40. Broom, D.M. 1981. Biology of behaviour. School Sci. Rev., 62, 442-451

The biology of behaviour

D. M. BROOM
Department of Zoology, University of Reading

In recent years there have been considerable changes in the questions asked about observable behaviour and the factors which affect it. The ethological approach, in which animal systems are studied by observing actions, was developed to the state where it is a valuable scientific method by Konrad Lorenz and Niko Tinbergen. Much of their early work concerned displays during the reproductive period and certain aspects of parent-offspring interactions. Concise description of a wide range of actions in a given situation is a technique which is now utilized for all those aspects of life in which behaviour plays a part. It is useful in laboratory experiments or in farm situations as well as in wild, undisturbed conditions.

A consequence of this broadening of ethological research is that its overlap with physiological, ecological and other biological and psychological work is now extensive. Behaviour, like anatomy and physiology, is seen to be an integral part of many functional systems in biology, hence behaviour observation is essential if a complete understanding of any system is to be obtained. These changes and the considerable increase in the amount which is known about all aspects of behaviour have significant implications for biology teaching. Behaviour is not an isolated topic but should be taught as a subject which is closely related to most other aspects of a biological course. It is indeed a key to the organization of the day-to-day life of the animal because decisions by the individual about apportioning time and energy to the various possible functional systems are most readily monitored by behavioural observation [1]. The considerable resurgence of interest in evolutionary mechanisms has concentrated especially upon behaviour because behavioural mechanisms play an important part in determining which individuals survive to breed and which have the most successful offspring. Some of the ideas which have helped us to understand behaviour better, which bridge gaps between biological topics and which emphasize the value of a biological approach to psychology are discussed below.

FUNCTIONAL SYSTEMS

1. *Feeding*

Before ingestion, most animals need to actively search for, recognize and acqure food. Elaborate behavioural strategies are used when hunting for animal prey or for widely distributed plant food sources. The hunting may be carried out by the individual which is going to eat the food or by a parent on behalf of its offspring. The food source of many insect larvae is located by the mother before she lays her eggs. The cabbage-root fly, an economically important species, lays its eggs next to the stem of a cabbage plant. Females about to lay eggs fly up wind when they detect the odour of mustard oil, which is produced by cabbage plants. They then approach objects producing this odour, especially if they are yellow and at a particular height from the ground. This information has been used to design traps to catch the flies and hence reduce the damage done to cabbage crops [2].

A detailed study of the food-searching behaviour of blackbirds and song thrushes can be carried out using little specialist equipment. A pair of binoculars and some pegs to mark out an area of grassland made it possible to describe the movements of the thrushes whilst they were hunting earthworms or artificial food which had been put out for them [3]. A series of movements, each about 40 cm in length and lasting about 0.5 s, were separated by pauses of about 5 s. If food was found the thrush was more likely to turn from its previous course and would often turn in the same way after two or more successive movements so that the overall path was circular. The path was straighter and faster if no food was found. This overall strategy is an effective way of dealing with a situation where the food cannot be seen from a distance and occurs in clumps of higher density. If the bird is not in such a clump it should move rapidly in a straight line until it gets to one, but if it is in a clump, turning will increase the chances that it will find another food item within that clump.

Another recent study has combined behavioural and physiological experiments with knowledge of ecology. Humming birds of some species feed principally on the nectar of plants whose corolla shape matches their bill shape and tongue length. What determines the timing of visits to flowers and the choice of feeding site? Measurements have been made [4] of the calorific value of the food, its rate of production and energy consumption by hovering and resting humming birds. When these measurements were related to observations of the feeding behaviour of humming birds, it was demonstrated that the humming bird behaves in such a way as to maximize the rate of the net energy gain. The amount of nectar taken in a meal and the frequency of meals are sufficient to adjust for the requirements of daily energy storage and maintenance energy during the day. An individual humming bird is likely to visit flowers which are fully open but the duration of foraging in a particular patch of flowers depends upon the average intake of nectar there in comparison with the quantities which it knows from previous experience to be available elsewhere. Once a flower has been visited, the bird will not visit it again until sufficient time has elapsed for further nectar secretion to have occurred. The feeding behaviour is thus seen to be dependent upon complex learning ability and the overall strategy is found to be very efficient in energetic terms.

