Social Behavior 1

- Costs & Benefits of Social Life
- Evolution of Helpful Behavior
- Inclusive Fitness
- Eusocial Behavior
Social living is actually rare, as the costs often exceed the benefits.

- Sociality is not a hallmark of an “advanced” species.
- Sociality is like any other trait and has costs & benefits.

<table>
<thead>
<tr>
<th>TABLE 13.1 Some potential costs and benefits of social living</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Costs</strong></td>
</tr>
<tr>
<td>Greater conspicuousness of clumped individuals to predators</td>
</tr>
<tr>
<td>Greater transmission of disease and parasites among group members</td>
</tr>
<tr>
<td>More competition for food among group members</td>
</tr>
<tr>
<td>Time and energy expended by subordinates in dealing with more dominant companions</td>
</tr>
<tr>
<td>Greater male vulnerability to cuckoldry</td>
</tr>
<tr>
<td>Greater female vulnerability to egg tossing, egg dumping, and other forms of reproductive interference by others</td>
</tr>
</tbody>
</table>
A cost of sociality in the colonial cliff swallow

• Colony size varies from ~100 pairs to several thousand pairs

• Ectoparasite loads of nestlings are higher in large colonies
  • swallow bugs are like bed bugs

• These ectoparasites feed on blood; can be thousands of swallow bugs per nest
A cost of sociality in the colonial cliff swallow

- Nestlings in large colonies have more parasites and lower body mass (correlation)

- In a large colony, experimental insecticide treatment increases nestling mass and survival
13.5 Effect of parasites on cliff swallow nestlings

Fig. 5. Typical nestling Cliff Swallow from a nonfumigated nest (left) and from a nest fumigated with an insecticide that kills swallow bugs (right) at a 345-nest colony. Both were 10 d old.
Glucocorticoid hormone levels increase with group size and parasite load in cliff swallows

SAMRAH A. RAOUF*, LINDA C. SMITH†, MARY BOMBERGER BROWN‡, JOHN C. WINGFIELD* & CHARLES R. BROWN‡

• 2 small colonies (90 & 110 nests): non-fumigated & fumigated

• 2 large colonies (3400 & 1600 nests): non-fumigated & fumigated

• Fumigation effect in large colony only – why?

Figure 4. Mean ± SE baseline corticosterone level (ng/ml) for nesting cliff swallows at a pair of small and large colonies, each of which contained one nonfumigated site (■) and one fumigated site (□). Sample sizes (number of birds sampled) are shown above the bars.
• 13 species of swallows and martins
• Size of spleen, bursa of Fabricius
• Wing web response to PHA
• Antibody response to SRBC
• Positive correlation between wing web swelling and colony size across species (esp. nestlings)
• In adults, similar results with SRBC test
• Investment in adaptive immune system
Social insects are especially vulnerable to parasites

- high number of individuals very concentrated
- high rates of contact between individuals
- high genetic similarity between individuals
- dependent on one individual for reproduction
Collective immune defenses

- division of labour
- guarding
- collection & production of antimicrobial substances
- waste management
- removal (and self-exile) of infected individuals

<table>
<thead>
<tr>
<th>status</th>
<th>species</th>
<th>MIC(100)</th>
<th>group size</th>
<th>$R$</th>
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<tbody>
<tr>
<td>solitary</td>
<td><em>Amegilla asserta</em></td>
<td>362.0 (± 28.9)</td>
<td>1</td>
<td>—</td>
</tr>
<tr>
<td>solitary</td>
<td><em>Amegilla bombiformis</em></td>
<td>280.2 (± 59.4)</td>
<td>1</td>
<td>—</td>
</tr>
<tr>
<td>semi-social</td>
<td><em>Exoneura robusta</em></td>
<td>38.2 (± 3.4)</td>
<td>6.4 (± 1.2)</td>
<td>0.312</td>
</tr>
<tr>
<td>semi-social</td>
<td><em>Exoneura nigrescens</em></td>
<td>17.3 (± 0.1)</td>
<td>8.2 (± 1.83)</td>
<td>0.468</td>
</tr>
<tr>
<td>eusocial</td>
<td><em>Exoneurella tridentate</em></td>
<td>68.3</td>
<td>14.1 (± 2.4)</td>
<td>0.664</td>
</tr>
<tr>
<td>eusocial</td>
<td><em>Trigona carbonaria</em></td>
<td>2.2 (± 0.3)</td>
<td>&gt;1000</td>
<td>0.695</td>
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Stow et al., 2007
Why are sheep red blood cells (SRBC) often administered to examine the immune response of an individual?

