Why Should Animals Be Social?

Ethology and Behavioral Ecology

Summary: This set of notes deals with some of the main ecological reasons that animals come together to form groups and also with reasons that tend to discourage group formation. It ends with a summary of the principal types of groups that have been identified by ethologists. The first part is review.

I. Why should animals be social?

A. Classical arguments for individual selection are easy to understand -- an animal should act in its own self-interest, which is to increase its direct fitness, W_D. Darwin and Wallace gave plenty evidence for how evolution would work in this type of situation and therefore it is not difficult to see why animals should engage in solitary behaviors.

B. Nevertheless, there is the perplexing problem presented by the fact that many animals do live in groups. Furthermore, these groups often appear to behave very cohesively and there often appears to be sacrifice on the part of some individuals for the benefit of others or even for the group. There are two general questions that arise from these observations:

1. Are our observations and inferences about what the animals are doing in the group or social interactions valid?

2. If we are correct in our observations, can we construct a theoretical framework to explain these actions?

C. Below are some general reasons that animals may join groups. There is also some experimental evidence presented that backs up some of these arguments for group formation.

1. These are very important since they form the basis for much of the rest of the course when we will look more at the diversity of social groupings, investigate how they work and propose reasons why they have evolved and been maintained -- that is, attempt to explain why social behaviors are adaptations.

2. Notice that we will start to use an approach that looks at **benefits** and **costs** to behaviors.

a. Both benefits and costs should be thought of in terms of fitness units; i.e., grandchildren, children or copies of genes. Thus a benefit of some action is the addition of some proportion of one of these while a cost is the loss of some proportion.

1. Other units that are related to fitness may sometimes be substituted for offspring or copies of genes, if they can be demonstrated to actually have some sort of effect on fitness. Examples include food, risk to life span, some resource, etc.

2. Notice that proportional gains/losses of offspring are used -- it is not necessary for whole offspring to be gained or lost since this is a probabilistic concept. Thus, individual's actions sum over a lifetime to allow them a certain whole number of offspring -- the benefits and costs of different actions make it more likely that a greater or smaller number of offspring will be produced by a certain actor.

b. We will examine benefit and cost using optimality theory (that's why we spent so much time on it).

c. It will be useful for us to remember the conditions where there is no selection for some trait. In that case:

eq. 1a: $B - C = 0$

Thus, to be favored by evolution:

eq. 1b: $B - C > 0$

or

eq. 1c : $B > C$

or

eq. 1d: $\frac{B}{C} > 1.0$

We will modify and expand this relationship soon, but for the moment it will suffice.

Reminder: the last formula is the one I warned you about earlier when we first discussed optimality. It is true only when only one "peak" B/C exists. If we have a function where there are several "max" B/C, the optimum is the one that gives the greatest difference between B and C (see the first graph in the optimality notes).

d. Finally, realize that in every situation we will consider that there will be a different dynamic of opposing benefits and costs and therefore the exact evolutionary outcome will be different.

C. Reasons for forming groups:

1. <u>Reproduction</u>

a. <u>*benefits*</u>:

i. increase chance and choice in mate finding

a. very solitary animals, especially if rare, have a difficult time locating mates

b. choice also is more difficult if solitary

ii. help in care of offspring

b. <u>*costs*</u>:

i. competition for mates

ii. competition with others and misdirected care

2. Avoidance of predators

a. <u>*benefits*</u>

i. greater alertness to predators

ii. better able to defend against predators

iii. selfish herds -- using other individuals essentially as shields against predators or bad environmental effects

iv. confusion effects -- similar to (iii) except that here the animals move individually in many different directions and thereby make it difficult for the predator to focus on one individual

v. glutting the predator-- self explanatory -- but how would you think that this would work -- could it work if the individuals were totally unrelated to each other?

vi. educating the predator -- similar to (v) except here the grouped individuals are either distasteful or dangerous to some degree -- the predator learns after one or two and avoids the others -- this protection is facilitated if there are a number of individuals together since typically learning involves several "trials" -- in this cases, several individuals being attacked. Often the individuals will be **APOSOMATICALLY** colored -- very conspicuous -- their vividness makes them easier to identify and perhaps also makes it easier to learn to avoid them.

