

EWA J. GODZIŃSKA

Laboratory of Ethology, Department of Neurophysiology

Nencki Institute of Experimental Biology

Pasteur St., 3, PL 02-093 Warsaw, POLAND

ETHOLOGY AND MECHANISMS OF BEHAVIOUR

ETHOLOGY

Ethology is the study of mechanisms and evolution of behaviour, focused both on accurate observation and description of behaviour and on its causation. Ethology is concerned with four main categories of causal factors of behaviour, the famous „four whys” outlined by N. Tinbergen, one of the pioneers of classical ethology. They include: (1) immediate mechanisms of behaviour (in particular, stimuli eliciting and modulating behavioural responses, factors influencing the motivational state of the animal, and factors related to the integration and organization of behaviour), (2) factors acting in the course of the ontogenesis of the studied individuals, (3) factors which acted in the course of the phylogenesis (the evolutionary history) of the studied species, and, lastly, (4) factors related to the function (adaptive significance) of the studied behavioural trait. The first two categories are now usually designated jointly as the proximate causal factors of behaviour, whereas the second two are called jointly the ultimate (evolutionary) causal factors of behaviour.

Sometimes ethology is also defined as the study of an animal's behaviour in its natural environment. As a consequence of their interest in the function and evolution of behaviour, ethologists often observe animals in their natural habitat or in environments designed to simulate it. However, modern ethological studies frequently involve highly sophisticated experiments carried out under strictly controlled laboratory conditions.

As another consequence of the emphasis laid on the evolution of behaviour, ethological research is often focused on genetically determined, inherited behavioural traits. However, ethology also contributed in a major way to the development of modern theories of learning processes. Numerous ethological studies dealt with the role of acquired factors in the ontogenesis of behaviour. Many of them demonstrated that animals may have remarkable learning abilities limited to specific contexts. The studies of the phenomenon of imprinting started by K. Lorenz demonstrated that not all forms of learning and behavioural plasticity fit into the conceptual framework of the theory of conditioning. Another eminent ethologist, W. H. Thorpe, was the first to demonstrate that species-specific

preferences of animals may not be determined genetically, but may arise as a result of early experience of the individual.

Ethological studies often involve comparisons among various species and phyla. In contrast to some other theories of behaviour, general theoretical concepts introduced by the classical ethologists arose as a result of comparative studies of many phylogenetically distant animal groups, both invertebrates and vertebrates.

Early ethological theory of behaviour introduced many important concepts, such as, for instance, fixed action pattern, sign stimulus, innate releasing mechanism, instinct, appetitive behaviour, consummatory act, vacuum activity, displacement activity, imprinting and critical period. Many of these concepts are still used in modern research on animal behaviour, although sometimes they are now hidden under a different label (for instance, fixed action patterns are now usually called motor programmes). Ethological theory of behaviour is still developing. New theoretical concepts proposed more recently are, for instance, equifinality, selective learning, and alternative tactics.

Ethology is not the sole branch of science concerned with the study of behaviour and its mechanisms. Two other important early approaches to the study of animal behaviour were zoopsychology and comparative psychology. Physiological psychology, neurophysiology (now transformed largely into a broader integrative scientific discipline, neurobiology), behavioural endocrinology, chronobiology, psychopharmacology and ethopharmacology contributed in a major way to our present knowledge concerning the proximate mechanisms of behaviour. Neuroethology is a particularly fruitful modern approach created on the boundary between neurobiology and ethology. Behavioural ecology and sociobiology are relatively young, dynamic approaches concerned mainly with the ultimate causation of behaviour. Still more recently founded are cognitive ethology and cognitivism, scientific disciplines focused mainly on cognitive processes in animals and humans. Numerous scientific disciplines (in particular, humanethology, psychology, psychiatry, ethnology and sociology) are concerned with human behaviour and its mechanisms.

As a result of the recent development of new approaches to the study of behaviour (in particular, behavioural ecology and cognitivism), ethology may seem to become relatively less attractive for modern students of behaviour. However, as pointed out by J. L. Gould, an ardent advocate of the ethological approach, we are just beginning to appreciate the full power of ethology's classic ideas and of its broad and integrative approach in unravelling how behaviour, both simple and complex, is organized and orchestrated. Only now we start to understand crucial links between neural mechanisms and the evolution of behaviour. Now more than ever before, ethology poses some of the most exciting intellectual challenges in modern biology while it offers the most powerful conceptual tools for answering them.

