton's Rule.

Social behavior will evolve under the following inequality:

$$rb > c,$$

where r is the measure of relatedness, b and c are benefits and costs, respectively.

Thus, behaviors that increase the chance of success of relatives may be favored by selection, even if those behaviors reduce the direct fitness of the individual. This is Kin Selection, and Sherman hypothesized that this drove the evolution and maintenance of alarm calling in *U. beldingi*.

In this case, females are philopatric. That is, females don't disperse and, therefore, a female is likely to reproduce in the same colony where she was born.

Males conversely do disperse among colonies and are therefore not likely to be related to colony members. All males eventually disperse (Holekamp & Sherman 1989. American Scientist, 77).

Kin selection theory would predict that only females give alarm calls, because only females will increase their inclusive fitness by doing so.

This is exactly what the squirrels do; call rates are much higher in females than males.

Furthermore, kin selection theory predicts that in colonies where females are more closely related genetically, there is a greater tendency to give alarm calls. That is, females must be able to discern relatives from non-relatives. This was supported by experiments; females call less frequently when there are fewer close relatives in the colony. Females can therefore ascertain relatedness of colony mates.