Animal Behavior
History II: from ~1960

1960s: The rise of behavioral ecology
1964 – W. D. Hamilton – papers on inclusive fitness
1966 – George Williams – *Adaptation and Natural Selection*
1960-70s – Richard Alexander & students
   1975 – E. O. Wilson – *Sociobiology*
   1970’s – John Maynard Smith – many seminal papers

Some Case Studies: E.O. Wilson

*Sociobiology* (1975)
Opposed at Harvard by his evolutionary biologist colleagues Steven J. Gould, Richard Lewontin
Attacked at talk Nov 1978 AAAS meeting: “Wilson, you’re all wet!”
Wilson: “I believe...I am the only scientist in modern times to have been physically attacked for an idea!”

“Science and religion are two of the most potent forces on Earth and they should come together to save the creation”.
A “scientific humanist” = “the only worldview compatible with science’s growing knowledge of the real world and the laws of nature”.

Dick Alexander
Had a huge influence on the field (30+ grad students, many postdocs, influenced many others as well ). Brought Hamilton to Michigan, also Trivers.
PhD students of Dick Alexander

Note: he influenced many others as well, including those who had him a committee member (e.g., Trish Schwagmeyer) or postdoc advisor (e.g., Jim Lloyd, Laura Beitzig), or who eavesdropped on his lectures (me, many others)

Mary Jane West

The modern study of animal behavior is generally thought to have begun in 1960’s, and Williams and Hamilton are often nominated as the ‘founding figures’.

Robert Trivers


Bob Trivers & Huey Newton

“The benefit of self-deception is the more fluid deception of others. The cost is an impaired ability to deal with reality.”

Trivers & Newton 1982

Huey Newton: political radical, co-founder of the Black Panthers

Williams’ major question: what is / is not an adaptation?

“Adaptation is often recognized in purely fortuitous effects, and natural selection is invoked to resolve problems that do not exist”. (p 4)

“Adaptation is a special and onerous concept that should be used only where it is really necessary. When it must be recognized, it should be attributed to no higher a level of organization than is demanded by the evidence.” (pp 4-5) [i.e., nix on group selection]

“The designation of something as the means or mechanism for a certain goal or function or purpose will imply that the machinery involved was fashioned by selection for the goal attributed to it. [e.g., vision is the function of the eye, reproduction and dispersal the function of the apple] When I do not believe that such a relationship exists, I will avoid such terms and use words appropriate to fortuitous relationships such as cause and effect”. (p 9)

ALTRUISM: behavior that benefits another individual at a cost to the altruist’s personal fitness (ability to produce offspring).

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Two key insights (Williams, Hamilton, others):
1. selection at the level of the individual (or gene, Dawkins)
2. Apparent altruism can be explained by kin selection

Early debate hinged on two questions
1. What is an adaptation? – Williams addresses this question
2. Altruistic traits – good for the group but bad for the individual (group selection, Wynne-Edwards)
   • Alarm calls – why do individuals put themselves at risk to protect others (not their offspring)
   • Reproductive restraint – why do individuals produce fewer offspring than they are capable of?
Group Selection and Reproductive Restraint

V. C. Wynne-Edwards, Animal Dispersion in relation to Social Behaviour (1962)

Lemmings are small mouselike rodents that live in the Arctic tundra. They are known for extreme fluctuations in population size. At high population densities, large number leave their homes to travel long distances. In the course of their journey, many die, some by drowning, as they attempt to swim across lakes and rivers. One popular explanation for their behavior is that the travelers are actually committing suicide to relieve overpopulation. The suicidal lemmings thus leave shelter and food for those that have stayed behind, and so save the species (or population) from extinction.

What’s the problem with this hypothesis?

The logical problem with group selection

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“Reproductive Restraint”

Table 1

<table>
<thead>
<tr>
<th>Year</th>
<th>Brood size</th>
<th>No. of broods</th>
<th>No. of young</th>
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<th>% lost</th>
<th>No. fledged/brood</th>
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Perrins 1965; Lack 1966

Fig. 1.3 The frequency distribution of the clutch size of great tits in Wytham Woods. Most pairs lay 8–9 eggs. From Perrins [1965].