As stressed by W. H. Thorpe, one of the most eminent pioneers of ethology, the strength of ethology resides in its prime concentration on the behaviour of the animal as a whole, and secondly on its fourfold approach to the subject of causation of behaviour. Ethology is an integrative science essential for the full

and satisfactory development of all other disciplines which are concerned with the whole animal.

THE PRESENT VOLUME

The present volume is composed of 24 review papers dealing with the behaviour of animals belonging to a broad spectrum of phyla. Numerous papers are devoted to the behaviour of insects, in particular, ants (GODZIŃSKA, GODZIŃSKA and WAGNER-ZIEMKA, KORCZYŃSKA, SZCZUKA, WOJTUSIAK), flying *Hymenoptera* (CHMURZYŃSKI, GODZIŃSKA and WAGNER-ZIEMKA, SZCZUKA), crickets and grasshoppers (GODZIŃSKA and WAGNER-ZIEMKA, GÓRSKA, KIERUZEL, PYZA), cockroaches (GODZIŃSKA and WAGNER-ZIEMKA, PYZA), mantises (GODZIŃSKA and WAGNER-ZIEMKA) and flies (PYZA). Reproductive behaviour of grasshoppers and water striders is also described by J. RADWAN. Regrettably, no paper deals with the behaviour of invertebrates other than insects, although the papers of E. PYZA and J. RADWAN contain some data concerning crustaceans.

The data on the behaviour of fishes, amphibians and reptilians are scarce: they are provided only in the papers of J. RADWAN and L. STEMPNIEWICZ on mate choice and mating systems in animals. Only one paper is devoted exclusively to the behaviour of birds: gulls and terns (BUKACIŃSKA and BUKACIŃSKI). However, numerous informations concerning mating behaviour of various bird species are also provided in the papers of J. RADWAN and L. STEMPNIEWICZ. Informations concerning various aspects of behaviour of birds can also be found in the papers of M. BIAŁY, J. BŁASZCZYK, T. JEZIEŃSKI, I. ŁUKASZEWSKA and K. TAJCHERT *et al.*

A large group of papers is devoted to the behaviour of mammals. The majority of them deals mainly or exclusively with the behaviour of rodents, and in particular the rat (BECK, BIAŁY, ŁUKASZEWSKA, PISULA and OSIŃSKI, POPIK, TAJCHERT *et al.*). Several papers are devoted to a single group of mammals: bats (FUZARA and FUZARA), *Carnivora* (KALETA) and shrews (RYCHLIK). Others provide the information about the phenomena observed in numerous mammalian species (BIAŁY, BŁASZCZYK, JEZIEŃSKI, STEMPNIEWICZ). The paper by W. KOSTOWSKI on the mechanisms of alcohol dependence deals with the phenomena which are important mostly as the mechanisms of human behaviour.

The papers presented in this volume deal with a broad range of topics ranging from molecular mechanisms of behaviour to applied ethology.

Neurobiological mechanisms of behaviour are discussed mainly in the papers included in the first part of the volume (KOSTOWSKI, BIAŁY, POPIK, PYZA, GODZIŃSKA and WAGNER-ZIEMKA, GÓRSKA, TAJCHERT *et al.*, BŁASZCZYK). More or less detailed data concerning neurobiological mechanisms of behaviour are also provided by T. JEZIEŃSKI, I. ŁUKASZEWSKA, W. PISULA and J. T. OSIŃSKI, and A. SZCZUKA.

The opening paper of W. KOSTOWSKI is devoted to the neurobiological mechanisms of ethyl alcohol (EtOH) dependence. The author discusses, among others, the interactions of EtOH with various brain neurotransmitters and their receptors and with the endogenous opioid system of the brain, the effect of EtOH administration on calcium L-channels, the mechanisms of the rewarding effects of EtOH and of the EtOH withdrawal syndrome, and the role of learning

processes in the development of EtOH dependence. He also reviews principal strategies of pharmacotherapy of EtOH dependence.