-

b. *costs*

(i) more conspicuous to predators -- groups are obviously more noticeable than individuals

(ii) become a more efficient target as far as the predator is concerned: concentrated resources (prey) are easier to harvest.

****

A nice set of studies were done by Hoogland and Sherman (1976 Ecol. Monographs v46) on the effects of group size and resistance to predation in a ground nesting bird, bank swallows. These birds form large breeding colonies where burrows are excavated in which young are reared. Individuals with adjacent nests are probably not closely related.

These birds defend their nests against terrestrial predators by a behavior common to many birds called **MOBBING**. In mobbing the object is for the birds to get close to the predator and harry it -- by making a lot of noise (the predators "know" they have been discovered and that their chance for success is probably lower) and by making mock attacks and occasionally attempting to rake it with claws or kick it -- this is obviously at some danger to the bird doing the mobbing, but they are careful to keep their risk reasonably low (many other studies have demonstrated this). Finally, mobbing is most effective when the number of birds mobbing increases.

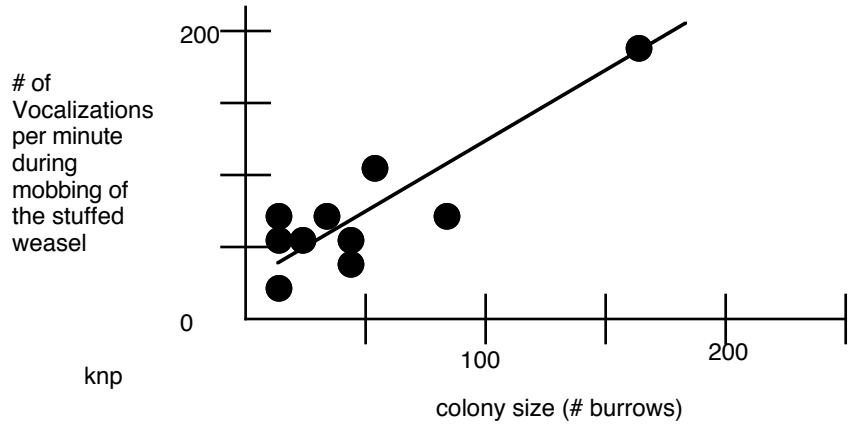
Hoogland and Sherman used a situation where they introduced a fake predator -- in this case a stuffed weasel. The weasel was used because the birds would recognize it as a threat -- they are preyed on by them -- and a stuffed one was used since its behavior was predictable and the birds seemed to treat it the same way they treated live ones (based on observations of real weasel attacks).

They looked at several different effects with the weasel, all of which are easily related to likelihood of a successful attack: the size of the mob, time till vocalizations (warning calls) started after the introduction of the weasel, and the number of vocalizations, all as a function of colony size. Here are their results:

Mob Sizes and Colony Size in Bank Swallows

Response Time and Colony Size

Number of Alarm Calls and Colony Size



Be able to explain how each of these effects favors the formation of large breeding colonies.
Be able to explain why the time and number of vocalizations are important.
What type of methodology were Hoogland and Sherman using? Explain.

****

3. Social foraging: form groups for the purpose of locating, subduing or utilizing food.

a. *Benefits*:

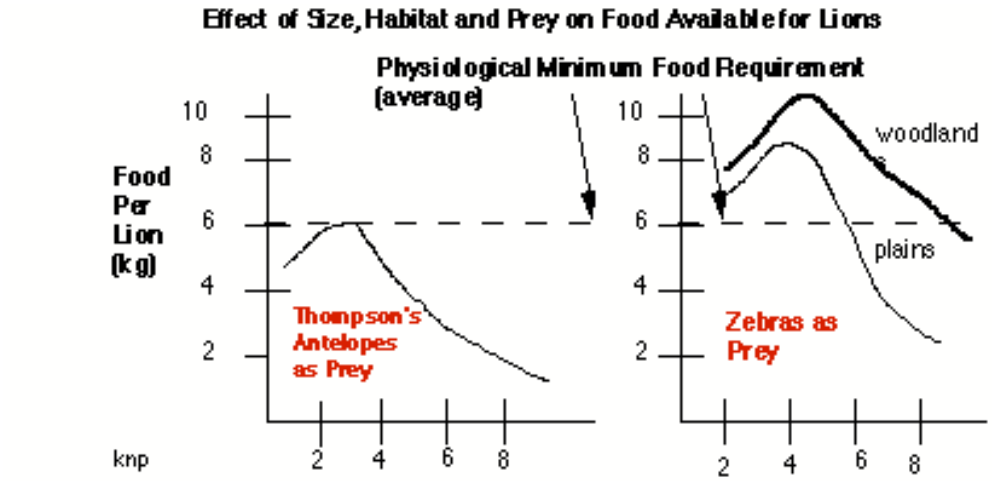
i. more searchers to help locate food
ii. use information obtained by others
iii. take on more difficult prey