2. *Predator avoidance*

Predators constitute a major hazard for most animal species and their existence has had a large effect on the evolution of behaviour in all species including man. Animals avoid large predators by concealment, keeping away from danger areas, flight, combat or combinations of these. The depredations of parasites are also countered by using some or all of these methods. Many anti-predator behaviour patterns are familiar to us because these are the commonest behaviours which we see in wild animals. Recent work on toads has provided evidence about methods of distinguishing predator from prey [5]. A toad will attack worm-like objects but shows escape responses when tall objects move near it. Experiments have shown that the same moving object oriented in different ways will elicit opposite responses. If a pencil-like object, oriented so that it is parallel with the ground, is moved horizontally near the toad, the toad attacks it. If the same object is moved in the same way but it is oriented so that it is vertical, the toad shows escape behaviour. Electrical recording from the ganglion cells of the toad's retina shows that the horizontal 'worm' and the vertical 'non-worm' cannot be distinguished at this level in the visual pathway. Recording further along the visual pathway in the caudal thalamus or the pre-tectal area has shown that there are 'enemy detector' cells which fire when a tall object like the vertical 'non-worm' is seen. If this area is lesioned, prey catching is shown to everything, including the 'non-worm' and the toad's own foot. Recording from the optic tectum has revealed units which respond to the 'worm', even if it is also vertically elongated, and others which do distinguish between 'worm' and 'non-worm'. These last units receive an excitatory input from tectal units which respond to 'worm' and an inhibitory input from the pre-tectal units which respond to 'enemy'.

3. *Hazard avoidance (a) chemical*
The ingestion of harmful substances and the accumulation of indigestible material or harmful metabolic products within the body must be minimized. The major components of this system are within the body: digestion, detoxification and immunological processes; but elimination is a frequent behaviour. The time and place of defaecation or urination are often precisely controlled, although the presence of very harmful substances in the gut may override normal constraints on the occurrence of the behaviour. The avoidance of harmful substances when feeding is a complex mechanism in which experience plays a large part.

4. *Hazard avoidance (b) physical*
Terrestrial animals encounter hazards such as falling, drowning and being squashed or buried. Aquatic animals may be stranded out of water, suffer lack of oxygen, or experience large pressure changes. Most of the methods of avoiding or minimizing the effects of these hazards are behavioural. Many experiments have assessed the responses of animals on a cliff which is apparent rather than real. When a rat or domestic chick is placed on a board with a shallow drop on one side but with glass, illuminated from below, over a deep drop on the other side, the 'deep' side is avoided. In a review of such 'visual cliff' experiments [6], it was shown that whereas most adult animals avoid the apparently hazardous drop, turtles do not. It seems likely that the turtles have adequate depth perception but that the deep side of a 'visual cliff' resembles a bank with water below it. Young mammals, such as kittens, whose eyes have opened recently do not avoid the deep side, however. Their depth perception ability is not sufficient to allow them to recognize the deep drop. If they are allowed practice at walking and co-ordinating their motor output and visual input, they start to avoid the cliff after a few days. The apparatus has been useful as a means of investigating mechanisms of depth perception.

5. *Body regulation and maintenance (a) osmotic*
Animals on land have to avoid dehydration whilst those in fresh water have to avoid loss of salts and other dissolved matter into the surrounding medium. Water conservation methods often involve behavioural components and, on land,

acquiring water by drinking inevitably involves complex behaviour. There have to be: receptors which detect changes towards dangerous levels of osmotic state, a decision-making mechanism which receives input from these receptors, a method of acting so as to return the state towards the optimum, and receptors which provide an input so that the correcting behaviour can be terminated. The homeostatic mechanism which regulates water balance in doves has been extensively investigated [7]. Day to day changes in body weight and water intake, during and following water deprivation in the Barbary dove can be explained in terms of a control system with two feedback loops. The conservation loop includes the kidney mechanism, which is regulated via the secretion of the hormone vasopressin from the hypothalamus, and the reduction of food intake, which is necessary since water is used up during feeding and digestion. In hot weather conservation can also be helped by avoiding places where panting might be necessary for thermoregulation. The major cue which is used to initiate drinking behaviour in some mammals, and probably in other mammals and birds, is a drop in the volume of blood reaching the kidney. Once a dove starts to drink. input to the control system from sensory receptors in the mouth and pharynx provide a positive feedback, which maintains drinking behaviour until there is negative feedback from sensory receptors in the crop.