M. BIAŁY provides the review of literature data on the role of acquired factors in the ontogenesis of sexual behaviour of male mammals. He also provides a detailed account of his own experimental data on the role of *c-fos* gene expression and of NMDA receptors in the plasticity of the sexual behaviour of male rats. His data provide an excellent example of fruitfulness of interdisciplinary research made possible thanks to joint application of methods of ethology and molecular biology.

P. POPIK reviews the results of research on the modulatory effects of posterior pituitary hormones, vasopressin and oxytocin, and of several vasopressin-related peptides on social recognition in rats (= the ability to acquire, store, and recall information concerning olfactory identity of juvenile individuals, involving most probably a form of working memory). The author also describes other olfactory learning phenomena used recently as models in psychopharmacological research on memory processes, in particular, the phenomenon of social transmission of food preferences in rats. A large part of the reviewed data are the results of the author's own research.

E. PYZA presents a detailed review of neurobiological mechanisms underlying insect circadian rhythms. In particular, she describes in detail the neuroanatomical substrate of circadian clocks in various insect species and in various *Drosophila* mutants. She also discusses the role of the *period* gene expression and of the neuropeptide PDF (pigment dispersing factor) in the functioning of insect circadian clocks. She also provides a detailed account of her own experimental research on two structural circadian rhythms detected by her in the visual system of the housefly — oscillations in the number of particular types of synapses in the first visual neuropile, and fluctuations in diameter of monopolar cell axons — and on the role of various neurotransmitters and of PDF in regulating the second of these two rhythms.

J. GÓRSKA describes in detail the phenomenon of phonotaxis in crickets and discusses its neurobiological mechanisms. Her paper provides, among others, the description of the sound-producing organs of the male and of the auditory system of the female (including the description of several classes of auditory interneurons involved in the phonotaxis). Of particular interest are the data on the role of the juvenile hormone JH III in the control of phonotactic responsiveness of female crickets (most probably carried out *via* genetic regulation of the response properties of the identified auditory interneurons).

E. J. GODZIŃSKA and A. WAGNER-ZIEMKA review in detail literature data on the role of opioids in insect behaviour. Although the role of these compounds in regulating insect behaviour was so far investigated in extremely few studies, the results of that research demonstrate already that opioids may influence in a significant way insect grooming behaviour, locomotory activity, feeding behaviour, various defensive responses triggered by noxious stimuli, and learning processes occurring within isolated thoracic ganglia controlling the movements of a single leg.

The paper of K. TAJCHERT, J. BŁASZCZYK and K. ZIELIŃSKI deals with the startle reflex, a reaction triggered by sudden intense stimuli. A particular stress is laid

on neurobiological mechanisms underlying the acoustic startle reflex (ASR). The authors also describe the phenomenon of the so called fear-potentiated startle paradigm, a new model used in pharmacological research mainly to evaluate the effects of various drugs on the level of fear and on the long-term memory. The authors also review their own experimental data on factors influencing the amplitude of the ASR in the rat.

The paper of J. BŁASZCZYK is devoted to neurobiological mechanisms of locomotion in mammals. The author describes, among others, various methods used in the studies of animal locomotion, and, in particular, a new method of simultaneous measurement of basic parameters characterizing quadruped locomotion developed at the Nencki Institute of Experimental Biology. He also discusses factors underlying the choice between various alternative gaits employed by mammals during locomotion, among others, energetic costs of various gaits. The paper also contains a discussion of the results of the author's own experimental data on physiological and neurobiological mechanisms involved in control of various parameters characterizing mammalian locomotion.

Another large group of papers (ŁUKASZEWSKA, PISULA and OSIŃSKI, CHMURZYŃSKI, KORCZYŃSKA, SZCZUKA and GODZIŃSKA) deals mainly with the role of environmental factors and stimuli in modulating and moulding animal behaviour. The main issues discussed in these papers are: exploratory behaviour, cognitive processes, learning processes, behavioural plasticity, behavioural flexibility and alternative tactics. The information about behavioural plasticity and learning processes can also be found in the papers by M. BIAŁY, E. J. GODZIŃSKA and A. WAGNER-ZIEMKA, T. JEZIEŃSKI, W. KOSTOWSKI, and P. POPIK. Alternative forms of behaviour are also discussed by J. BŁASZCZYK, M. BUKACIŃSKA and D. BUKACIŃSKI, and L. STEMPNIEWICZ.