“Reproductive Restraint”
“Reproductive Restraint”

Fig. 1.4 (a) In larger broods of great tits the young weigh less at fledging because the parents cannot feed them so efficiently. (b) The weight of a nestling at fledging determines its chances of survival. Heavier chicks survive better. From Perrins [1969].

Fig. 1.5 Experimental manipulations of the number of young in a nest show that the optimal brood size for a pair of great tits is between 8 and 12 eggs. This is the brood size which maximizes the number of surviving young. From Perrins [1979].

Fig. 1.6 The influence of adult mortality on the optimal clutch size. The number of young produced versus clutch size follows a curve, as in Fig. 1.5, with being the clutch size which maximizes the number of young produced per brood. Increased clutch size, however, has the cost of increased adult mortality, shown here for simplicity as a straight line. The clutch size which maximizes lifetime reproductive success is , where the distance between the benefit and cost curves is a maximum. This is less than the clutch size , which maximizes reproductive success per brood. From Charov and Kraus [1974].

Back to Hamilton...

“Bill Hamilton’s 1963 and 1964 inclusive fitness articles are easily the most cited articles in the entire field of behavioral evolution, and his work on altruism and kinship spurred endless dissertation projects and hundreds of published articles, both theoretical and empirical. When modern behavioral ecologists and sociobiologists are asked to mark the birth of the field, many respond by citing Hamilton’s 1963 and 1964 articles.”

ALTRUISM & KIN SELECTION

Three factors are important in the spread and maintenance of an altruism gene by kin selection:

1. benefit to recipient, $B$
2. cost to altruist, $C$
3. degree of relatedness between altruist & recipient, $r$

Hamilton’s Rule states the conditions under which altruism will spread. In its simplest form it is:

$$rB > C$$

When should you be altruistic?
When $B > C/r$

<table>
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<th>Recipient</th>
<th>$r$</th>
<th>$B &gt; C/r$</th>
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<tr>
<td>identical twin</td>
<td>1</td>
<td>$B &gt; C$</td>
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<tr>
<td>1 parent</td>
<td>1/2</td>
<td>$B &gt; 2C$</td>
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<tr>
<td>full sib</td>
<td>1/2</td>
<td>$B &gt; 2C$</td>
</tr>
<tr>
<td>half sib</td>
<td>1/4</td>
<td>$B &gt; 4C$</td>
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<tr>
<td>niece/nephew*</td>
<td>1/4</td>
<td>$B &gt; 4C$</td>
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<tr>
<td>uncle/aunt **</td>
<td>1/4</td>
<td>$B &gt; 4C$</td>
</tr>
<tr>
<td>1st cousin</td>
<td>1/8</td>
<td>$B &gt; 8C$</td>
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</table>

* assumes your sib is full sib
** assumes your parent’s sib was full

Hamilton’s take on altruism anticipated by Haldane

Question: Would you lay down your life for your brother?

“No, but I would for two brothers or eight cousins”

J.B.S. Haldane
Empirical Studies

Jerram Brown – Mexican jays [helpers at the nest & kin selection]

Paul Sherman – Belding’s ground squirrels [kin selection]

Jerry Wilkinson – Vampire bats [reciprocity]

Table 1

<table>
<thead>
<tr>
<th>Area</th>
<th>References</th>
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<tbody>
<tr>
<td>Split sex ratios in social insects</td>
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<td>Local mate competition theory</td>
<td>Hamilton, 1967; West et al, 2005</td>
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<td>Kin discrimination in cooperative breeding vertebrates</td>
<td>Hamilton, 1964; Griffin &amp; West, 2003</td>
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<td>Worker policing in social insects</td>
<td>Ratnieks &amp; Visscher, 1989; Wenseleers &amp; Ratnieks, 2006</td>
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<td>Parent-offspring conflict</td>
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<td>Cooperation in microbes</td>
<td>Griffin et al., 2004; Gilbert et al., 2007</td>
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<td>Genomic imprinting</td>
<td>Haig, 2002</td>
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From Gardner et al 2008

West talk on group selection:
http://www.vimeo.com/8202768

Pagel talk on group selection:
http://www.vimeo.com/8504335

Alarm calling is potentially risky (exposes caller to danger) but valuable to unaware ground squirrel that hears it = “Altruism”