6. *Body regulation and maintenance (b) temperature*
Behavioural mechanisms and physiological mechanisms combine in temperature regulation. Although especially important in warm-blooded animals, the dangers of being unable to show activity at low temperatures have resulted in the existence of many body-temperature modifying behaviours in cold-blooded animals. When the sun first appears on a cool morning, butterflies open their wings and hold them at right angles to the direction of the sun's rays. When the air temperature increases and direct heat from the sun may be dangerous for the insect, the wings are held closed over the back and are pointed at the sun. Lizards also bask in the sun after a cool night and they avoid overheating by moving into shade or, like the butterfly, by presenting a small surface area to the sun. It seems likely that the fossil mammal-like reptiles with a large fan on their backs, such as *Dimetrodon*, used these fans for thermoregulation in the same way. Mammals and birds also use behavioural methods of regulating body temperature. Studies in which rats, pigs and sheep were able to switch on heaters in cold surroundings by pressing a lever or breaking a light beam with the nose, showed that such energetically cheap behavioural methods of temperature control were preferred to physiological methods. In field situations the physiological methods might sometimes be preferred because the behaviour might render the individual vulnerable to predation.

7. *Body regulation and maintenance (c) cleaning*
Birds must maintain their wing feathers in order to fly. Grooming, preening and cleaning behaviour are also important as means of maintaining the efficiency of other forms of locomotion, sensory functioning and display. They also minimize the incidence of disease and parasites. Recent interest in the control of action patterns has centred on grooming behaviour. It was possible to describe seven distinct components of face grooming by careful analysis of films of mice [8].

These components were usually combined with one another in one of five recognizable sequences which were called units. After any given unit there was a fifty per cent chance that another particular unit would follow. Sensory input did not modify the form of the components but it could sometimes alter the composition of units and it readily affected sequences of units. The next step in this type of research is to relate more effectively the detailed observations of behaviour to the functioning of the cerebellum and motor cortex of the brain.

8. *Reproduction*
All of the functional systems mentioned so far operate in such a way that individual survival is maximized. The functional system in which reproduction and the survival of offspring or other relatives is promoted, operates at the same time as those promoting individual survival and may conflict with them. Behaviour in which there is such a conflict is often called altruistic. The system includes behavioural mechanisms for mate finding; mate recognition; display and other methods of persuasion (Figure 1); parental care, and other means of

Figure 1. Male fiddler crab, *Uca rapax*, displaying to mate or rival at the mouth of his burrow in a Jamaican mangrove swamp (photograph G. F. Warner)

increasing the chances that offspring and other close relatives will survive and breed. This last function incorporates elements of many of the functional systems which promote individual survival.

9. *System selection*
If an animal is feeding it may at any moment stop feeding and set off to find water, or act so as to change its body temperature, or carry out an activity which reduces the chances of predation. What determines this transition from one type of activity to another? Various changes within the food or water regulatory systems may precipitate such a behavioural change. For example there may be a critical change in a blood-sugar level monitor, a stretch receptor in the gut, a body-fluid concentration monitor, a control centre in the hypothalamus, or in a controller of short-term patterns of feeding or drinking behaviour. Techniques of physiology,

physiological psychology and behaviour analysis must be combined in order to understand what is happening. The decision as to which functional system determines current behaviour must depend upon biological priorities.

Behaviour changes depend upon changes in motivational state, a term which requires definition. Sensory inputs to the brain are analysed and the output from the analysers acts as a causal factor which may affect behaviour. Other causal factors include outputs from pace makers and homeostatic control systems as well as from regions of the brain affected by hormones. If the levels of two causal factors are plotted against one another, the state of the individual with respect to each of them can be pinpointed at any moment. In time the position in the causal factor space will change. Since there are many causal factors there will be many dimensions but it is possible to consider the state, at any moment, with respect to each of them. Motivational state is the position of the individual in that multidimensional causal factor space [9].

