The life of vertebrates and the survival value of intelligence

It may be a comforting and valid truism that the brain integrates and controls behaviour, but clearly we ought to be able to say something rather less vague in the context of the theories of brain evolution which I discussed in the last chapter. The basic biological requirements are to survive and multiply. Animals, both vertebrate and invertebrate, are distinguished first of all by movement, and this entails in itself a special imperative for the organisation of behaviour. Functions such as nutrition, excretion, respiration and reproduction are universal, and criteria based on the psychological processes by which these are accomplished are as important as any others for distinguishing animals from plants, vertebrates from invertebrates, and classes of vertebrate from each other. Our concern is whether there are systematic differences between vertebrate species in the way in which the brain operates, and more specifically whether there are differences between vertebrates which can be related to the high degree of intelligence we would like to attribute to animals most like ourselves. Some account must be taken then of the natural behavioural categories of moving, feeding and breeding—is there anything in these which implies an evolutionary necessity for the development of more and more elaborate psychological processes? First we might examine what ought to be a simpler question—is there any logical progression to improvements in the purely physical apparatus of the body which underlies a progression of methods by which it is governed?

Bodily evolution and brain evolution

Analysis of gradual improvements in bodily efficiency—via the evolution of better limbs, better digestive systems and so forth—is as fraught with theoretical difficulties as the argument for successive improvements in mental abilities (Simpson, 1953; Rensch, 1959). However, it is often stated that there is a phylogenetic trend towards physical independence from the environment. There are certainly particular instances, at least, where an emancipation from the demands of exterior geography seems to have occurred: amphibians and reptiles 'conquered the land'; the higher vertebrates, being warm-blooded, are less dependent on external temperature and climate. The distinction between the higher, warm-blooded (homiothermous) classes and the lower, cold-blooded
(poikilothermous) classes is especially interesting, as it provides a correlation between a major metabolic change and a possible psychological step. If there is a qualitative jump in psychological capacity from the cold-blooded reptiles to the warm-blooded birds and mammals, then an obvious hypothesis is that brain efficiency was in some way substantially improved by the faster energy metabolism of the latter. Since documenting the qualitative difference in brain efficiency in psychological terms is so difficult, such hypotheses are not easily tested.

However, a curious principle is illustrated by the shift to better internal temperature control, the principle being that the higher vertebrates can as readily be seen to have superior vegetative or mechanical properties as psychological or mental ones. The higher animals may have better ‘reflex programming’ as well as, or even instead of, improved cognitive abilities. Recent investigations of reptiles have shown that many species go to elaborate behavioural lengths to ensure a similar degree of control of internal temperature as that achieved much more easily by birds and mammals. Reptiles such as lizards and snakes may spend a considerable proportion of the day in basking in the sun, altering body posture, or else burrowing to cooler levels of sand, in order to maintain body temperature. I would argue that the brain functions required to govern these behaviours involve more, rather than less, cognition, compared to the methods of temperature control evolved later by mammals. These include shivering, raising and lowering of fur, sweating, and ‘non-shivering thermogenesis’ (internal metabolic production of heat): these are brainstem reflexes while the reptilian methods seem purposeful by comparison. The instrumentality of reptilian temperature-changing behaviours is attested to by large numbers of experiments in which external temperature is used as a goal to support learned artificial responses (Burghardt, L977). Lizards will learn to press levers to turn on a gently warming sun-lamp, and in other experiments have learned to respond appropriately to a buzzer used as a conditioned warning signal for an imminent unpleasant degree of heat (by moving out of the way in time—Yori, 1978). Mammals, of course, are just as capable of performing simple learned acts to ensure a comfortable external temperature: the point is that they have superior peripheral and autonomic methods of temperature control as well. It should be noted that perspiration is as much an indication of human uniqueness as the more valued faculty of inspiration in intellectual and artistic endeavours: anthropoid apes do not have sweat glands like ours and thus their skin is more obviously non-human than their brains (Weiner, 1971).

Specialised bodily devices to serve the needs of particular species are of course innumerable, from worm-like appendages which lure prey to the mouths of fishes and reptiles to the retractable claws of the cat family. It is not obvious that such specialisations follow progressive phylogenetic rules, or that they can be related to changes in brain organisation, although in many cases psychological
adaptations must exist to allow a species to take advantage of its external equipment. Two physical types of advance may be mentioned, however, which apply to vertebrate classes, and therefore might be considered to have phylogenetic implications, although in both cases the bodily mechanisms appear to simplify the demands placed on the brain.

First, the mechanical advantage of neutral buoyancy in water that is enjoyed by teleost fish has received many plaudits. Because of their possession of a ‘swim bladder’, relatively little body movement is needed to maintain orientation in modern teleosts. On the other hand, sharks and other elasmobranchs sink to the bottom if sufficient lift is not given by swimming movements. The hydrodynamics are pretty straightforward, but the central nervous system of sharks has to be capable of continuous operation in the case of swimming movements. The movement coordinating structure—the cerebellum—is extremely prominent in sharks, but this may have more to do with skill than with continuous operation.

Second, consider the task of programming reproductive behaviours in the higher vertebrates. The supreme evolutionary achievement of mammals could be said to be the development of psychologically foolproof reproductive devices, while birds need very elaborate behavioural organisation and control to achieve the same ends. The mammalian placenta and breast require minimal motor skills or cognitive sophistication for their effective deployment, and in the majority of species relieve the male from any parental responsibilities whatsoever. But the birds, lacking these organs, need behavioural programs for nest-building, and highly sophisticated strategies for incubation, then feeding, of the young. These activities typically require the active co-operation of both parents. Without labouring this point, it should be clear that the mammalian pattern of reproduction involves physical, as much as mental, adaptations, and that, rather than necessitating superior mental abilities, it could be argued that the physical evolution of mammals is such that fewer demands are placed on the brain. One has to say, therefore, that if mammals are cognitively superior to other classes, it is as much because the brain is freed from the more immediate biological duties as because features such as warm-bloodedness and breast-feeding would be logically impossible in the absence of superior intelligence.

Clearly, speculation about biological needs for intelligence is extremely hazardous. On the one hand, natural selection via the survival of the fittest seems to imply that everything that has evolved has been absolutely necessary for survival, and that anything inessential will eventually be lost. On the other hand, the most potent condition for adaptive radiation, and thus evolutionary invention, is lack of competition, when interesting divergences may be rewarded rather than punished (Rensch, 1959). It is perhaps a better universal rule that whatever is sufficient, survives: and the criterion for sufficiency is always a complex combination of habitat, relations with other species, and specialisation. Various sufficient
solutions to common problems of behavioural control may be achieved in different vertebrate (and invertebrate) classes; and therefore a statement of the problem does not imply a universal solution. Nevertheless, something may be gained from reviewing general categories of task which vertebrate life may present to the brain, and the most elementary categories are movement, food-finding, and reproduction.

Movement and knowledge of space

Seasonal migration, defence of home territory, and systematic search for food by foraging or predation are common vertebrate characteristics and may require navigational skills and spatial memory to varying degrees. One of the jobs of the vertebrate brain can therefore be said to be the detection and storage of geographical information and its use in directing locomotion. This is sometimes merely taken for granted, but a specific proposal is that mammalian brains at least are constructed so as to contain ‘cognitive maps’ of the outside world, which may be consulted as the need arises. The comparative question is whether fish, amphibians, reptiles and birds have less reliable or accurate maps, or some more primitive method of accomplishing adequate orientation in space. Migration and the defence of territory are not, of course, confined to mammals. Reproductive migrations occur in lampreys as well as, more dramatically, in eels and salmon and other teleost fish, and in some frogs, and reptiles such as the green turtle. This animal swims 3,000 miles to a small Pacific island to lay its eggs, the young then having to swim 3,000 miles back to the South American coast. It has been suggested that in this case the migration results from the geological movement of the breeding islands over many generations (Carr and Coleman, 1974).

