

of the predominantly monogamous indigo bunting *Passerina cyanea* reveals that at least 14 per cent of 256 offspring sampled have genotypes incompatible with one of the putative parents. Because females do not lay eggs in each other's nests in this species, extra-pair copulations are probably responsible for fathers helping to raise offspring that are not their own (although in the indigo bunting, direct paternal care is minimal).

Such findings have tended to provoke a revisionist movement, replacing the view that 90 per cent of bird species are monogamous with the view that essentially none are. But if a male has a sufficiently high probability of fathering the offspring in his territory, selection will favour him helping to raise them. Some monogamous species copulate more frequently than others, with the frequently copulating species having relatively larger testes but fewer sperm per ejaculate⁸. Perhaps monogamous birds can be divided into two categories: those with few extra pair copulations and reduced sperm competition (infrequent maters); and those with relatively high levels of extra-pair copulations and sperm competition (frequent maters).

Because the last male to mate is more likely to fertilize the eggs, the male's strategy in those species with high levels of extra-pair copulations would be to mate with his mate frequently, and particularly after she has taken part in an extra-pair copulation, as in the case with indigo buntings¹⁷ and zebra finches¹⁸. Because, in zebra finches at least, the sperm of the last male to copulate have a precedence of about 84 per cent, and pairs mate about 12 times during the production of a clutch, such species may be as close to monogamy as can be reasonably expected in an imperfect world. □

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Nikolaas Tinbergen (1907-1988)

NIKOLAAS Tinbergen, who received a Nobel prize for Biology and Medicine in 1973, died on 21 December 1988. As a student in the Netherlands Tinbergen was an outstanding hockey player, but was not otherwise regarded as showing great promise. He nonetheless began studies on several species of birds and insects, in which he quickly revealed an exceptional capacity for meticulous, detailed observation. An autobiographical volume, *Curious Naturalists* (1958), gives an agreeable account of many of the field enquiries in which he took part. At the end he typically questions the value of what he had been doing, but concludes that nobody "need be ashamed of being curious about nature".

Tinbergen, like Darwin, was interested not only in the variety of living things, but also in developing general concepts which allow us to impose order on diversity, and especially in proposing how the many forms of species-typical behaviour have arisen. But, unlike Darwin, he was also a skilful experimenter: his elegant experiments on insects and birds in the field, and on sticklebacks in aquaria, remain models for textbooks of ethology.

His large output of published work, part of which is collected in the two volumes of *The Animal in its World* (1972, 1973), includes many papers on the analysis of fixed action or motor patterns, especially social signals. These are accompanied by scrupulous comments on method, and provide much of the foundation of current social ethology. Empirical findings on behaviour are presented in a darwinian framework; but Tinbergen distinguished, with exemplary clarity, between experimentally validated findings, on the one hand, and hypotheses about the past action of natural selection, on the other.

Tinbergen's studies of gulls, carried out with many colleagues, illustrate the several facets of his method. Long periods of watching and filming in the field led to intimate understanding of the natural history of each species. Ingeniously designed models were used to analyse social interactions, including those of parents and young, and to reveal the significance of minutiae, such as the coloured spot on a herring gull's beak. An ecological component is exemplified by investigations on defence against predators. Among the items closely scrutinized was the removal of broken eggshells from the nest. This apparently trivial manoeuvre, reported on in three papers, led to discussion of difficult questions on the nature and functions of stereotyped acts, and of the complexity of the 'anti-predator system' of black-headed gulls.

Although, as Tinbergen wrote, even "common descent is a matter of conjecture", one aim was always to suggest how the behaviour recorded had evolved. Hypotheses on phylogeny were made plausible

by comparing the behaviour patterns of a number of closely related species.

Tinbergen moved from Leiden to Oxford in 1949, and there founded a school of able pupils among whom he inspired affection as well as respect. Their influence is now felt throughout the world. Two years later *The Study of Instinct* was published; this, the short Methuen monograph *Social Behaviour in Animals* (1953), and his notable study of a single species, *The Herring Gull's World* (also 1953), provided the themes for many new university courses in animal behaviour. Tinbergen was, indeed, a teacher of the front rank: as he wrote, he was "at heart a missionary".

Converting the English to ethology was easy. American behavioural scientists, accustomed to laboratory experiments on habit formation by domestic species, found the untidy world of nature disconcerting and the study of 'instinct' baffling. They were therefore slower to accept Tinbergen's message, but eventually did so on a large scale. Tinbergen's success in the United States was probably helped by his lecturing style, for he held close attention without flamboyance or gimmickry: the art that conceals art. Some appreciative North Americans also offered cogent criticisms of early ethological theory, especially the neglect of ontogeny. These Tinbergen discussed and partly accepted without strident controversy — an aspect of his readiness to modify his views as knowledge advanced. As a result, leading North American experimental psychologists joined the International Ethological Congress, of which Tinbergen was a prominent founder.

Tinbergen's characteristic restraint was also shown in his contributions to the human sciences. He held that a combination of modern ethology with darwinism could tell us much of value about humanity, from the social lives of infants to the anti-social violence of adults; and he was tolerant of "naked-apey" among his colleagues and pupils. But he did not take part in the movement to provide a thoroughgoing biological interpretation of humanity. In 1968 he wrote: "What we ethologists do not want, what we consider definitely wrong, is uncritical application of our results to man".

Today, it may seem strange that a career in behavioural science of historical significance could be founded entirely on observation of whole animals, with little physiological analysis and no use of the algebra of evolutionary theory. A fitting memorial would be for students and workers in the behavioural sciences to return to Tinbergen's works, and to study them with the kind of critical appreciation which he himself applied to the works of others.

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