Motivational systems have evolved just as other biological characteristics have done. When a predator is detected, an animal which is feeding must rapidly stop eating and initiate predator avoidance behaviour, if it is to survive. If there were two genotypes within a population of animals, such that the possessors of one set of genes were likely to switch more rapidly from feeding to predator avoidance than were the individuals with the other set of genes, the first set of genes would be more likely to spread in the population than the second.

OPTIMALITY AND FITNESS

In the above survey of functional systems, assumptions are made about the way in which biological systems work. One assumption is that biological mechanisms are efficient because genes which promote efficient mechanisms are likely to survive in the population. Although the basic idea stems from Darwin it has become sophisticated as a result of the writings of those concerned with population ecology and evolution [10]. Much behavioural and ecological work is now influenced by the belief that the assessment of the costs and benefits of actions is of paramount importance in determining how behavioural mechanisms work, what an animal does at any moment and, as a consequence, how animals become distributed. The mechanisms which were originally discussed in this way were those concerned with the utilization of food resources but cost-benefit analysis and optimality theories are now being applied to all behavioural problems [11].

If behavioural or physiological mechanisms, which achieve a particular end, are being compared, how should benefit be measured? In early studies of feeding, energy gain from food seemed a logical measure but food of a given calorific value might be a life-saver to one individual but not to another. A further factor which must be considered is effect on reproductive potential. A large meal may result in an increase in the number of offspring produced. The benefits of an action have therefore been thought of by many authors as improvements in the fitness of the individual. This concept of Darwin's encompassed the survival of the individual and its subsequent breeding. The more recent idea of 'inclusive fitness' [12] emphasizes that the ultimate assessment of benefit must be in terms of gene survival. Since the genes are the replicators, the measure of the success of an action, which can occur only if a certain combination of genes is present in the individual, is the number of individuals in future generations which have this combination of genes [13]. In practice, it is seldom possible to measure costs and benefits in this way, so for many behavioural functions, estimates of efficiency of the kind that an engineer might make are a useful approximation.

When considering the evolution of many aspects of behaviour the concept of the 'evolutionarily stable strategy' (ESS) is useful [14]. Suppose that a population exists in which there are two classes of members which show different strategies in a given situation and the two strategies depend upon different genetic programmes. After many generations natural selection will result, usually, in the survival of one of these genetic programmes (A) in the population. If the strategy which results from (A) is the best possible, given the limitations of the animal and the general conditions in which it lives, then other genetic programmes (B, C, etc.), arriving as mutants or migrants, cannot invade a population of (A) and (A) is an ESS. One example of a theoretical set of alternative genetic programmes arises from studies of strategies for contests between evenly matched individuals competing for a mate. Consider four strategies: 'hawks' which attack as soon as a contest is initiated, thus inevitably incurring quite high costs but sometimes benefiting by victory; 'doves' which threaten initially when a contest starts but always give in, with consequently low costs but no victories against attackers; 'bullies' which attack initially but give in if the attack is returned; and 'retaliators' which threaten initially and attack only if they themselves are attacked. When assumptions are made about the costs and benefits of serious injury, slight injury, winning, and saving or losing time, the average net result of each possible encounter can be calculated. Populations of individuals showing 'hawk', 'dove' or 'bully' strategies are each seen to be vulnerable to invasion by animals showing one or more of the other strategies. A population of 'retaliators', however, cannot be invaded so in these conditions 'retaliator' is the evolutionarily stable strategy. The area in which the ESS concept is particularly useful is that in which the playing of a particular strategy has consequences as to which alternative strategy by another individual is subsequently most effective. It is applicable in situations in which the contestants are unequal [15]. Examples of such situations, where there is interaction between individuals, include competition for food or for other resources as well as direct encounters. If your competitors are all eating spinach it will pay to concentrate on cabbage [16].

THE UNIVERSALITY OF ENVIRONMENTAL EFFECTS ON BEHAVIOUR

The fact that details of behaviour evolution and genetics are discussed, e.g. [17], does not imply that any behaviour is completely predetermined and independent of environmental effects. Arguments about behavioural characteristics refer to the average individual which has a certain genotype. The population of such individuals may vary considerably. All characteristics of organisms, including behaviour, are the result of interaction between genetic programmes and environmental variables so that it is not valid to refer to any behaviour as being genetically determined or environmentally determined. The environmental input to genetic programmes may be relatively constant from individual to individual or very variable.