If any class is especially prone to migrations, it is of course the birds, who possess the physical capacities for extensive travel, and have in some cases insectivorous feeding specialisations that make migration, if not hibernation (Aristotle’s explanation for the absence of swallows in winter), mandatory. The study of bird migration has tended to be a specialised subject area, not always fully examined for its psychological implications (Dorst, 1962; Mathews, 1955; Schmidt-Koenig, 1975; Schmidt-Koenig and Keeton, 1978). The main point is that behavioural programming by the central nervous system must be very considerable for any systematic migrations, but that some processes, such as the following of chemical traces suspected to be used by salmon, may be regarded as less complex than the celestial navigation and the use of memorised visual landmarks which are among the methods used by bird species. It is also important to note that birds are sometimes very flexible when it comes to migration—probably much more flexible than lower vertebrates. Many European species not dependent on summer flying insects appear to make individual or group decisions about
whether to make winter migrations, or stay put. The individual
decisions may be determined primarily by climate, since a major
source of variation is that the same species may have quite different
patterns of migration, depending on its breeding locations: the robin,
which sits through the winter months in England, abjures the more
severe Northern European winters, and migrates from Scandinavia
to North Africa, and to the Near East from Russia. This is not only a
matter of inherited regional differences, since in Germany some
robins migrate while others do not. In populations exhibiting this
sort of ‘partial migration’, there is usually a tendency for females to
travel more than males, and young birds sometimes migrate in
populations where the older birds are more sedentary.

In any event it is clear that avian brain design must incorporate a
substantial capacity for storing geographical information, and this
may be done in a more sophisticated way than that employed by
lower vertebrates. Little is known of what brain structures might be
involved in the direction of bird migrations, although in mammals
the hippocampus is supposed to be the major repository for spatial
information (O’Keefe and Nadel, 1978). The spatial functions of the
hippocampus have not been investigated in other vertebrates, and it
does not appear to be anatomically prominent in birds (Pearson,
1972), but it is a reasonable guess to suppose that forebrain
structures play some part in navigation and landmark recognition in
birds, if not in all vertebrates.

As always, the problem is that species with what we would
assume are vastly different cognitive capacities display superficially
similar behavioural patterns—I strongly suspect that the
psychological mechanisms used to direct long-distance travel in the
robin are more complex than those utilised by the eel, but I cannot
prove it. Long distance migration is perhaps the most spectacular
example of a behavioural ability which is difficult to tie down in
terms of cognitive aspects of brain function, but spatial ability in
general tends to share this feature. Movement in space is an ever-
present part of animal life, and so one can hardly claim that
advanced cognitive mechanisms are necessary to achieve it.

Another conventional subdivision of spatially-directed
behaviour, apart from migration, is ‘territoriality’. This has been
widely canvassed as an underlying motivational factor in animal
behaviour, but rather less attention has been given to the intellectual
requirements of categorising geographical stimuli sufficiently well
for them to acquire their emotional significance. Even for
invertebrates, some sort of home base can be seen to direct
movements, as in the systematic, if slow, peregrinations of limpets
to and from the same spot (the consensus is that limpets and other
molluscs follow their own mucus trails on their homeward journeys;
Cook and Cook, 1975; Mackay and Underwood, 1977). The
occurrence of such apparent spatial competence in organisms with
little apparent means of neurological

support should be a caution against reading too much into the spatial
characteristics of movement in lower vertebrates, but territory
defence in the stickleback, whose behaviour is relatively well
known (Tinbergen, 1951; Van Iersel, 1953), goes beyond limpet-
like routines, since it involves constructed, visually detected
landmarks. The male stickleback digs out small holes around the
circumference of its territory as a by-product of social interactions
with its neighbours—border disputes include mutual digging
activities. In a sense the most ubiquitous territorial landmark is other
species-members—if a certain distance is always kept between
individuals, this in itself establishes ‘personal space’. Particular
instinctive cues may simplify the task of species recognition: colour
(redness for the robin and stickleback); vocalisation, pre-eminently
in bird-song but also in frogs; and scent—many mammalian species
have scent glands which are rubbed on the ground or on trees to
provide cues of location and possession, or an economy is achieved
by pressing other bodily functions into geographical service, as in
the pungent urination of dogs and cats. One might ask, to what
extent does the olfactory discrimination of the social significance of
urine by dogs demand higher cognitive capacities than the use of
colour by fish? Phylogenetic theory would imply that social
interactions in fish are reflexive and mechanical, whereas
mammalian behaviour must be more flexible and cognitive. This
might be supportable by sufficiently detailed experimental
comparisons, and we should expect to be able to show higher
divisions of the brain are involved in the territorial behaviour of
mammals. However, such sketchy data as exist suggest that it would
be premature to assume that territorial behaviour in fish is under the
control of the brainstem, whereas leg-cocking in dogs is cortical: it
has been found both that subcortical mechanisms are involved in the
sociosexual behaviour of dogs and that forebrain centres regulate
instinctive behaviour in fish (Hart, 1974; Aronson, 1970).

It is worth putting in another word at this point about the
bird/mammal distinction. Birds display a very noticeable collection
of complex species-specific behaviours, and thus have often been
regarded as being dominated by fixed and stereotyped instincts,
‘with little of the learning capacity which in mammals is associated
with the development of the expanded cerebral cortex’ (Romer,
1949, p. 585). I shall discuss later ( Chapters 7 and 8) the
performance of birds on laboratory tests of learning, but we can note
here the considerable flexibility of many avian species in selection
of breeding habitat—in

particular their use of the human urban environment. The
resemblance of buildings to cliffs is probably responsible for the
large urban populations of pigeons and house-martins, but even so,
the shift from cliffs to cities implies a certain range within any
stereotopy adapted originally to a particular type of territory. The
rapidity of the transition of a species to a man-made adaptive zone is
illustrated by the herring gull, whose ‘fixed action patterns’ of social
behaviour were documented by Tinbergen (1953) on sand dunes in
Holland, but which has been seen in growing numbers as a roof-top
nester in coastal towns in Britain (and in Central London) during the
last few years. Gulls nest on cliffs, as well as on dunes, and so could be said to be capitalising on natural instincts; but the capability to nest and establish family and flock social organisation on either dunes, cliffs, or town buildings, suggests some rather more subtle adjustments to ecological opportunities than would be provided by a very rigid set of fixed behavioural patterns.

A distinction needs to be made, of course, between adjustments to new environments by genetic change through selection, which may occur in the simplest of organisms (as in the emergence of drug-resistant strains of bacteria) and the behavioural variations possible within a genetically homogeneous population. One interpretation of the advantages of a larger or better central nervous system is that the same brain can cope with a wider range of environments—either by containing a larger set of instinctive behaviours, or by providing the means for learning from experience.

**Locomotor and manipulative skills**

Given that movement in space occurs at all, a further variable is simply mode of locomotion. The biologically most primitive way of getting about for vertebrates is the lamprey-like undulation of a long body, used by many invertebrates, and returned to successfully by eels and snakes. The emergence of paired fins, and then paired limbs, has been thought to require more sophisticated muscular control, but the spinal cord and hindbrain alone can accomplish a satisfactory degree of limb co-ordination: birds whose forebrains have been removed can manage flight, as well as bi-pedal walking (though not the trickier manoeuvres of take-off and landing). It might be suspected that the primate facility for tree-climbing and two-legged running should be associated with outstanding brain power, but both activities are performed with considerable success by lizards.

The prominence of the cerebellum in the delicate programming of postural balance and rapid movements has already been alluded to, and is usually confirmed by at least temporary motor incapacities following cerebellar lesions. Considerable recovery of ability often follows initial losses due to cerebellar lesions, however, even in the case of climbing by racoons or primates (Wirth and O’Leary, 1974). A strong anatomical case can still be made for the encephalisation of motor control in mammals, because of the presence of the pyramidal tract direct from the motor cortex to the spinal cord. This is not an absolutely clear mammalian prerogative since analogous, if less substantial, connections have turned up in birds and reptiles, and even sharks (Ebner, 1976; Ebbesson and Northcutt, 1976). It has always been obvious that shark, teleost, reptile, bird and mammalian brains can all be used for fast swimming, just as analogous streamlining of the body has evolved in the relevant species, but the acrobatics of dolphins and seals may manifest an additional dimension of muscular control superimposed on the basic necessities by large mammalian brains.
It is possible that higher vertebrates in general are capable of more complex motor control than lower, and have more varied methods of locomotion available within a single species. One could cite in support of this the multiple gaits of horses, or the walking, running, climbing and swimming of man, and the rat. But to be fair, one would also have to consider the multimodal locomotion of the duck, which can swim, dive, walk and fly, and the frog, which can both jump and swim. Reptiles, though often appearing ungainly, can show a good turn of speed when necessary. Crocodilians and turtles are elegant and skilled underwater, if clumsy on land, and the change of gear from slow four-legged walking to fast two-legged running in frilled lizards may be an example of reasonably complex reptilian locomotion. Fish might be thought limited by their watery environment, but some species (e.g. lung-fish and mud-skippers) have useful if rudimentary land-going abilities. Lampreys as well as salmon leap into the air in the course of their up-river migrations, and the flying fish can traverse up to 400 metres in a single airborne glide. Even casual observation of a domestic goldfish is sufficient to reveal an extraordinary number of combinations of fin and tail movements. It is thus difficult to be convinced that complexity of locomotion as such was the driving force behind brain evolution.