A. They are not pathogenic
B. They do not initiate an immune response in most animals
C. They are foreign and trigger an immune response
D. They can be easily administered
E. A, C and D
Outline

• Costs & Benefits of Social Life

• Evolution of Helpful Behavior

• Inclusive Fitness

• Eusocial Behavior
Evolution of helping

• One benefit of social living is the helping behavior of others. How can helping evolve?

• Until the 1960’s, many thought that helping was for the good of the species (group selection).

• We now think that natural selection acts mainly on individuals (or at least the genes carried by individuals), which makes the evolution of helping an interesting puzzle.
### Types of social interactions

#### TABLE 13.2  The direct reproductive success of individuals that engage in different kinds of social interactions

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*aYou should not be surprised that spiteful behavior is almost never observed in nature; you should be surprised that altruism is not uncommon despite the loss of reproductive success experienced by altruists.*

- **Mutualism** is an interaction in which both participants benefit, although the benefit may not be equal.
Mutualism in Lazuli buntings

- **Yearling** male lazuli buntings may be dull, intermediate, or bright blue.
- The bright males get the good territories and chase away all other males **except** dull males.
- Why tolerate the dull males? Lazuli buntings have high rates of EPC’s, but bright males are cuckolded **less** than dull males. The dull males present little threat, and their mates provide possible EPC’s for the bright males.
- The dull males raise some of the bright males’ young, but dull males benefit by getting to breed on high-quality territories.
### Types of social interactions

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Reciprocity

- Reciprocity is a social interaction where favors are returned at a later date.
- Reciprocity is relatively rare, probably because it is vulnerable to cheating.
- Under most circumstances, cheating may be the best choice, as suggested by the prisoner’s dilemma (see textbook)
So how can reciprocity work?

- Reciprocity may work when individuals interact with each other repeatedly over an extended period of time (and have individual recognition).
- Thus, someone who cheats may get cut off.
- E.g., vampire bats
- If foraging is successful, they return to the roost engorged with blood (visibly bloated)
- Can share with others at low cost; high benefit to others (die if no food for 3 nights in a row)
- How to manipulate experimentally??

Frans de Waal:
http://www.ted.com/talks/frans_de_waal_do_animals_have_morals.html
Oxytocin increases trust in humans

Michael Kosfeld\textsuperscript{1*}, Markus Heinrichs\textsuperscript{2*}, Paul J. Zak\textsuperscript{3}, Urs Fischbacher\textsuperscript{1} & Ernst Fehr\textsuperscript{1,4}

\textbf{Figure 1 | The trust game.} Both subjects receive an initial endowment of 12 monetary units (MU). The investor can send 0, 4, 8 or 12 MU to the trustee. The experimenter triples each MU the investor transfers. After the investor’s decision is made, the trustee is informed about the investor’s transfer. Then the trustee has the option of sending any amount between zero and his total amount available back to the investor. For example, if the investor has sent 12 MU, the trustee possesses 48 MU (12 MU own endowment + 36 MU tripled transfer) and can, therefore choose any back transfer from 0 to 48 MUs. The experimenter does not triple the back transfer. The investor’s final payoff corresponds to the initial endowment minus the transfer to the trustee, plus the back transfer from the trustee. The trustee’s final payoff is given by his initial endowment plus the tripled transfer of the investor, minus the back transfer to the investor. At the end of the experiment, the earned MU are exchanged into real money according to a publicly announced exchange rate (see Methods). Each subject made four decisions in the same player role while paired with four different, randomly selected interaction partners.
Figure 2 | Transfers in the trust and the risk experiment. Each observation represents the average transfer amount (in MU) over four transfer decisions per investor. 

a, Relative frequency of investors’ average transfers in oxytocin (filled bars) and placebo (open bars) groups in the trust experiment (n = 58). Subjects given oxytocin show significantly higher transfer levels.

b, Relative frequency of investors’ average transfers in oxytocin (filled bars) and placebo (open bars) groups in the risk experiment (n = 61). Subjects in the oxytocin and the placebo group show statistically identical transfer levels.
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Altruism and indirect selection

- Altruism does not benefit an individual’s reproductive success directly, but is beneficial indirectly if the “altruist” is helping relatives who share the altruist’s genes.

- Natural selection of traits that influence survival of an individual’s own offspring is termed direct selection.

- Natural selection of traits that influence survival of nondescendant kin is termed indirect selection.

- Together, direct and indirect selection comprise kin selection.
Altruism and indirect selection

- “I would gladly lay down my life to save 2 sons or 8 cousins.”
  - JBS Haldane, famous British biologist (after a few pints at the pub)

- E.g., “cooperative breeding” in some bird species
  - offspring delay breeding
  - instead, stay with parents and help parents raise more chicks (siblings)