The paper of I. ŁUKASZEWSKA is devoted, on one hand, to novelty responses and exploratory behaviour of animals, in particular the rodents, and, on the other hand, to the phenomenon of habituation of responses to novel stimuli. The author provides an exhaustive review of literature data and of her own experimental data concerning these phenomena and their neurobiological mechanisms. Of particular interest is her discussion of the major function of exploratory activity — creating and updating of „cognitive maps”, internal representations of environment. Her paper contains also an account of her numerous experiments dealing with neurobiological and neuropharmacological mechanisms of exploratory behaviour, spatial attention and habituation in the rat.

W. PISULA and J. T. OSIŃSKI provide a detailed account of their experiment on the exploratory behaviour of the laboratory rat. The animals were tested in a special chamber providing the environment richer in stimuli than the classical „open field” setup; their behaviour was analysed by means of the hierarchical cluster analysis. The authors discuss, among others, the relevance of their results for the theoretical model of the stimulus seeking behaviour of the rat proposed by J. Matysiak. They also put forward many open questions raised by their research. Their paper provides an example of the approach of experimental psychology to the study of animal behaviour.

The paper of J. A. CHMURZYŃSKI is devoted mainly to the role of various types of flights in the acquisition of information by flying *Hymenoptera*. The author reviews literature data and his own experimental data demonstrating that certain forms of flights are triggered in *Hymenoptera* in response to novelty/change, and that these insects memorize visual stimuli perceived during these flights. A particular stress is laid on learning processes occurring in the context of foraging and homing. The author also reviews the results of his experiment on various alternative modes of flight employed by the digger wasp, *Bembix rostrata*, which demonstrated that the speed and ceiling of flight are mutually interrelated in a way maximizing the ability of the insect to discriminate visually the details of its surroundings. He also discusses a possible relationship between the tendency to perform exploratory flights and hypothetic negative emotional states appearing in *Hymenoptera* in response to novelty/informative uncertainty.

J. KORCZYŃSKA discusses the role of acquired factors in the ontogenesis of environmental and food preferences in the ants. A particular stress is laid on the ontogenesis of preferences determining the choice of the nesting site in various ant species, and on the plasticity of foraging behaviour in the harvester ants. The author also provides an account of her own experimental data on the role of acquired factors in the ontogenesis of illumination preferences in the ants, and describes in detail the research of GODZIŃSKA, KORCZYŃSKA and SZCZUKA on the processes occurring in the course of familiarization of the harvester ants with novel seeds.

The paper of A. SZCZUKA is devoted to the phenomenon of behavioural flexibility in the ants. The author explains the distinction between the behavioural plasticity and behavioural flexibility and provides numerous examples of various forms of behavioural flexibility in the ants; in particular, she describes the phenomena of social regulation and behavioural elasticity. Of particular interest is her account of the data concerning the neuroanatomical and hormonal changes appearing in the honeybees as a consequence of the transition from the role of nurse to the role of forager, triggered experimentally by modifications of the social structure of the colony. These data provide an excellent example of the bidirectionality of the cause-effect relationships between neuroanatomy and behaviour, demonstrating that behavioural modifications triggered by the events occurring on the social level of organization may lead to profound neuroanatomical changes on individual level.

The paper of E. J. GODZIŃSKA is devoted to hunting techniques and tactics employed by the ants. The author describes techniques of prey capture and transport which have evolved in various ant species, and alternative hunting tactics employed by the ants of a given species in various situations. Of particular interest are the data on the secondary disappearance of the fundamental difference between intra-specific aggressive behaviour and predatory behaviour, which occurred in the course of the phylogenesis of some ant species. The author also provides an account of her own experimental data on responses of various ants to prey equipped with chemical antipredatory defense systems, on hunting and transport tactics of the African ants of the genera *Oecophylla* and *Polyrha-*

chis, and on the so called „pseudostinging behaviour” of the harvester ants of the genus *Messor*.