Manipulation may be a special category of muscular co-ordination. Primate handgrips of varying degrees of precision have been the subject of detailed study (Napier, 1960) and the use of the forelimbs for manipulation rather than locomotion has been given considerable emphasis in theories of the origin of human intelligence. In general higher vertebrates use all four limbs for locomotion but both primates and rodents (and dinosaurs and kangaroos) use the forelimbs also for pushing, holding or digging. As rodents are usually thought of as a rather lowly order of mammals, the fact that they possess manipulatory skills provides another perturbation on the phylogenetic scale. Beavers rival birds in instinctive architectural abilities and young mice and rats can be surprisingly adept at ape-like brachiation, when they swing from the roof bars of cages, or are trained to climb wires. Some aspects of manipulation in mammals are undoubtedly controlled by the pyramidal tract from the cerebral motor cortex. Heffner and Masterton (1975) rated 69 species of mammal for ‘digital dexterity’ and found a correspondence between this rating and the anatomical intimacy of pyramidal fibre terminations with spinal motor neurons, although there was no correlation with the thickness of the tract. Either the lack of forelimbs or the absence of the pyramidal tract may preclude manual dexterity, but the emphasis on hands may be slightly misleading, since it disguises the fact that the behavioural purposes served by the forelimbs are in some vertebrates equally well administered by the nose, mouth, trunk or bill. Among mammals, the trunk of the elephant and the nose of the dolphin may be exceptional, but many herbivores use snout, horns or lips in a manipulatory fashion (the llama has independently mobile separate halves of the upper lip and, in each cerebral hemisphere large independent somato-sensory projections for the ipsi- and contra-
In birds the bill is a manipulatory device, and an extremely effective one for use in nest-building, food carrying, preening, digging and tool handling (in the Galapagos finch/woodpecker). Two examples may be given to illustrate interesting analogies between bill-use and hand-use. The European oystercatcher uses its bill to open up shell fish—a task requiring some skill in humans equipped with a hand and a knife. The unexpected aspect of this is that it is a learned rather than inborn skill in the oystercatcher, with the magnitude of the educational problem indicated by the need for several months of supervision and supplementary feeding of the young by the parents, by the variation in the opening techniques finally mastered, and, most emphatically, by the high mortality rate among slow learners (Norton-Griffiths, 1969). Given the high mortality rate in the young who never learn the shell opening skill, one would have thought that oystercatchers should be in the throes of developing a stereotyped and species-specific fixed action-pattern for this purpose, but the advantages of trial-and-error learning over fixed instincts may be manifested in the fact that the oystercatchers studied by Norton-Griffiths were feeding on mussels, not oysters: trial-and-error allows more ecological flexibility. An apparently unique lack of flexibility in bill-use occurs in the New Zealand wryneck, whose beak curves strongly to the right. This kind of built-in ‘handedness’ is extremely rare in vertebrates, and appears to be associated with the manipulation of pebbles: the wryneck inserts its bill under the left side of pebbles and turns them over to the right.

Many species of fish manipulate stones or vegetation, either in the course of foraging, or more elaborately in the construction of nests. The mouth in these species is the manipulatory organ —fish mouths are obviously not the equivalent of bird bills in this respect but some fish, including the much-studied stickleback, build quite respectable nests. Modern reptiles do not appear to utilise manipulative skills in any sense of the term, and heaps of vegetation (cobras) and holes in sand (turtles) represent the extremes of reptile nest-building. But numerous extinct reptiles including many dinosaurs and many species implicated in mammalian evolution (therapsids) are assumed to have walked on their hind legs, and to have had forelimbs specialised for manipulative clawing. Control of forelimb movements is no doubt more skilled and expert in mammals such as rodents and primates (and in carnivores like bears and raccoons) than it was in extinct reptiles. But detailed control of head movements, involving the cranial nerves, is also an example of sophisticated motor programming, especially in birds.

**Feeding strategies**

Type of feeding is one of the major candidates for the determination of behaviours by aspects of ecology, as opposed to
The broadest distinction can be made between carnivorous and herbivorous habits, but there are several useful subcategories within each of these, and a further line to be drawn between specialised and omnivorous species. The first point is that most types of feeding occur within each extant vertebrate class, with the possible exception of modern amphibians (the initial amphibian radiation having become largely extinct). Quite clearly different problems of behavioural control are presented by reliance on an unconcentrated but stationary diet of grass or leaves on the one hand, and a specialisation in catching highly nutritious but alert and mobile prey, on the other. But both types of problem have been effectively solved in fish, reptiles, birds and mammals. All these classes include foragers and browsers, and predators of various kinds. A meaty diet will not involve the excitements of the chase if it is acquired by scavenging on already dead prey or on shellfish. But capture by stalking, chasing or ambush is sometimes supposed to require the development of cunning or intelligence. A standard explanation for the explosion of human intelligence beyond the already high standards of the primate order is that our ancestors underwent an ecological transition from a fruit eating arboreal primate, via a foraging terrestrial ape, to a cooperative hunting hominid (Jolly, 1972; Pilbeam, 1972).

Intelligent and co-operative pack hunting is found in wolves and other canids, but pack hunting as such works successfully in dogfish and the teleost barracuda (although claims of intelligent herding or ‘nursing’ of prey by sharks and barracuda should perhaps be treated sceptically). It is curious that although birds are often intensely social and communicative, there do not appear to be any co-operative hunting species, although there is often group activity for defence against predators (mobbing) and some hawks and falcons, as well as vultures, have very gregarious habits. Solitary ambush and stalking may be associated with cunning or foresight when these techniques are utilised by mammals, but individual hunters such as the pike or eagle (or any number of lower vertebrate or invertebrate predators) may occupy a similar ecological niche without the benefits of mammalian cognition. The main assumption is that mammalian predators depend more on learning, and the practising of their skills, especially through play, while those in other classes rely on fixed instincts of attack. However, many attack patterns are definitely inborn in mammalian carnivores, since appropriate behaviours can be elicited by the electrical stimulation of the brains of naive animals (Roberts and Berquist, 1968) and species-specific actions such as neck-biting can appear fully-formed without practice, as has been observed in the polecat (Ewer, 1973). No doubt parental tutelage, and practice, refines these skills.

Clearly intelligence is not a necessary condition for ecological status as a predator, and thus if intelligence of some kind is associated with mammalian hunting practices, it is the phylogenetic mammalian
characteristic, rather than the ecological role, which is important. Even if it were possible to show that it was the requirements of hunting which led to the development of cunning and foresight in mammalian carnivores, this would still leave the problem of how to account for the brains of mammalian herbivores. Consumption of vegetation often sustains large bodies, and as a consequence some mammalian herbivores, such as the elephant and elk, have enormous and elaborately convoluted brains. In my view it is unnecessary to try and identify ecological needs served by these large brains, since I believe that their size and organisation are determined mainly by phylogenetic factors—any large mammal will have one. However, it has been suggested that brain power in mammalian herbivores can be put to the uses of (a) defence against predators (Jerison, 1973); (b) locating and remembering sources of food; and (c) maintaining social organisations which facilitate (a) and (b).

