## A Tribute to William Donald Hamilton (1936–2000)

Biologists around the world were shocked to hear that W. D. Hamilton was admitted to intensive care after contracting malaria during a trip to the Congo, and then deeply saddened to learn of his death on 7 March 2000. We all felt a great loss at his passing because he was "... one of the greatest evolutionary theorists since Darwin. Certainly, where social theory based on natural selection is concerned, he was easily our deepest and most original thinker." (Trivers 2000)

Hamilton died as he had lived, in search of answers to our most perplexing questions in biology. His trip to the Congo was to evaluate first hand Edwin Hooper's contention, laid out in his recent book The River: A Journey to the Source of HIV and AIDS that the current AIDS pandemic can be traced back to contaminated polio vaccines administered in central Africa in the late 1950s. For generations to come, Hamilton will be revered for his seminal work on inclusive fitness (Hamilton 1963, 1964) and his deep insights into the causes of skewed sex ratios (Hamilton 1967). Further, his contributions to the genetics of senescence (Hamilton 1966), the influence of parasites on sexual selection and on the maintenance of sex in host populations (Hamilton 1980, Hamilton & Zuk 1982), and his insights into the existence and consequences of selfish, spiteful, altruistic and cooperative behavior (Hamilton 1970, 1971, 1972, Axelrod & Hamilton 1981) will continue to inspire the work of biologists for generations to come.

We paid tribute to the memory of W. D. Hamilton by organizing a symposium held in Berkeley, California, 20-21 October 2000. Our priority was to hold this memorial symposium as soon as possible after his death, and then to rapidly publish this special issue of the Annales with as many papers as possible. All participants unstintingly covered their own costs to come from countries as far away as Australia and Finland for the opportunity to honor Hamilton's memory and his work. Twenty-four talks were presented during the two-day symposium, of which twelve are published here. These twelve papers by no means reflect developments covering the full range of topics championed by Hamilton. The range of papers in this issue is broad and includes the topics of inclusive fitness, sex ratios, sexual selection, and evolutionary questions relating to sex, polyandry, altruism, and spite.

During the next several years, we are sure that other W. D. Hamilton memorial compendiums will be published. There is no doubt in our minds that future generations will regard Hamilton as the most important figure in theoretical evolutionary biology during the second half of the 20th century. W. D. Hamilton has inspired us, as he has a generation of biologists. Equally important, he has taught us that one pathbreaking paper, of which he has had several, is worth more than a lifetime of pedestrian research no matter how voluminous.

Wayne M. Getz, Robert E. Page Jr. & Philip T. Starks

May 2001, California

## References

- Axelrod R. & Hamilton, W. D. 1981: The evolution of cooperation. — *Science* 211: 1390–1396.
- Hamilton, W. D. 1963: The evolution of altruistic behavior. — *The American Naturalist* 97: 354–356.
- Hamilton, W. D. 1964: The genetical evolution of social behaviour I and II. — *Journal of Theoretical Biology* 7: 1–16 and 17–52.
- Hamilton, W. D. 1966: The moulding of senescence by natural selection. — *Journal of Theoretical Biology* 12: 12–45.
- Hamilton, W. D. 1967: Extraordinary sex ratios. Science 156: 477–488.

- Hamilton, W. D. 1970: Selfish and spiteful behaviour in an evolutionary model. — *Nature* 228: 1218–1220.
- Hamilton, W. D. 1971: The geometry of the selfish herd. — Journal of Theoretical Biology 31: 295–311.
- Hamilton, W. D. 1972: Altruism and related phenomena, mainly in social insects. — Annual Review of Ecology and Systematics 3: 193–232.
- Hamilton, W. D. 1980: Sex versus non-sex versus parasite. — Oikos 35: 282–290.
- Hamilton, W. D. & Zuk, M. 1982: Heritable true fitness and bright birds — a role for parasites. — *Science* 218: 384–387.
- Trivers, R. 2000: Obituary: William Donald Hamilton (1936–2000). *Nature* 404: 828.