The third large group of papers (RADWAN, STEMPNIEWICZ, KIERUZEL, BECK, BUKACIŃSKA and BUKACIŃSKI, FUSZARA and FUSZARA, WOJTUSIAK, KALETA, and RYCHLIK) deals mainly with the inter-individual interactions and social behaviour of animals. The information about these issues can also be found in the papers of M. BIAŁY, E. J. GODZIŃSKA, J. GÓRSKA, T. JEZIERSKI, J. KORCZYŃSKA, P. POPIK, and A. SZCZUKA.

The paper of J. RADWAN is devoted mainly to the ultimate causal factors of mate choice in animals. The author provides a detailed account of various hypotheses concerning these factors and of experimental data which support these hypotheses. A particular stress is laid on the analysis of the evolutionary costs and benefits of mate choice. The paper provides also numerous examples of factors influencing mating behaviour and mate choice in various animal species and of proximate mechanisms underlying mate choice.

The paper of L. STEMPNIEWICZ provides a classification of mating systems encountered in vertebrates. A particular stress is laid on mating systems employed by birds and mammals. The author provides numerous examples illustrating the diversity of mating systems employed by bird and mammalian species. He also discusses various factors underlying the flexibility of vertebrate mating systems. Of particular interest is his discussion of alternative mating strategies/tactics of vertebrates and of factors influencing their evolution.

M. KIERUZEL reviews literature data and her own data on behaviour of the house cricket (*Acheta domesticus*) during various types of encounters with conspecifics. In particular, she describes sexual behaviour, aggressive behaviour and the so-called parasocial behaviour of these insects. Her paper contains also an account of her own experimental data on the expression of aggressive behaviour in food deprived females fighting for access to food, on the ontogenesis of territorial behaviour of males, and on spatial distribution of individuals kept together in laboratory cages. She also discusses literature data and the results of her own research on the effects of intense contacts with conspecifics — the so-called „group effects” — on the speed of ontogenetic development of the house cricket.

J. BECK provides a review of literature data and of his own experimental data on sexual behaviour of the rat. His paper contains a detailed description of courtship and copulatory behaviour of male and female rats. He also provides a detailed account of his own experimental research on cooperation between the male and the female during the sexual behaviour, and discusses his hypotheses concerning the character of the rewarding properties of various elements of the sequence of courtship and copulatory behaviour of male and female rats. Of particular interest are his data on the expression of male copulatory behaviour in rat females.

M. BUKACIŃSKA and D. BUKACIŃSKI describe various forms of intra- and interspecific aggressive behaviour displayed by gulls and terns. The stress is laid mainly on various functions of aggressive behaviour in these birds, and on hypothetical proximate mechanisms underlying the choice between various alternative forms of aggressive behaviour taking place in conflict situations. The

paper also contains a brief account of the authors own experimental data on the territorial behaviour, breeding success, and female guarding in various gull species.

E. FUSZARA and M. FUSZARA provide a review of literature data on mating behaviour and parental care among the bats. The authors describe mating behaviour and mating systems of numerous bat species living in various climatic zones. They also provide a description of parental care and mother-young communication in various bat species. Of particular interest are the data on the ontogenesis of vocal signals emitted by bats and on the role of observational learning in the ontogenesis of mating, social and foraging behaviour of these animals.

J. WOJTUSIAK provides a detailed account of the social organization of weaver ants of the tropical genus *Oecophylla*. These ants attained one of the pinnacles of the ability for cooperative behaviour in the whole animal kingdom. The author describes in detail the cooperative nest-building behaviour, territorial behaviour, predatory behaviour and communication systems of these ants. His paper contains also a brief discussion of his own experimental data on the nest-repairing behaviour and on the predatory behaviour of the African weaver ant, *Oecophylla longinoda*. That research provided, among others, an account of some of the most spectacular cases of individual and cooperative transport of large objects ever observed in ants.

The paper of T. KALETA is devoted to the social systems of *Carnivora*. The author describes in detail social systems encountered among *Carnivora* and territorial behaviour of various species belonging to that group. A particular stress is laid on the causal relationships between, on one hand, various features of feeding behaviour of these animals (in particular, prey size, food availability, diurnal versus nocturnal foraging) and, on the other hand, the type of their social system.

The paper of L. RYCHLIK is devoted to social systems of shrews. The author puts forward his own classification of social systems of these animals based, on one hand, on literature data and on his own experimental data and, on the other hand, on his hypotheses which remain still open for future investigations. He also discusses his own hypotheses concerning the evolution of social systems of shrews.