There are special difficulties in accounting for why primates should require more brain power than other orders of mammals, and in assigning the human-like brains of the great apes ecological causes. Because of its large size the gorilla suffers from little predation and the adult orang-utan prefers solitude to elaborate social interactions. Although the gorilla forms ‘extended family’ social groups, interactions within these groups are not noticeably more complex than those found in lizards, chickens or rodents. Gorillas also appear to be less playful and curious than their smaller relatives, the chimpanzees, their daily life being a repetitive round of eating, digesting and heedlessly defecating enormous quantities of vegetable matter (Schaller, 1963). Several observers have concluded that the gorilla is a stupid animal, but training with gestural sign-language suggests that it has abilities equivalent to those of the more obviously alert chimpanzee (Patterson, 1978) and the development of cognitive capacities during the first 18 months of life is much the same in gorilla and human infants (Redshaw, 1978). Although we might expect that such measured intelligence should exist because of its survival value to the species, the lifestyle of the gorilla suggests a contrary hypothesis—that intelligence as assessed by these methods is purely incidental to the ecological niche occupied by the species.

The problem of apparently useless organs is not unfamiliar in evolutionary theory—blind species may retain eyes, and appendages such as the antlers of deer may reach a size out of all proportion to their superficial usefulness. It often has to be assumed that vestigial organs or other anatomical features are retained only because they are genetically linked to other more useful structures (Simpson, 1953), and Darwin supposed that some anomalies, such as the webbed feet of nonaquatic geese, were evolutionary accidents, supporting the haphazard element in natural selection. Darwin’s alternative explanation for anatomy or behaviour that lacked conspicuous survival value was that it arises from sexual selection, which may be at odds with more mundane utility. The antlers of deer are selected
for during male competition for females (predators being kicked rather than butted). Sexual benefit may outweigh other biological costs, or species may be sufficiently well adapted to carry otherwise unnecessary secondary sexual apparatus. Conceivably, therefore, some form of sexual selection acts on primate intelligence. In the case of the gorilla, at least, the social structure revolves around a dominant male, who has first call on both food and sexual partners (Schaller, 1963). However sexual activity itself is extremely perfunctory and infrequent in gorillas, and so sexual competition between males is not a very obvious factor.

To return to feeding strategies, the gorilla is an example of a species with quite a varied diet, even though it only eats plants. In general it is assumed that omnivorous species need to be more flexible in their food selection, and more amenable to trial-and-error learning, than specialised feeders. As many as 100 different plant species may be eaten by the gorilla (Schaller, 1963) and perceptual identification of these, together with knowledge of their location and the season when they are available, and the skills involved in their collection (such as tree-climbing, bark stripping and digging), could be put forward as the tasks to which gorilla intelligence is directed. Classification of plant species has sometimes been said by anthropologists to be an early and important form of human cognition (Levi-Strauss, 1962) and it might not be too far-fetched to consider gorilla communities as utilising a similar kind of knowledge, in a non-verbal form. Among birds, the crow family have large brains for their size, and typically consume a wide range of edible materials. Jackdaws for instance may take eggs or young from other birds’ nests, pick insects from the backs of sheep, and forage for fruit, worms, shoots and grain, and anything else that is going. Such habits are sometimes said to be indicative of advanced phylogenetic status. But many birds have similarly catholic tastes, especially those commensal with man such as sparrows, pigeons and seagulls. There are plenty of omnivorous or scavenging fish, and modern amphibians have been characterised as ‘not particular in choice of diet’ (Young, 1962).

At one end of any dimension based on diet selection one would have to put filter-feeding Baleen whales, possessors of the largest known brains, whose feeding strategy of swimming with an open mouth through seas rich in small invertebrates seems almost equivalent to breathing food, and would hardly be put at the top of a list of activities requiring high brain power. Similarly, living in trees and eating whatever leaves and fruit come to hand seems an undemanding, even idyllic, existence. But this is a rough description of the ecological niche of South American monkeys, and a fairly accurate account of the feeding habits of one such species, the Howler monkey, which is the fortunate beneficiary of a digestive system which can cope with mature leaves and unripe fruit, as well as more palatable ripe and juicy fruit and tender shoots and buds. Typically tree-living primates drop half their food to the ground, and eat only a small fraction of what is readily available—they are
not ‘food-limited’ (Jolly, 1972). This relationship to the food supply does not suggest a selection pressure to evolve intelligence in order to gather food more efficiently. If anything it prompts the speculation that the lack of selection pressure allowed the emergence of primate intelligence as a luxury not available to species more hard-pressed. Cognition may, like other civilised pursuits, be a product of surplus, leisure and excess, and not a consequence of struggle, deprivation and need.

In any event, the idea that diet determines destiny, in terms of brain evolution, is difficult to sustain except by hand-picked examples. The most common example has it that man shares intelligence with primates because of arboreal fruit-eating, and with wolves because of co-operative game hunting. But there is little systematic evidence that fruit-eating, or hunting, is associated with intelligence in other instances. Even the more general idea that flexibility in diet selection is somehow correlated with brain development runs into difficulties in accounting for apparently intelligent specialists (aquatic mammalian fish-eaters) and comparatively dull all-rounders (such as the rat).

Reproduction and other social interactions

Reproduction, and genetic reduplication, must be the most fundamental of all biological imperatives. The reproductive success of a species, more than anything else, is of immediate importance for its survival and adaptive evolution. It is therefore worth asking whether reproductive strategies have any bearing on brain evolution. The aspect of reproduction which at first sight has phylogenetic implications is parental care, since this is prominent in mammals and birds but relatively rare in lower vertebrates. Except in very unusual cases, fertilisation, usually via copulation, is indispensable for all vertebrates, but courtship and mating take various forms, ranging from completely indiscriminate mating with external fertilisation in many teleost fish, to elaborate courtship with permanent pairing of the couple, which is common in birds and occurs occasionally in mammals. It should come as no surprise that there is no clear correlation between reproductive strategy and phylogenetic status.

Cyclostomes

The sexual behaviour of lampreys is relatively well known, and certainly involves minimal post-natal parental duties, since the two adults invariably die after mating (Breder and Rosen, 1966). Marine lampreys migrate up rivers, in some species several hundred miles, to mate. Although these fish represent the most primitive vertebrates, there is an interesting complication in their mating, since they construct, sometimes communally, circular egg-laying sites. The lampreys make use of their jawless sucking mouths to remove quite large stones from the circular area, and place them
round the circumference to form a low parapet. If enough stones are available, some are also used to form a barrier upstream from the circle. A single pair or, more often, several pairs, share in the construction of this spawning site: recognition of species and sexual identity is an obvious perceptual requirement, and is probably aided in many species of lamprey by colour cues, since variegated colouring appears during the reproductive season. The motor coordination needed for copulatory spawning is simplified by the male being able to attach its mouth to the female’s head. Excited, violent and repeated copulation, which produces synchronised ejaculations of eggs and sperm, begins on completion of the nest construction, and extends to permutations of couplings when several pairs have made the same site. These ritual acts of the most primitive vertebrates, taking place within a laboriously constructed circle of standing stones, are strangely reminiscent of some ideas about human Mesolithic relics such as Stonehenge. Without succumbing to biological mysticism, it is possible to point out that migration, colour vision and social co-operation to produce constructed environments appear at the lowest phylogenetic vertebrate stage that we can now observe. This should emphasise that we must look for subtle changes in the cognitive control available to other species, and that a behaviourist principle of examining only the most superficial characteristics of actions is likely to be of little use in the comparative study of brain evolution.

Sharks

The reproductive biology of sharks poses another problem for theories of progression in phylogeny, since it is evident from the existence of male intromittive organs that fossil sharks relied on internal fertilisation, and modern sharks either lay skinned, reptile-like eggs or, in other species, give birth to live young. In some of these the foetal young are nourished by a mammal-like placental organ. The psychological implications of this ‘advanced’ biology are not clear, since there is no reason why reproductive sophistication should not be accompanied by primitive behavioural reflexes. It is maintained that no parental behaviour occurs in sharks, but this is based on lack of observations of the newborn, rather than positive identification of parental apathy (Breder and Rosen, 1966). If we were to use the argument popularised by Dawkins (1976b; Hamilton, 1964) we would expect that the investment of the genes in internal fertilisation and maternal nourishment during gestation should be followed by protective parental behaviour to guarantee reproductive dividends. For instance, the basking shark, a large filter-feeder, endures a pregnancy of two years to produce a single offspring. It would seem foolishly parsimonious not to program some maternal interest in the post-natal welfare of the infant. In fact it is suggested that female sharks generally do indeed seek out favourably shallow waters in which to give birth, but it would not be surprising if some social
interaction between mother and infant were eventually to be discovered.