b. *Costs*:

i. greater chance of being noticed by prey
ii. division of any resource that is found

Here is a set of measurements that look at the benefits and costs involved in social foraging -- in this case by lions. The study was done by Caraco and Wolf, 1975 (Am Nat. v109) and looked at the effects of group size, prey type (a small gazelle vs. zebra) and habitat on the payoff in food per lion.

A minimum long-term requirement was for the lion to remain in good health (**a constraint**). They found that about 6 kg of meat was required per lion per day. This was considered the physiological requirement that must be met for social foraging to be favored. Here are their results:



from Caraco and Wolf, 1975, Am Nat

? Under what conditions would solitary hunting be favored?
Group hunting?
Is the amount of food the only consideration when determining whether to hunt solitary or in a group? (stick to predation here -- don't bring in arguments about reproduction etc.)
Why is there a difference in payoff as a function of habitat?

4. Social Facilitation: This is when the presence of a large number of individuals tends to reinforce the performance or timing of certain behaviors. Thus, social facilitation (along with other environmental events not involving the behavior of conspecifics -- such as appearance of certain preferred food species, or changes in day length) often serves to help **synchronize** behavior. This is often very adaptive as will be shown below. First, an analysis of benefits and costs that result from social facilitation and therefore determine the extent to which it favors the evolution of social vs. solitary behavior:

1. *Benefits*:

a. social facilitation that improved synchronization of activities such as mating may well result in an increase in reproductive success (the synchrony could then be an anti-predator or a way to avoid bad environments)

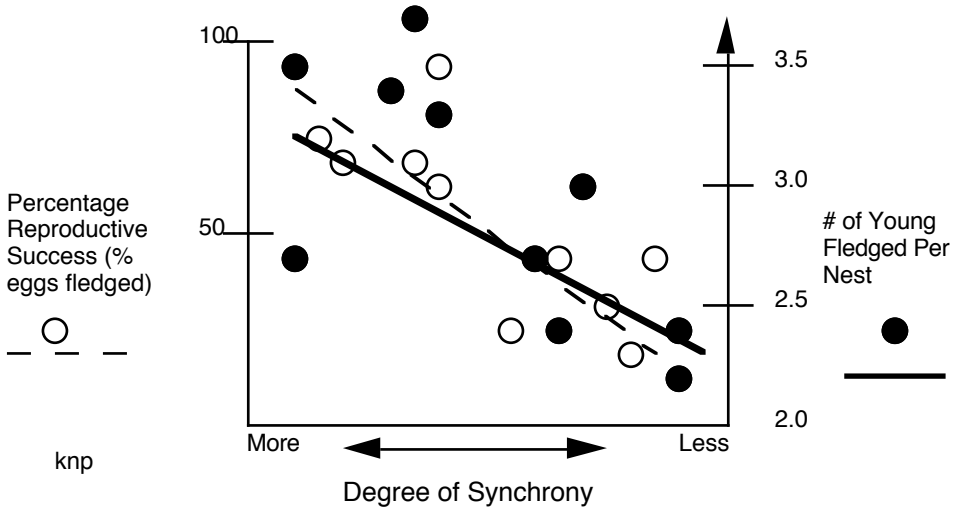
b. conditioning the environment: many animals using the same area can convert it into a place that is more livable for the others -- examples-- the construction of trails through overgrown or dangerous areas as the result of a number of individuals using the same area at about the same time -- any one of them would not be able to make the trail yet all together can. The same is true with excavations of nesting sites that can be used year in year out.

