envelope by budding from the plasma membrane; HBVs are considerably smaller, with a glycosylated surface protein that can be independently secreted; and CaMV is a naked icosohedral nucleocapsid that accumulates in the intracellular inclusion bodies. On the other hand, the genetic organization of these viruses reinforces conviction in their similarities: in each case, all the known coding information is present in the single RNA strand thought to be used as template for DNA synthesis. Is it possible that the three classes have evolved from a common virus or cellular element, adopting very different strategies for entering and leaving host cells?

Before such elusive notions are considered, however, some straightforward enzymology is needed to place the new view of the CaMV life cycle on firmer ground. Unlike the situation with retroviruses or HBVs, DNA polymerase activity has not been described in mature CaMV particles, though there is recent rudimentary evidence for the predicted activities in extracts of infected leaves[10]. It is also not yet apparent whether the predicted enzyme is likely to be virus-encoded; however, most CaMV-coding domains are still unassigned[11]. It is difficult to imagine a more inviting target for a restless enzymologist. ☐

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Animal behaviour

From Skinner box to the field

from John R. Krebs

TEN years ago operant psychology and behavioural ecology would have seemed most improbable bedfellows; but a recent meeting* bringing practitioners of the two disciplines together showed that after all, *afficionados* of the Skinner box and field workers peering through binoculars at foraging animals in the wild are studying essentially similar problems. Operant psychologists have concerned themselves with elucidating the behavioural rules governing the relationship between reinforcement (often food) and response while behavioural ecologists have attempted to formulate and test general rules governing choice made by foraging animals between different kinds of prey or between differing feeding sites. There is an obvious parallel between choice by a pigeon in a Skinner box with two keys, one offering a food reward every 10 pecks and the other a reward every 100 pecks, and the choice of a wild pigeon to feed in a field replete with newly sown barley instead of a nearby field with a scattering of natural grass seed. There are good grounds for expecting the rules of choice to be similar in the two contexts, and exactly how similar was one of the discussion points of the meeting.

An important difference emerged in the kinds of models of choice developed by operant psychologists and behavioural ecologists. The former are interested in describing at the behavioural level the proximate rules or immediate criteria governing choice, while the latter model choice by trying to deduce from evolutionary first principles what the criteria of choice ought to be if the individual is to survive and do well in its natural environment. The behavioural ecologist might account for the pigeon's choice of the barley field or the high reward-rate key in the Skinner box by postulating that animals are designed by natural selection to forage efficiently, since efficient foraging ultimately reflects itself in reproductive success and survival. A mathematical model along these lines might be based on the hypothesis that choice maximizes overall rate of food intake, subject to some specified constraints. The operant psychologist's approach is to investigate the nature of immediate rules guiding the pigeon's choice — for example the pigeon might be influenced by the immediate probability of reinforcement at the two sites or by the rate over a short time period. The two kinds of explanation are not, of course, mutually exclusive and one might expect the animal's proximate rule for responding to be one which ultimately produces an adaptive outcome from the evolutionary stand-point.

A response rule discussed extensively at the meeting, first proposed by R.J. Herrnstein and W. Vaughan (in *Limits to Action*; ed. Staddon, J.E.R.; Academic, New York, 1980), is melioration, choosing the alternative with the higher (or highest in multiple choice) local rate of reinforcement. Given a standard criterion for defining 'local rate of reinforcement' melioration is quite successful in describing choice for food rewards offered on different schedules in a Skinner box. From the point of view of the behavioural ecologist it is interesting to note that an animal using melioration as its choice rule often ends up maximizing overall rate of reinforcement (or coming close to this) which is equivalent to the choice criterion of many ecological models of foraging. Experiments in which melioration does not lead to overall maximizing tend to be ones in which the animal is set a highly artificial choice task (for example, pecking at key A to get rewards from site B), in which the simple rule of thumb does not do well (Mazur, J.E. *Science* **214**, 823; 1981).

The complexities of food choice in the real world were illustrated by T.C. Moermond's and J. Denslow's (University of Wisconsin) account of neotropical frugivorous birds such as the genera *Euphonia* and *Manacus*. When tested in captivity with local fruits in Costa Rica the birds show transitive preferences in pair-wise choices (A>B>C) based on sugar concentration (high > low) or size (big > small). However when a large or sugar-rich fruit is made less accessible by hanging it below a perch, the bird's preference switches: rather than hang at full stretch below the perch to eat the big one (which they are physically capable of doing) the birds take the small fruit. Moermond and Denslow suggested that the energy- or nutrient-based preference is overcome because the birds avoid putting themselves in the vulnerable upside-down position. Psychologists such as R.J. Herrnstein (Harvard University) pointed out that these results could equally well be described by saying that the birds' choices are based on melioration and hanging the fruit below the branch decreases its reinforcement value. The problem with both accounts is that they are based on *post hoc* rationalization of the data. By careful analysis of costs and benefits in the field, behavioural ecologists hope that it may be possible to come up with *a priori* accounts of the rules of choice, based on functional considerations. ☐

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