**Reptiles**

This last guess is nourished by the fallibility of the traditional belief in the incapacity of reptiles for parental responsibilities. It is true that in the case of the vast majority of modern reptile species biologists pay far more attention to the reptilian amniote eggs (as the precursor of the reproductive methods of higher vertebrates) than do the reptile parents. Nevertheless, forms of incubation of the eggs are found in some species of the squamata (lizards and snakes) and elaborate parental care occurs, it is now believed, in most crocodilians. The Nile crocodile mother guards with a high degree of maternal intensity the mud nest in which the eggs have been laid, responds to vocalisations from the young to assist emergence from the eggs, and then ensures their safe transition to water by carrying them to it in her mouth (Pooley, 1977). One cannot claim, then, that the reptile brain as such is incapable of sustaining maternal instincts.

**Teleost fish and amphibians**

Reproductive habits in these lower vertebrates are marked by incredible diversity, and it is certainly not possible that they suffer from behavioural simplicity. Extensive accounts are available (Breder and Rosen, 1966; Noble, 1931) but we may note the well-documented responsibilities of the male stickleback for nest-building, egg-fanning, and nest-protection, and the organised vocal competitiveness of many anurans (frogs and toads) during courtship. In non-mammals the female is not anatomically predestined to provide post-natal care for the young, and most conceivable possibilities of single-parent and two-parent involvement with eggs and young can be found in some or other teleost or amphibian species. Mouthbreeding, and production of milk-like secretions by both parents are examples from teleosts, and in amphibians, though typically neo-natal survival is guaranteed by large numbers of free-swimming larvae, there are salamanders which are viviparous, a tree-frog in which eggs develop in a womb-like sac under the skin of the mother’s back, and a tongueless aquatic South American toad (*Pipa*) in which the young grow in individual pits in the mother’s back, emerging only when metamorphosis is complete. In other such ‘marsupial’ species of toad the bearing of the young, either on the back or, less conveniently, in the mouth, may be the prerogative of the father; similarly in the European ‘midwife’ toad (under suspicion of non-Darwinian tendencies for other reasons) it is the male which carries the eggs wrapped around its legs for safe-keeping.

**Birds**
The extremely taxing parental duties of most birds are attributable perhaps to the liabilities of warm-bloodedness in the absence of mammalian organs for the internal and external nutrition of the young. Behaviourally a binary division has been made between altricial (or nidiculous) avian species, in which the relatively helpless young are fed in the nest for protracted periods, and those which are precocial (or nidifugous), where more mobile young can leave the nest immediately after hatching to search for their own food. In these latter, the connection between parent and young is not broken after hatching: considerable interest has been attracted to the apparently haphazard process by which the young form social attachments to (usually) the female parent during the first day or so of their posthatching life. The interest is in the importance of individual experiences: the young will ‘imprint’ on almost any suitably sized, but preferably moving object which is presented to them during the ‘critical period’ (Sluckin, 1964; Hind; 1970). In other words, there is little in the young by way of an instinctual perceptual image of the species parent, and it is left largely to chance that the thing they imprint upon will have appropriate social consequences—but of course in the absence of human intervention this is usually a fairly safe bet.

Partial features of the natural parent may assist the imprinting process, especially in ducks, where the ‘following response’, which is the initial behaviour required, is elicited more readily if a waddling movement and a regular quack-like sound accompany the artificial stimulus-object used in imprinting experiments (Ramsay and Hess, 1954; Hess, 1959). However, the crucial psychological mechanism appears to be the formation of a memory of whatever is responded to first during the first few hours when movement is possible after hatching, and this allows for unnatural stimuli to be substituted for the species parent (notably the figure of the ethologist Konrad Lorenz, who first drew attention to the phenomenon).

In the case of nest-rearing species, it is the natural instinctual cues which elicit the responses given by the infants to the parents which are given pride of place. The classic ethological studies of nestling herring gulls and thrushes by Tinbergen showed that certain visual cues in the profile of the adult’s head are crucial ‘trigger features’ which elicit the begging responses of the young. These in turn stimulate the adults to place food into the mouths of the most insistent nestlings, if necessary after first regurgitating it. In the herring gull, the trigger features which attract the young’s response of pecking at the parent’s bill include the redness and contrast of a small patch on the bill, to which pecking is directed. There are certain variations in such stimulus factors among even closely related species of gull (Weidmann, 1961)

but begging and parental feeding show some constancies in form over many groups of altricial birds, which is sufficient to ensure
cuckoos a choice of foster-parents. Transfer of affectionate and
caring emotions across species is of course not unknown in
mammals and in primates: Tinbergen has gone as far as to suggest
that there are aspects of the appearance of the young which have
very general effects in calling forth appropriate emotions in adults—
in mammals he supposes that smallness of the body and roundness
of the head serve as ‘releasing stimuli’ of this kind.

The finding that there appear to exist instinctively coded
stimulus response connections in young birds was used by
Tinbergen (1951) to support his concept of the ‘Innate Releasing
Mechanism’: this idea is simply that particular vertebrate species
will respond in fixed ways to only Certain innately determined
stimuli. The impression that only rigid inbuilt reflexes are available
to the species studied is, however, false. A careful reading of
Tinbergen’s methods reveals evidence of the normal plasticity and
change in ‘species- specific’ behaviours due to individual
experience which is not always made use of in ethological
theorising. For instance, Tinbergen and Kuenen (1957) reported that
they used great caution in feeding young thrushes during tests of
their reactions to artificial stimuli, since if a very natural stimulus
was presented without subsequent feeding the infants very quickly
refused to respond to it as they should, whereas if by chance a
‘wrong’ stimulus was given just before feeding, the fledglings
tended to treat the wrong stimulus thereafter as a natural releaser.
There is no reason to doubt that nestlings come equipped with
appropriate instinctive preferences, but the readiness of nestlings to
learn at least as flexibly as precocial young in reaction to novel
experiences is often ignored (Eibl-Eibesfeldt, 1970). Conversely,
precocial young have need of instinctual preferences and fixed
action patterns if they are to be successful in their first foragings for
food. Mallard ducklings have been shown to have a preference for
pecking at green, rather than at other hues, which is rather
unexpected, since they initially eat dark invertebrates and not green
vegetation; but it is conceivable that reactions towards greenness
assist in directing their behaviour to where these may be found
(Oppenheim, 1968).

In general, the social interactions of parents and young suggest
that the brains of birds must encode a considerable amount of innate
information in terms of both releasing stimuli and the organisation
of instinctive fixed-action patterns. However, these brains must also
be

well adapted to the behaviour-controlling method of learning from
experience. Apart from the refinement of motor skills, the main
category of experiential learning involves perceptual recognition of
known objects. The imprinting process in precocials such as young
geese or chickens is a clear example of this, but it is likely that
young nestlings often learn to recognise their own parents. In
herring gulls the young learn to recognise the individual
vocalisations of their own parents (Tinbergen, 1953; this also occurs
in term—Stevenson et al., 1970).
The use of vocalisation in birds for species and individual recognition and for social communication is of course a rich and highly specialised area of study (Thorpe, 1961), and is not exclusively related to reproduction, but I would like to draw on it here for implications concerning the capacities of bird brains. First, bird vocalisation clearly requires elaborate control of the vocal organs, and there must be similarly complex auditory analyses for the recognition of distant songs and chirps, and for the monitoring of self-produced output. As we have seen, there is evidence that in some species at least the two halves of the brain are unequally involved in the control of vocalisation (Nottebohm, 1977), a design characteristic which is also typical of the human brain. A further question is whether the efficiency of bird vocalisation is determined by in-built genetic specification, or whether it is educable by individual experience alone—this also has some interest in the context of debate about the neurological underpinnings of the complexities of human language (Lenneberg, 1967). A subtle balance of advantages between reliable and rigid pre-wiring of behavioural outcomes on the one hand, and the variable but plastic results of determination by experiential factors on the other, is illustrated by the varying weights attached to these two influences on vocalisation in different bird species. At one extreme young birds completely isolated from all external sounds, from birth, are able to produce extremely complex songs specific to their species, given time for maturation and individual practice (for example, the song sparrow; Mulligan, 1966). More commonly, a rudimentary version of natural songs (or a complete vocal repertoire in species with only a crude range of sounds) may be possible in individual birds deprived of the opportunity for vocal learning. Sound production of this kind may occur even when individuals are isolated from the sound of their own voice, by neo-natal deafening (deafened juncos and white-crowned sparrows produce rudimentary songs --- Konishi, 1963, 1965; domestic chickens and ring-doves show a relatively complete range of species-specific vocalisations after neo-natal deafening---Konishi and Nottebohm, 1969). In some species, young reared in groups but isolated from adults can develop normal species-specific songs by singing at each other, even though individuals reared alone produce abnormal and idiosyncratic sounds (white-crowned sparrows---Marler, 1970). In all these cases the species involved are obviously relying to a large degree on genetic inheritance of detailed motor patterns, or of ‘auditory templates’ as the goals for vocal practice (Marler, 1970). This is probably more a matter of executive brain routines than peripheral constraints in the sound-producing apparatus, since the structure of the distinctive avian sound-producing device, the syrinx, changes very little from species to species.

