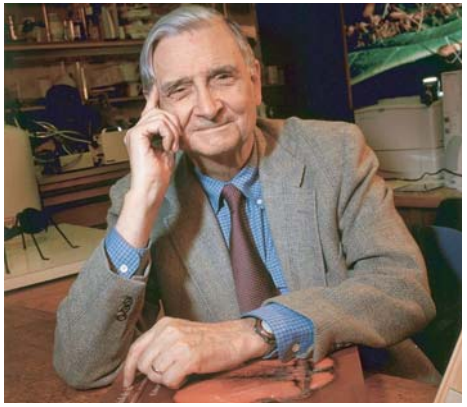
Animal Behavior

History II: from ~1960

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".

1960s: The rise of behavioral ecology

1964 – W. D. Hamilton – papers on inclusive fitness

1966 – George Williams – *Adaptation and Natural Selection*

1970-1976 – Robert Trivers – many seminal papers

1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46: 35-57.

1972. Parental investment and sexual selection. In Campbell, B. (ed.), *Sexual Selection and the descent of man*.

1975. Parent-offspring conflict. *American Zoologist* 14: 249-264.

1976. (with Hare, H.) Haplodiploidy and the evolution of the social insects. *Science* 191: 249-263.

1960 -70s – Richard Alexander & students

1974. The evolution of social behavior. *Annual Review of Ecology & Systematics* 5: 325-383.

1975 – E. O. Wilson – *Sociobiology*

1976 – Richard Dawkins – *The Selfish Gene*

1970's – John Maynard Smith – many seminal papers

1973. (with George Price) The logic of animal conflict, *Nature* 246:15-18

Dick Alexander

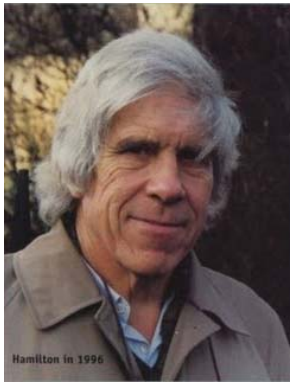
Had a huge influence on the field (30+ grad students, many postdocs, influenced many others as well). Brought Hamilton to Michigan, also Trivers.

Kenneth Shaw	Mary Jane West
Dan Otte	Mitchell Weiss
Ann Pace	Harry Power
Paul Sherman	John Hoogland
Rick Howard	Marianne Feaver
Gerry Borgia	Katie Noonan
David Foltz	Cynthia Kagarise
Nancy Moran	Marlene Zuk
David Queller	Joan Strassman (UG)
Alex Mintzer	Bernard Crespi
Richard Connor	Beverly Strassman
Stan Braude	Eileen Lacey
Andy Richards	John Pepper
John Cooley	David Marshall
Deborah Ciszek	Anna Bess Sorin
Bret Weinstein	Laura Howard