The mistaken belief that an individual's behaviour is determined by its genes is dangerous for it may result in people giving up trying to modulate aspects of their own behaviour.

An important change in attitude to behaviour which is gradually gaining ground is the view of learning as a continuous process throughout life rather than an occasional phenomenon [18]. All interactions between an individual and its environment are occasions for potential modification of that individual. Using the word learning in a broad sense, it is apparent that everyone who studies behaviour sees learning occurring.

They may not always recognize it because the behaviour change is subtle or because the environmental change and its consequences are widely separated in time. The problem facing those attempting to analyse the effects of experience on behaviour is to determine why behaviour changes so infrequently rather than just to consider what does make behaviour change. The differences between cues which do elicit behaviour modification and those which do not is, again, a matter of biological priorities. The impressive ability of wild rats to avoid poison and inadequate diets must involve relating cues from eating to later cues from the effects of eating that food [19]. Such learning ability is very important for survival. The ease with which various associations between a supposed reinforcer, such as food, and an activity can be made, varies according to the biological likelihood of the association. When food was presented to hamsters on successive occasions when they were carrying out one of seven activities, the subsequent frequencies of some activities were changed but those of others were not. The activities where frequencies were changed, e.g. digging or rearing, were activities which might be related to food finding whilst the frequencies of washing or scent marking were not changed [20].

The ways in which experience affects behaviour are often best studied in developing animals [21]. One conclusion which can be drawn from the extensive array of behaviour development studies is that environmental factors may act on a given system at any stage from zygote formation onwards and studies which consider only those factors which are obvious after birth or hatching may be inadequate. Another conclusion is that it is essential to consider function in the developing individual as well as function in the adult.

THE EVOLUTION OF SOCIAL BEHAVIOUR

The first step in the evolution of social behaviour must have been the appearance, in the population, of genes which promoted the initiation of aggregation or which slowed down separation after reproduction. The most likely occasion for aggregation is when there is a local abundance of food. Once this has been found by one or more individuals, others may be best able to find it by recognizing the presence of those individuals. Those genes which promote the recognition of and approach to conspecifics will be likely to spread in the population. Once an aggregation is formed, predator avoidance can be improved by ensuring that there is always another individual between you and the predator. Where the predator does not eat too many prey individuals at once, genes which promote the behaviour pattern whereby prey individuals place themselves between conspecifics, spread in the population [22]. Another benefit of group living could be in the acquisition of information about food finding. An individual which knew of no food source could follow another member of the group when it departed, for it might be heading towards food [23]. In some circumstances, food acquisition is much more efficient if the animals remain in groups and they return to the group if separated from them. An example is the brittle-star *Ophiothrix fragilis* which feeds on suspended matter in currents and can use more arms for feeding if it can hold on to other brittle-stars (Figure 2) [24, 25].

Social groups also provide opportunities for apparently altruistic behaviour. As mentioned earlier, selection acts on gene expression. Group selection is unlikely to be an important mechanism and it is not meaningful to argue that a characteristic is 'for the good of the species' (as many biology books do). A gene complex which makes likely altruistic behaviour towards brothers and sisters will, by

Figure 2. Brittle-stars *Ophiothrix fragilis* on the seabed off the coast of south Devon. The individual not touching others cannot raise its arms to feed or it will be swept away in the current whereas those holding on to other brittle-stars can feed (photograph G. F. Warner)

definition, survive in the population if the behaviour results in a net increase in the number of such genes. This is quite likely to happen because siblings are related by a factor of 0.5. Hence genes will spread if they promote altruistic acts which save two siblings so that they can produce viable offspring. In the same way, similar altruistic acts which save four grandchildren, nephews and nieces, or even eight cousins will be favoured. These ideas [12] have been elaborated with reference to social insects and the important possibilities of reciprocal altruism are under investigation [26]. All this leads to elaborate social behaviour. Experience certainly affects social behaviour in many ways and the necessity to learn complex relationships in long-lived social groups may have been the major factor, during evolution, in determining brain size.