At the other extreme, imitating species such as parrots and mynah birds quite clearly are capable of producing sounds that are not genetically programmed. It now seems likely that these species are not so unusual in their capacity for auditory imitation as they are
in their readiness to use human sounds as their model. Many other species pick up sounds as they go along, but imitate conspecifics, which makes the imitation very much less obvious to the human observer (Marler, 1970; Waser and Marler, 1977). The functions of vocalisation include isolation of local groups within a particular species as well as species recognition and the identification of individuals: the function of imitation is presumably partly to promote the learning of local or familial dialects. Various aspects of the auditory pattern may be used for different purposes: the decision ‘that is not my species’ must be a lot easier than ‘this is an unfamiliar member of my tribe of my species’. For species recognition, genetically built-in determinants of vocal production and auditory perception is a possibility and very rapid learning of slight individual variations may be imposed on this. The speed with which recognition of individual parents can be acquired is illustrated by the ‘His Master’s Voice’ experiments performed by Stevenson et al. (1970) on young terns: these responded immediately to tape-recordings of their own parents (by cheeping a greeting, and walking towards the loudspeaker) but ignored other tern calls, even those recorded from other adult members of their own colony.

Vocal recognition among the adults of some species may be more arduously acquired. There is an East African shrike in which two members of a pair learn to duet with one another and, while adopting certain phrases and rhythms which are characteristic of the locality, work out between themselves duets which are sufficiently individual to enable the bird to distinguish and keep contact with its mate by singing duets with it (or, to be more exact, singing antiphonally with it) in the dense vegetation in which they usually live. (Thorpe, 1974, p. 116: see Thorpe, 1966, 1972)

This involves a clear element of song composition in addition to imitation. However, both the composition and the imitation are constrained within a range peculiar to the species. In general, if imitation in any species is to be useful, it is important for the young to imitate the right thing. Marler (1970) refers to the inherited ‘auditory template’, which may not be sufficient to generate complete song in isolated birds, but enables young in the natural environment to single out the noises produced by their own species instead of trying to imitate the entire dawn chorus. The experimental basis for this concept is that isolated white-crowned sparrows learned by imitation if they were played tape-recordings of adult song of their own species, but paid little attention to the songs of other species. The force of the concept is therefore attenuated by the fact that the experiments were performed on nestlings which had had several days of natural existence—and feeding by their natural parents—before they were removed from the nest and artificially reared (Marler, 1970). Bearing in mind the extreme rapidity of visual imprinting in ducks and geese, and of visual learning in nestling thrushes (Tinbergen and Kuenen, 1957) and that term appear to recognise the individual voice of their parents when only four days old (Stevenson et al., 1970), early experience in the nest could be at least partly responsible for the later recognition of species-specific song in white-crowned sparrows.
However, it is a safe generalisation that innate factors at least partly determine the form of song in most species; but that it is also very common for young birds to imitate the vocalisations of individuals with whom they have social interactions. This may in some degree be due to mere propinquity, as is imprinting in parent-following species, but selective imitation is the norm. Nicolai (1959) found that a male bullfinch fostered by canaries was prepared to imitate canary phrases, but this did not prevent him from successfully courting a female of his own species, which allowed the observation that the canary phrases were transmitted second-hand to the next generation. Human whistled tunes, remote from any natural template, were also transmitted through bullfinch generations in this way. Other finches selectively imitate whatever paternal model is provided (Immelman, 1969).

The same sort of imitation is the basis of the extraordinary performances of domesticated parrots and mynah birds (and budgerigars) since in the wild these species learn the vocal signals of their own families or communities (Bertram, 1970). There are also well-known species which, although giving less spectacular impressions of human speech in captivity, mimic other species of bird in the wild (the mockingbird and the starling). Mimicry tied within genetic relationship is more obviously functional, and whether starlings or mockingbirds gain any biological advantage from their vocal promiscuity is difficult to establish. Imitating other species might be the result of general imitative tendencies gone awry, and raises the issue of vocalisation in excess of natural utility. Given an adaptive value for the production of vocal signals, either instinctive or learned, there may arise an independent motivational system for vocalisation, which under some conditions could produce vocal performance far in excess of the marginally usefully biological requirement. Thorpe, a distinguished authority, has suggested that such a dissociation between drive and utility can be seen in the singing of the blackbird, which emits hurried, imperfect and less pleasing songs during the crucial phases of courtship, nest-building and parental care, but indulges in more elaborate, inventive, and well-practised sound sequences when freed from these reproductive responsibilities by the end of the breeding season (Thorpe, 1972).

Mammals

The biological techniques employed for mammalian reproduction could equally well be assumed to minimise the cognitive load placed on the brain, as to require a newer and higher psychological level. This is especially true in the case of cooperative parental care, which is typical of birds, but rare among mammals even in primates. However, the dependency of mammalian infants on their mothers provides greater opportunities for social learning than usually occur in lower vertebrates. Yet the constancies of mammalian anatomy support a certain diversity in
patterns of parental care and social structure. The tree shrew, which is sometimes used to represent a primitive primate for the purposes of comparative brain anatomy

(although this is a very dubious practice—Campbell, 1966) has an absolute minimum of parental care. The infants are born in a nest separate from that used by the parents for sleeping, and left entirely unattended except for a ten-minute period once every two days, when the mother returns to perfunctorily squirt milk (a highly concentrated type) into their mouths (Jolly, 1972). Unusually limited maternal activity also occurs in some small New World monkeys, in which the father carries and cares for the infant continuously except for the short intervals when it is handed over to the mother for breast feeding. On the whole, though, the involvement of the male parent with the care and rearing of the young is extremely limited in primates (Mitchell, 1969). This is also the case with herbivorous mammals, where males of some species form separate groups, and only interact with females during the formation of harems or of mating pairs.

It is possible that a line should be drawn between carnivorous mammals and all others, for patterns of parental care. Certainly neonatal carnivores are less able to fend for themselves than the young in hard herbivores, which are up and about soon after birth. Similarly the transition to grazing after weaning can be accomplished without very much parental attention, but providing food and training for infant meat-eaters which are as yet incompetent to hunt for their own food is a major task for the carnivore parent which, like many birds, must bring solid food to the young at some stage of their development. The most elaborate parental and community organisation is found in the canids (dogs, foxes, jackals and wolves), where males will hunt to bring back food for both young and the maternal females (Fox, 1975). This has been taken to suggest that human sex roles evolved while hunting was the main source of food, although the appeal of the analogy with wolves is somewhat reduced by their habit of food-sharing by regurgitation. The forming of social attachments between pairs (‘pair bonding’) may be needed to ensure parental cooperation in canids and may be facilitated by the nature of copulation in these species. Typically in a watchful mammalian ungulate, although there will be great competition between males to establish sexual access to females, copulation itself is brief and perfunctory—in some species faster than the human eye can follow (Grant’s gazelle: Walther, 1972) —and clearly requiring little by way of interpersonal relationships. In carnivores generally copulation is a more protracted and involved activity, and in the canids prolonged personal contact is guaranteed by an anatomical copulatory lock, produced by a

bulbous expansion at the end of the penis. Although in domesticated dogs wolf-like male responsibilities have been lost, it may be assumed that in wild canids physical attachments reinforce even
more lasting social bonds. It should be noted that while ‘two-parent’
families appear to be universal in canids, but do not occur in our
close relatives the chimpanzee and the gorilla, the gibbons (the
‘lesser’ apes) are found in nuclear family groups (one adult male,
one adult female, and their young). The diet of gibbons—fruit and
leaves which they find in trees plus some insects and bird’s eggs—
does not differ dramatically from that of chimpanzees, and it is
therefore a mistake to assume that it was necessary for an ape to
become a co-operative hunter before the two-parent family group
could make an appearance in the larger primates.