The paper of T. JEZIERSKI is devoted to the current advances in the applied ethology of farm animals. The author discusses mainly the role of ethological and neurobiological research in improving the welfare of farm animals. He also provides an account of ethological research on the ontogenesis of food preferences of these animals. His paper also provides a brief account on his own experimental research in the domain of applied ethology (the effect of stress on milk productivity of cows, the effect of handling on development of young rabbits, the effect of genetic and hormonal factors on homosexual behaviour of young bulls, and a new method of oestrus detecting in cows by a trained dog).

ETHOLOGY IN POLAND

In Poland, the main centre of the research on animal behaviour and its mechanisms is the Nencki Institute of Experimental Biology of the Polish

Academy of Sciences in Warsaw (represented in this volume by the papers by BŁASZCZYK, CHMURZYŃSKI, GODZIŃSKA, GODZIŃSKA and WAGNER-ZIEMKA, KIERUZEL, KORCZYŃSKA, ŁUKASZEWSKA, SZCZUKA, and TAJCHERT *et al.*). In Warsaw and its surroundings behaviour is also investigated, among others, at the Institute of Ecology of the Polish Academy of Sciences in Dziekanów Leśny (BUKACIŃSKA and BUKACIŃSKI, FUSZARA and FUSZARA), Warsaw University (PISULA and OSIŃSKI), Warsaw Medical Academy (BECK, BIAŁY), Institute of Genetics and Animal Breeding of the Polish Academy of Sciences in Jastrzębiec (JEZIEŃSKI), Warsaw Agricultural University (KALETA), and Institute of Psychiatry and Neurology (KOSTOWSKI). In Cracow, large centres of research on behaviour are the Jagiellonian University (GÓRSKA, PYZA, RADWAN, WOJTUSIAK) and the Institute of Pharmacology of the Polish Academy of Sciences (POPIK). Other important centres of the research on behaviour and its mechanisms are the University of Gdańsk (STEMPNIEWICZ), University of Łódź, University of Wrocław and the Mammal Research Institute of the Polish Academy of Sciences in Białowieża (RYCHLIK).

The first scientific society created by Polish ethologists, the Ethological Section of the Polish Zoological Society, was founded in 1987. In 1991 it transformed itself into an independent Polish Ethological Society (PTetol.)¹.

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Ewa J. Godzińska

¹The address of the Society is: Polish Ethological Society, Nencki Institute of Experimental Biology PAS, Pasteur St. 3, PL 02-093 Warsaw. Monthly meetings of the PTetol. take place at the Nencki Institute of Experimental Biology of the Polish Academy of Sciences in Warsaw, Pasteur St. 3, as a rule on third Thursday of each month, starting at 14.30.

Presently, the following persons form the Council of the PTetol.: Jerzy A. Chmurzyński — President (e-mail: jch@nencki.gov.pl); Ewa J. Godzińska — Vice-President (e-mail: ejg@nencki.gov.pl); Piotr Jabłoński — Secretary (e-mail: piotrjab@plearn.edu.pl); Anna Szczuka — Secretary (e-mail: szczuka@nencki.gov.pl); Julita Korczyńska — Treasurer (e-mail: jk@nencki.gov.pl); Marek Kozłowski — Member of the Council (e-mail: kozlowsk@alpha.sggw.waw.pl); Elżbieta Pyza — Member of the Council (e-mail: pyza@zuk.iz.uj.edu.pl) and Janusz Wojtusiak — Member of the Council (e-mail: wojt@zuk.iz.uj.edu.pl). Ewa J. Godzińska is also acting as the present delegate of Poland to the ICE (International Council of Ethologists).

Informations about funding sources for ethological research can be found *via* INTERNET in the document „The directory of the funding sources for promotion of the ethological research: research projects, travel and conference grants, schools and workshops, pre- and postdoctoral fellowships, senior scientists fellowships, cooperation with foreign laboratories”, prepared in 1995 by Ewa J. Godzińska, Charles Snowdon and Madeleine Paillette (address: gopher.cisab.indiana.edu or <http://www.cisab.indiana.edu/ABS/di-recpr.html>).