All the topics mentioned in this article are explained at greater length elsewhere [27].

References

1. McFarland, D. J., 'How animal behaviour became a science', *New Sci.*, 1976, **72**, 376–9.
2. Finch, S. and G. Skinner, 'Some factors affecting the efficiency of water-traps for capturing cabbage root flies,' *Ann. Appl. Biol.*, 1974, **77**, 213–26.
3. Smith, J. N. M., 'The food searching behaviour of two European thrushes. I. Description and analysis of search paths', *Behaviour*, 1974, **48**, 276–302.
4. Hainsworth, F. R. and L. L. Wolf, 'Feeding: an ecological approach', *Adv. Study. Behav.*, 1979, **9**, 53–96.
5. Ewert, J.-P., 'The neural basis of visually guided behaviour', *Sc. Am.*, 1974, **230**, 34–42.
6. Gibson, E. J. and R. D. Walk, 'The visual cliff', *Sc. Am.*, April 1960.
7. McFarland, D. J., *Feedback Mechanisms in Animal Behaviour* (Academic Press, 1971).
8. Fentress, J. C. and F. P. Stillwell, 'Grammar of movement sequence in inbred mice', *Nature*, 1973, **244**, 52–3.
9. Sibly, R. and D. McFarland, 'A state-space approach to motivation', in *Motivational Control Systems Analysis*, ed. D. J. McFarland (Academic Press, 1974).
10. MacArthur, R. H. and E. R. Pianka, 'On the optimal use of a patchy environment', *Am. Nat.*, 1966, **102**, 381–3.
11. McCleery, R. H., 'Optimal behaviour sequences and decision making', in *Behavioural Ecology an Evolutionary Approach*, ed. J. R. Krebs and N. B. Davies (Blackwell, 1978).
12. Hamilton, W. D., 'The genetical evolution of social behaviour', *J. Theor. Biol.*, **1964**, **7**, 1–16.
13. Dawkins, R., 'Replicator selection and the extended phenotype', *Z. Tierpsychol*, 1978, **47**, 61–76.
14. Maynard Smith, J. and G. R. Price, 'The logic of animal conflicts', *Nature*, 1973, **246**, 15–18.
15. Yasukawa, K., 'A fair advantage in animal confrontations', *New Sci.*, 1979, **81**, 366–8.
16. Maynard Smith, J., 'Evolution and the theory of games', *Am. Sci.*, 1976, **64**, 41–5.
17. Dawkins, R., *The Selfish Gene* (Oxford University Press, 1976).
18. Hinde, R. A., 'Constraints on learning—an introduction to the problems', in *Constraints on Learning*, ed: R. A. Hinde and J. Stevenson Hinde (Academic Press, 1973).
19. Rozin, P. and J. W. Kalat, 'Specific hungers and poison avoidance as adaptive specializations of learning', *Psychol. Rev.*, 1971, **78**, 159–489.
20. Shettleworth, S. J., 'Food reinforcements and the organization of behaviour in golden hamsters', in *Constraints on Learning*, ed. R. A. Hinde and J. Stevenson Hinde (Academic Press, 1973).
21. Hinde, R. A., *Biological Bases of Human Social Behaviour* (McGraw-Hill, 1974).
22. Hamilton, W. D., 'Geometry of the selfish herd', *J. Theor. Biol.*, 1971, **31**, 295–311.
23. Ward, P. and A. Zahavi, 'The importance of certain assemblages of birds as "information centres" for food-finding', *Ibis*, 1973, **115**, 517–34.
24. Broom, D. M., 'Aggregation behaviour of the brittle-star *Ophiothrix fragilis*', *J. Mar. Biol. Ass. U.K.*, 1975, **55**, 191–7.
25. Warner, G. F., 'On the ecology of a dense bed of the brittle-star *Ophiothrix fragilis*', *J. Mar. Biol. Ass. (UK)*, 1971, **51**, 267–82.
26. Trivers, R. L., 'The evolution of reciprocal altruism', *Quart. Rev. Biol.*, 1971, **46**, 35–57.
27. Broom, D. M., *Biology of Behaviour* (Cambridge University Press, in press).