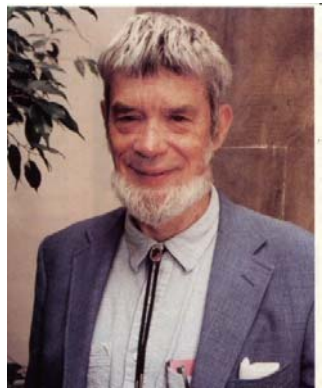
PhD students
of Dick Alexander
←

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

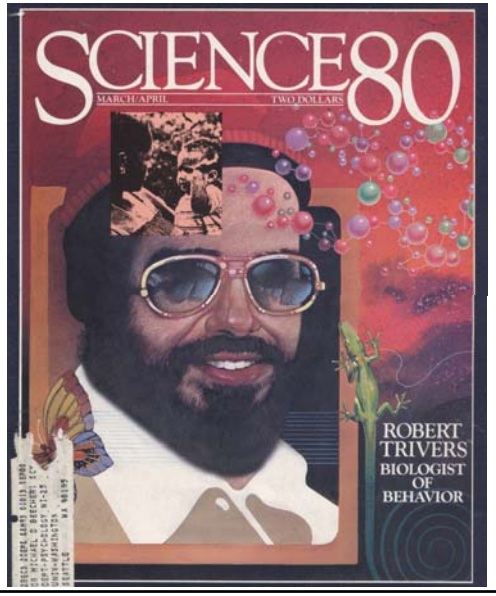


W. D. Hamilton

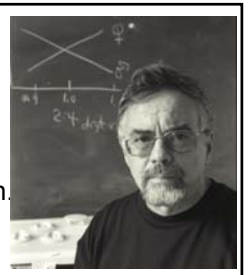


George Williams

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



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1976. (with Hare, H.). Haplodiploidy and the evolution of the social insects. *Science* 191: 249-263.

1982. (with Newton, H.P). The crash of flight 90: doomed by self-deception? *Science Digest* 111: 66-67.

2011. *The Folly of Fools: The Logic of Deceit and Self-Deception in Human Life.* Basic Books.

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

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'.

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?

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 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]

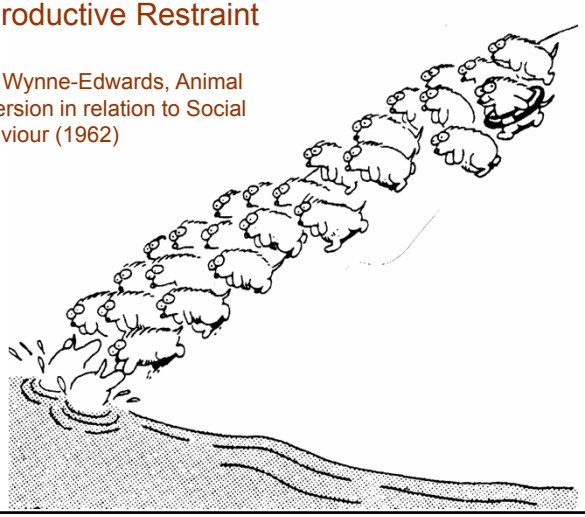
"The designation of something as the *means* or *mechanism* for a certain *goal* or *function* or *purpose* will imply that the machinery involved was fashioned by selection for the goal attributed to it. [e.g., vision is the function of the eye, reproduction and dispersal the function of the apple] 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).

- C Altruist → + B Recipient

Group Selection and Reproductive Restraint

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



The logical problem with group selection

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?

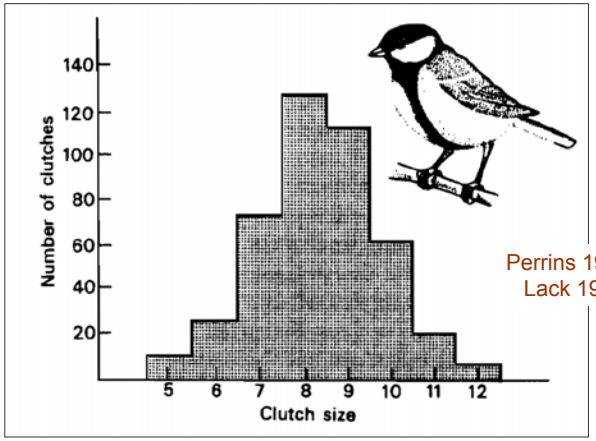
"Reproductive Restraint"

Table 1

Year	Brood size	No. of broods	No. of young	No. lost	% lost	No. fledged/ brood
1958	1	7	7	2	28·6	0·71
	2	21	42	2	4·7	1·95
	3	4	12	1	8·3	2·75
	4	2	8	4*	50·0	2·00
1959	1	10	10	0	0	1·00
	2	15	30	0	0	2·00
	3	4	12	0	0	3·00
	4	4	16	5	31·2	2·75
1960	1	6	6	0	0	1·00
	2	18	36	2	5·6	1·89
	3	6	18	4	22·2	2·33
	4	5	20	14	70·0	1·20
1961	1	7	7	0	0	1·00
	2	18	36	1	2·8	1·95
	3	6	18	4	22·2	2·33
	4	5	20	13	65·0	1·40