Here are some data that show that social facilitation can be important in real populations. This the same study by Hoogland and Sherman on bank swallows.

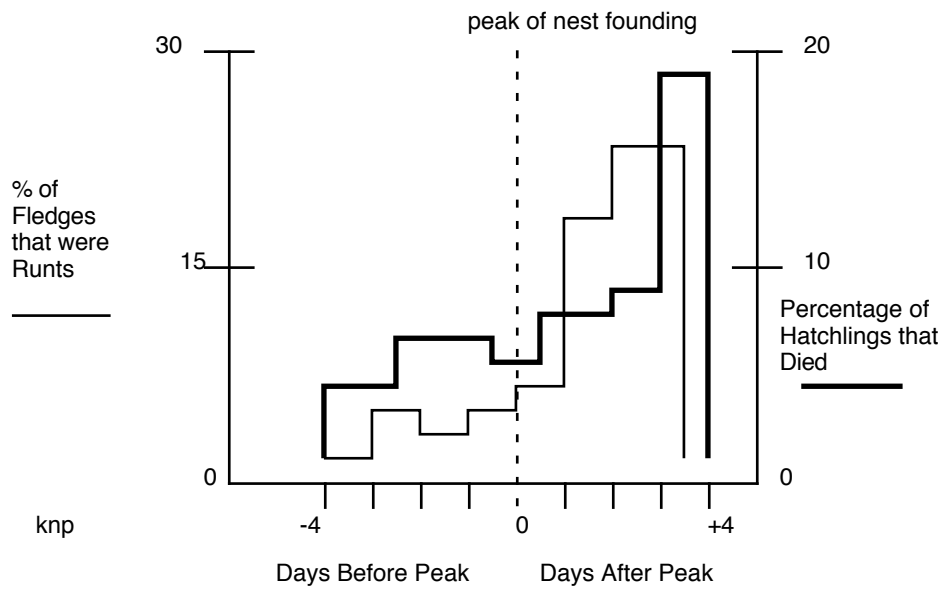
Here the effect of synchrony of breeding was examined in terms of degree of synchrony (how advanced or delayed was the founding of a nest or laying of eggs compared to the colony average). It was known that the birds are to a significant degree influenced as to the exact timing of these events by what other birds in the colony are doing (they are also influenced by their own assessment of the environment, probably by their own particular genetic predisposition, and by the physiological state they arrive at the breeding colony in):

(I) This graph looks at the reproductive success as (a) the percentage of eggs that actually result in a fledgling bird (dotted line) and (b) the number fledged per nest (solid) both as a function of synchrony where more means the eggs were laid close the colony peak and less means either earlier or later than the peak:

Measures of Reproductive Success as a Function of Synchrony



(II) The second graph looks instead at the effect of lack of synchrony on the likelihood of producing a runt (light line) and of death as a nestling (birds that hatched but did not fledge):



? Do these results support the idea that synchrony in reproductive activity is adaptive in bank swallows?
Do the data demonstrate social facilitation? Explain your answer. What more would be desirable to better demonstrate social facilitation? Suggest an experiment or natural experiment.

2. Some *cost*s: *Note that both of these are also potentially important any time a group is formed, however, they may well be made worse by synchronizing group activity and thus they are specially listed as costs to social facilitation:*

a. pollution: if everyone is using the same area in the same way at the same time there is a great chance of despoiling the area for instance with waste (as occurs in bird colonies or at watering holes) or by causing soil damage and erosion, etc.

b. disease and parasite transmission: this one goes hand in hand with the previous since degraded conditions often increase the likelihood of disease transmission; in addition, if everyone is doing the same thing at the same time and the parasite requires certain specific conditions to be transferred from one individual to another, social facilitation will increase the likelihood of transmission.

5. The advantages of numbers in group vs. individual interactions and in large vs. smaller groups conflicts. This one is self-explanatory and as humans we are very familiar with the effects of numbers. Thus the most obvious benefits and costs:

a. *benefits*: larger groups are usually more able to secure resources when in competition with smaller groups or individuals and all members of the larger group can potentially share in this bounty.

b. *costs*: competition within the group can decrease the rewards for some group members -- essentially, some may be exploited (think about soldiers vs. industrialists or other non-combatants in wars).