Where there is any social organisation at all in mammalian
species, it may be said that a network of social relationships in the
family, pack or herd needs to be mastered by each individual and
that this is the primary task for which mammalian intelligence
evolved (Humphrey, 1976). However, it is difficult to support this
by comparisons between relatively solitary mammalian species and
their more gregarious counterparts (such as comparisons between
orang-utans and chimpanzees): indeed it is not immediately obvious
that mammalian social structures are such that they would require
more elaborate forms of cognition than those of birds or lower
vertebrates. Complex social hierarchies can of course been seen in
the ‘pecking orders’ of birds (and are very highly developed in
corvids such as the jackdaws studied by Lorenz, 1966), and social
hierarchies can be observed in reptiles (particularly in the social
lizards: E. O. Wilson, 1975). Therefore it is not very plausible to
suggest that social organisation as such is the prime mover behind
the evolution of intelligence, even though it may well be the case
that the range of learned social relationships which occurs in higher
vertebrates can exceed that which is possible in lower vertebrates. It
could be that it is the gradual learning of individual social
relationships, rather than simply the existence of social interactions,
which distinguishes mammals from other vertebrate classes. The
imprinting of parent-following birds on artificial objects seen soon
after hatching is certainly more abrupt than the imprinting of hand-
reared sheep and goats on their human foster-parents or the
identification with humans which develops in the domestic
carnivores (cats and dogs). Any line drawn between birds and
mammals on this count must,

however, be blurred, since Klinghammer (1967) has shown that
gradual and cumulative social learning takes place in many altricial
birds, and very early experiences are important in the taming of
mammals (Scott, 1962). The general view is that gradual learning
from experience is supremely important in mammals, but on the
other hand it is assumed that most of the social signals in mammals
are innately programmed (e. g. ‘appeasement gestures’ and the
social significance of tail position in wolves, and facial expressions
in primates: Lorenz, 1966; Eibl- Eibesfeldt, 1970). The soundest
hypothesis would seem to be that both birds and mammals make use
of a large amount of social learning, by comparison with lower
vertebrates.
Aggression and altruism

No account of social relationships in vertebrates would be complete without due consideration of aggression and competition between members of the same species, and the relation of such hostile interactions to an opposite category of co-operation, affection and self-sacrifice. It should first be emphasised that either hostile or cooperative interactions between members of the same species should be kept distinct from between-species factors. Predation, and defence against predation, provides an obvious example of what would appear to be competition between species, and there are many subtle cases of parasitic or symbiotic relations between species. But it is relationships between individuals of the same species which have most immediate theoretical interest. It is clear that many vertebrates have very systematic and time-consuming forms of ritual competition and fighting between individuals of the same species. The rituals frequently include ‘appeasement’ mechanisms involving submissive gestures, which may prevent fights between species members extending to the death of the losers (Lorenz, 1966). It is certainly common practice to conduct hostile interactions with the weapons of proud display, strutting and threatening postures, and mutual vocal abuse. But biting, kicking and goring are also resorted to, and fairly serious wounding, sometimes obvious from the scars of successful veterans, takes place in species as far removed as fighting fish, domestic chickens, and elephant seals.

As usual, we may ask if there is any evidence for a phylogenetic progression in the utilisation of aggression, and to what extent aggression requires higher forms of intelligence. And, given the prevalence of within-species aggressive interactions in all vertebrate classes and orders, we can again dismiss the idea that a particular category of behaviour will distinguish one class from another, even though the human species may exhibit interspecies hostility to a very pronounced degree. It is likely, of course, that in lower vertebrates interpersonal unpleasantness is based on innate and reflexive reactions while higher vertebrates and mammals especially may make use of greater foresight and cunning to implement malevolent intentions. But equal weight could be given to the proposition that even in higher vertebrates aggression is predominantly reflexive, emotional and innate, and that even in man violent impulses provide evidence for the retention of primitive methods of behavioural control (though insight and imagination may in some instances be employed in the service of reflexive revenge and resentment).

A stronger argument can be made for a phylogenetic progression in the use of altruism, particularly if one assumes, optimistically, that human individuals show exceptional care and concern for fellow species members (when they are not being callous or cruel). Care of the sick and injured as well as the young and helpless is
certainly a characteristic of human, as opposed to animal, societies. However, one cannot adopt this as a source of more general phylogenetic hypotheses. In the first place, the analysis of the genetic basis of altruistic behaviour has to be made independently of the ancestry of a particular species, following the argument that altruism should only be programmed towards individuals closely related to the benefactor, irrespective of the behavioural or psychological mechanisms involved (Hamilton, 1964; Dawkins, 1976b). Also there is a confusion between altruistic motives and the means or tools available for putting them into practice.

The distinction between means and ends was very clearly expressed by Lorenz (1966) in his discussion of aggression, and the same point applies equally well to altruism. According to Lorenz, man is not necessarily more dominated by aggressive motives than other species, but has access to weapon-making skills and social institutions which vastly amplify the damaging results of individual aggressive feelings. The same could be said of more laudable behavioural categories: it is difficult to decide whether the human species has exceptionally powerful helpful impulses, or merely unique medical and social technologies for improving the welfare of others. It would be reassuring to believe that the increased mammalian capacity for cognition improves the expression of friendly impulses by allowing more imaginative identifications with the predicaments of others, but it is always difficult to disentangle emotion and cognition. It is usually convenient to assume that such altruism as may occur in lower vertebrates (as in the parental behaviour of sticklebacks and toads) is merely a product of mechanical reflexes, whereas in higher animals emotion and cognition develop hand in hand. But there is a well-grounded alternative opinion that emotions and instinctual drives are biologically stronger and phylogenetically more primitive than the rarefied realms of cognition. According to this, animals are both more emotional, and less intelligent, than people. It seems reasonable that cognitive abilities should always be to some extent the servants of emotion. While in lower vertebrates very highly charged behaviours may be directed by relatively simple perceptions, emotional drives in brains better equipped for cognition should be modified by imagination and inference.

One can only say that behaviour in all vertebrate classes appears to be very well organised within the category of aggression and competition, whereas the category of affectionate and co-operative social interactions is more problematical, but is sufficiently well represented to account for social affinities and group behaviour in a wide variety of vertebrate species.

**Reward and punishment**

In theories of animal behaviour deriving from laboratory experiments there is a fundamental division between the motivational systems for reward and punishment, which cuts across
natural categories of behaviour such as food-seeking or social interaction (Hilgard and Bower, 1975; Mackintosh, 1974; Gray, 1975). A similar division has been proposed from the standpoint of neuroanatomy (Riss, 1968b). Rewards imply a motivational system for the maintenance and repetition of activities which satisfy some criterion of value while punishment should serve to reduce and discourage disadvantageous or dangerous behaviours. A major feature of theoretical accounts of animal behaviour is the proposition that one or both of these motivational systems promote the learning

of relatively arbitrary responses (Hull, 1943; Mackintosh, 1974; see Chapter 3, this volume). But it has been much emphasised recently that natural, species-specific behaviours are closely entwined with supposedly arbitrary reward and punishment (e.g. Seligman, 1970; Hinde and Stevenson-Hinde, 1973; Bolles, 1972). Indeed it is possible to start at a purely reflexive level, and yet categorise inbuilt and automatic behaviours as either positive and ‘appetitive’ (causing increased contact with eliciting stimuli) or negative and aversive (reducing contact with environmental signals): this is the initial step suggested by Riss (1968b). The question is how far natural vertebrate behaviours arise from automatic elicitation of responses which are appropriate for the feeding strategies, reproductive patterns and all other necessary activities. In the case of higher vertebrates at least, the apparent direction of behaviour with respect to external goals, and the relationship between organised actions and ostensible needs, are usually taken to imply that inner motivations modulate elicited reactions to external stimuli.