Perrins 1965 (Swifts)

"Reproductive Restraint"



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"

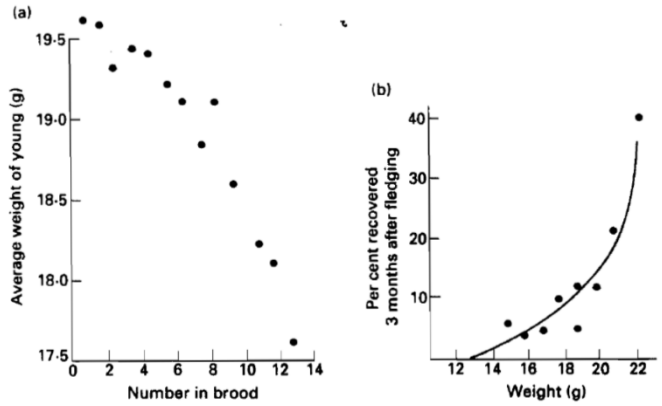


Fig. 1.4 (a) In larger broods of great tits the young weigh less at fledging because the parents cannot feed them so efficiently. (b) The weight of a nestling at fledging determines its chances of survival. Heavier chicks survive better. From Perrins (1965).

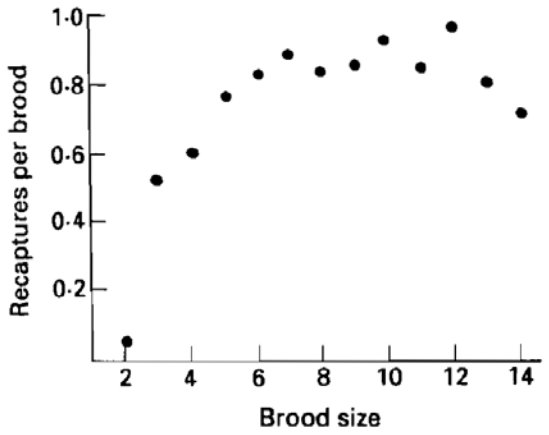


Fig. 1.5 Experimental manipulations of the number of young in a nest show that the optimal brood size for a pair of great tits is between 8 and 12 eggs. This is the brood size which maximizes the number of surviving young. From Perrins (1979).

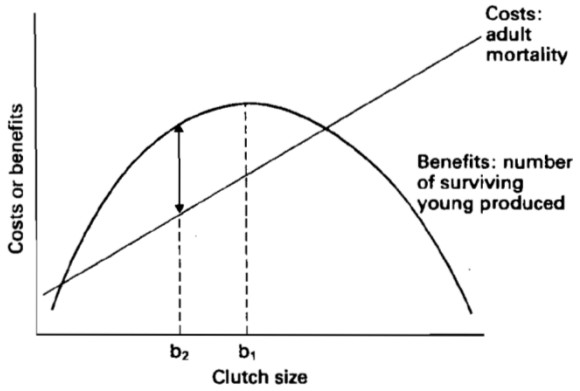


Fig. 1.6 The influence of adult mortality on the optimal clutch size. The number of young produced versus clutch size follows a curve, as in Fig. 1.5, with b_1 being the clutch size which maximizes the number of young produced per brood. Increased clutch size, however, has the cost of increased adult mortality, shown here for simplicity as a straight line. The clutch size which maximizes lifetime reproductive success is b_2, where the distance between the benefit and cost curves is a maximum. This is less than the clutch size b_1, which maximizes reproductive success per brood. From Charnov and Krebs (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."

Dugatkin, L. A. (2007) Inclusive Fitness Theory from Darwin to Hamilton. *Genetics* 176: 1375-1380.