6. Division of labor: solitary individuals cannot specialize successfully for a wide range of activities (this is always relative -- obvious in some species individuals are more capable of this than in others, but nevertheless there are always limits). This is because specialization involves behavioral and often morphological adaptations that are costly or limiting in terms of other activities. For instance, large wings good for gilding do not allow an animal to move around freely through the leaf litter; likewise the size of brains is limited and complex behaviors and the structures required to support them take up this space. In a group, certain individuals can specialize on different activities and if individuals cooperate, all may benefit from each other -- the cooperation along with the specialization is what gives the benefit, although even without cooperation, the reduction in competition between individuals would also help. thus:

a. greater efficiency of the unit and each member, often an ability to do more types of things well. The classic example of this is the behavioral and morphological specialization in the eusocial insects -- complete with the differentiation of the sexes into reproductives, workers often of many types and sizes, and soldiers (also of several types). An even more extreme example is the specialization of polyps in colonial hydrozoans such as the Portuguese-man-of-war or in genera such as *Vellia* . Sessile animals become pelagic and capable of utilizing a number of different types of food in these **Clonal colonies or clonal organisms** (see below).

b. a reduced fitness of those less specialized for reproduction; this is probably not a problem in the most eusocial of animals but might well be in other groups such as in some of the primitive social wasps (we will discuss this in more detail later)

7. Social transmission of information: as has been mentioned above, anytime animals are in groupings, information can be transmitted or sought. This can either be a by-product of groups formed mainly for some other reason or it in itself can be a main reason for forming the group. However, in most cases, this very important potential advantage of sociality is probably a reinforcing mechanism and is not the lone or main reason for the formation of the group -- the more immediate reasons for group formation were discussed above.

a. *Benefit*: The advantage to group information transmission can be put simply -- the gain in information from others' experiences without the risks

b. *Cost*: anytime individuals come to utilize information from others the opportunity for the sender to deceive the receiver or to manipulate its behavior in some way that is not to the benefit of the receiver while it does benefit the sender presents itself. More about this later.

II. Types of Social Groupings: There are classically a number of different types of groups that are referred to in ethology. You should be familiar with each of these and be able to classify a group into one or more of these categories:

A. Aggregation: a group formed by simultaneous attraction to some common resource rather than to each other and/or the result of physical factors operating on individuals

examples: birds following a plow
gulls at a dump
humans at political rally

B. Survival Groups: groups formed by non-breeding, randomly related individuals based on a mutual attraction

examples: schools of fish or most herds
night roosts of birds (there are often plenty of places to roost but the birds prefer to roost together)

C. Mating groups: groups that are specially formed for the purpose of reproduction, anything from pairs, extended families (when offspring remain with parents), troops (several males and several females) to harems.

There are so many familiar examples that there is no reason to mention all of them.

D. Colonial Groups: groups formed by breeding pairs that are distinct from each other; on the other hand, these pairs seek each other out -- although it is also possible that the habitat tends to reinforce the coming together.

examples: bird colonies, especially with sea birds and some specialized nesters (such as cliff nesters and weaverbirds)
human communities

E. Unisexual Groups: usually male groups, formed as a by-product of the breeding system, (i) to attract mates (lekking groups) or (ii) due to failure to attract mates or as a result of being excluded from a harem

examples: **lekking** in turkeys and other gallinaceous birds --
bachelor groups in large ungulates, lions, seals and perhaps human frats and sororities?

F. <u>Clonal Groups</u>: formed by asexual reproduction, usually the individuals remain in very close physical contact, for instance often possessing partially linked digestive, nervous and circulatory systems

examples: colonial hydrozoans (hydra-like organisms),
anthozoans (corals), and bryozoans ("moss animals")
some asexually reproducing organisms such as
summer generations of aphids
perhaps all multicellular organisms can also be
viewed as clonal groups

? In what sense are organisms clonal groups? Explain the parallels between them and the cnidarian clonal organisms.
Should cnidarian organisms be considered as types of societies or colonies or are they an organism or are the lines between all of these terms indistinct?