Hamilton's take on altruism anticipated by Haldane

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

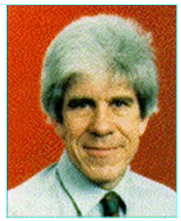
"No, but I would for *two* brothers or *eight* cousins"

J.B.S. Haldane

ALTRUISM & KIN SELECTION

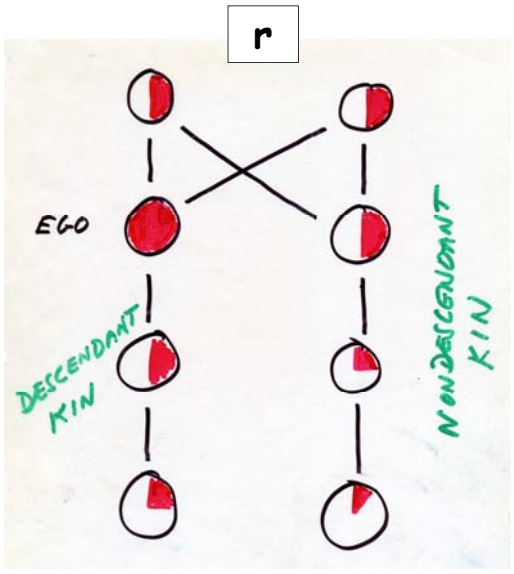
Three factors are important in the spread and maintenance of an altruism gene by kin selection:

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

Recipient	r	B > C/r
identical twin	1	B > C
1 parent	1/2	B > 2C
full sib	1/2	B > 2C
half sib	1/4	B > 4C
niece/nephew*	1/4	B > 4C
uncle/aunt **	1/4	B > 4C
1st cousin	1/8	B > 8C

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

Table 1 The great success stories and flourishing areas of kin selection. This table summarizes some of the most productive and successful areas of social evolution theory – in all cases these have developed from kin selection theory and not group selection. The references given are a mixture of pivotal original papers and more recent reviews or comparative studies.

From Gardner et al 2008

Area	References
Split sex ratios in social insects	Boomsma & Grafen, 1991; Chapuisat & Keller, 1999
Local mate competition theory	Hamilton, 1967; West *et al.*, 2005
Kin discrimination in cooperative breeding vertebrates	Hamilton, 1964; Griffin & West, 2003
Worker policing in social insects	Ratnieks & Visscher, 1989; Wenseleers & Ratnieks, 2006
Parent–offspring conflict	Trivers, 1974
Sibling conflict	Mock & Parker, 1997
Selfish genetic elements	Hamilton, 1967; Burt & Trivers, 2006
Avoidance of cannibalism	Pfennig *et al.*, 1999
Cooperation in microbes	Griffin *et al.*, 2004; Gilbert *et al.*, 2007
Genomic imprinting	Haig, 2002

West talk on group selection:

http://www.vimeo.com/8202768

Pagel talk on group selection:

http://www.vimeo.com/8504335

Empirical Studies

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

1970. Cooperative breeding and altruistic behaviour in the Mexican jay. *Animal Behavior* 18: 366-378.

1974. Alternate routes to sociality in jays - with a theory for the evolution of altruism and communal breeding. *American Zoologist* 14: 63-80.

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

1977. Nepotism and the evolution of alarm calls. *Science* 197: 1246-1253.

1985. Alarm calls of Belding's ground squirrels to aerial predators: nepotism or self-preservation? *Behavioral Ecology & Sociobiology* 17: 313-323.

Jerry Wilkinson – Vampire bats [reciprocity]

1984. Reciprocal food sharing in the vampire bat. *Nature* 308: 181-184

1990. Food sharing in vampire bats. *Scientific American* 262, 2: 64-70.

Paul Sherman – Belding's ground squirrels

1977. Nepotism and the evolution of alarm calls. *Science* 197: 1246-1253.

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