It is here that behavioural flexibility and arbitrary learning become important as criteria for the necessity of inner motivation. If a mammal maintained its body temperature only by changes in metabolism, shivering, and raising or lowering its fur, that might not be sufficient to convince us that there was any need for body temperature to have psychologically motivating properties. If on the other hand it is shown that the animal will learn to turn a wheel to alter the intensity of a heat lamp used in laboratory experiment, it is hard to resist the conclusion that the arbitrary response of wheel turning is motivated by the goal of physical comfort. It is true that the sucking reflexes of a newborn mammal, or the efforts of a newly hatched cuckoo to turn out all other eggs from the nest in which it finds itself, may appear to be motivated, but any stereotyped and rigid sequence of responses could surely be satisfactorily pre-programmed as a set of inbuilt reflexes.

There is little likelihood of establishing clear and agreed definitions of whether a given behaviour should be regarded as motivated or not, and all speculation about inner drives which may provide causal explanations for observed behaviours is open to criticism (Hinde., 1959). However, apart from the criterion of arbitrary learning and behavioural flexibility, it is possible in some cases to anchor psychological processes of motivation to particular kinds of brain process. It is generally supposed that shifts in emotional mood, and
the selection of behavioural priorities, are a function of the forebrain limbic system. Electrical activation of various parts of the limbic system can provoke natural behaviours such as attack and copulation in birds and mammals in a way which suggests that normal moods and drives are being mimicked (Glickman and Schiff, 1967; Valenstein et al., 1970). The most revealing phenomenon is, however, that experimental animals will perform relatively arbitrary behaviours if electrical stimulation of points in the limbic system is used for reward or punishment. In higher vertebrates it is possible to suggest that limbic pathways correspond to subjective pleasure and pain, since electrodes surgically implanted in their brains appear to provide internal sources of reward and punishment which are detached to some degree from inbuilt motor patterns. Animals desist from any action which results in stimulation of the ‘pain centres’ and energetically repeat simple behaviours which are made to bring about activation of the ‘pleasure centres’ (Olds and Milner, 1954; Olds and Olds, 1963; Benninger et al., 1977). It is regrettable that the vast majority of experimental studies of this ‘self-stimulation’ phenomenon have been confined to mammals and in particular to the rat and the monkey. Several attempts to reproduce self-stimulation in birds have been successful (e.g. Macphail, 1966; Andrew, 1967; Delius et al., 1976; Zeigler et al., 1978), but systematic comparisons of a greater number of species, from all vertebrate classes, in terms of their susceptibility to this artificial source of motivation, would be extremely valuable. At present there is very little evidence to suggest whether self-stimulation, of the kind found in mammals and birds, can be successfully reproduced in any lower vertebrate species. The existence of ‘pain’ and ‘pleasure’ centres in the brains of goldfish has been reported (Boyd and Gardner, 1962) but without any convincing behavioural data, and there does not appear to have been any investigation of self-stimulation using reptiles or amphibians.

Sleep and dreams

If the most obvious and universal feature of vertebrate behaviour is apparently purposeful activity, the next most general aspect of vertebrate behaviour is a regular alternation between periods of rest and periods of action. Vertebrates are hardly exceptional in this respect, but we are reminded daily that many mammals spend a considerable proportion of their lifetime in a peculiar sort of suspended animation, marked by unresponsiveness to external events, in direct contrast to the characteristics of alertness and intelligence. I am referring of course to the daily cycle of sleep and waking, rather than seasonal hibernation. The problem of the function of sleep still remains to be solved. One extreme theory is that sleep has no function, other than to ensure conservation of energy during periods of enforced idleness in species which can
only engage in their normal activities during part of the day/night cycle (Meddis, 1975). Alternative theories suggest that the special activities of the brain during sleep are intimately related to its successful function during wakefulness (Oswald, 1962; Jouvet, 1975). Apart from theories concerned with purely physiological needs (for instance, for some sort of recharging of stores of neuronal transmitter substances) the most interesting theories for present purposes concern the role of thought during sleep, in the form of dreams. Vivid and memorable human dreams have always provided compelling evidence of thought processes detached from action, and from immediate reality, although as often as not dream content ‘is assumed to have a deeper meaning, or a greater psychological significance, than more mundane waking experience. However, why dreams should occur at all presents a biological puzzle. Are dreams a spurious and unnecessary artefact of sleep, or are they crucial biological events, sufficiently important to require long periods of ‘down-time’ for the normal brain? It is still rather uncertain how far the human brain suffers a serious loss of efficiency if it is deprived of sleep, whether by the demands of an experiment, idiosyncratic personal routines, or clinical abnormalities (Meddis, 1975; Dement, 1960; Oswald, 1962). There is certainly a disparity between the strongly felt need for sleep which most of us experience, and the difficulties experienced by psychologists trying to demonstrate fundamental deficits resulting from temporary sleep-deprivation. By and large, keeping people continuously in bed with absolutely no form of distraction (‘sensory deprivation’), that is imposing ideal conditions for sleep, even for a few days, is more likely to produce psychological disturbances than keeping them awake, and bombarded with sensation, for a similar period of time. It is possible that the biological need for sleep is somewhat less fundamental than our individual drives might lead us to believe. If so, this would support the speculation that the ‘sleep instinct’ exists to serve a diurnal cycle for the regulation of physical activity rather than to set the stage for dreaming, or to

support a necessary form of mental or physical restoration.

However, a strong hypothesis has been put forward by Jouvet (1967, 1975), who has been responsible for localising some of the brainstem mechanisms which control sleep and dreaming. This hypothesis is that dreams function as mental rehearsals for instinctive performances. The main reason for supposing that dreams are a running through of built-in perceptual, motor and emotional programs, rather than a consolidation or organisation of life memories, is that sleep and dreaming are most prevalent in the newborn and young (in man and other mammals). However, this is not a strictly necessary deduction. One could equally well put forward the theory that neonatal (and even prenatal) experiences and sensations are sufficiently radical and new as to require more consolidation and organisation, via re-running and compiling during sleep, than the predictable happenings of adulthood. An intermediate position would be that mental rehearsal could
accomplish both a running-in phase for instinctual programs and a means for repetition and elaboration of individual life experiences. An obvious source of evidence for deciding the relative importance of instinctual and experiential factors in dreaming is of course phylogenetic comparisons, and received opinion here is definitely that it is the species which are presumed to rely most heavily on learning from experience, that is mammals and pre-eminently man, in which dreaming sleep is most apparent.

Before looking more closely at the comparative psychology of sleep, we need to define some relevant terms a little more clearly. Electroencephalography,—the measurement of rhythmic fluctuations of electrical potentials picked up from surface or implanted electrodes on or inside the head—is the technique used to make relatively unambiguous and quantitative assessments of sleep. It can be combined with direct observation of rapid flickering movements of the eyeballs which is a convenient outward sign that inner events reportable as dreams are taking place. In a normal sleep sequence, before any dreams are to occur we must close our eyes and wait for a special sort of muscular relaxation, most evident in the neck. EEG recordings (electroencephalograms) show that if we are awake with the eyes open, there are fast (about 40 cycles per second), desynchronised (irregular) and shallow (low voltage) brain rhythms. Once the eyes are closed, but depending on our state of relaxation, a more regular medium frequency and medium voltage rhythm appears—this is the famous alpha rhythm aspired to as a measure of the success of meditative techniques of self-control. During the first hour or so after dropping off to sleep there is a gradual transition to ‘slow-wave sleep’ in which there are long (5 per second) waves on the EEG record of a distinctly higher voltage than alpha rhythms or the desynchronised waking pattern (200—300 micro volts as opposed to 30—50). It is customary to distinguish four stages of depth of sleep during the transition from drowsiness to slow-wave sleep, but these are rather arbitrary distinctions imposed on a continuous shift. The most interesting change in sleep state, which is quite unmistakeable, occurs normally when one and a half hours of the drift down to slow-wave sleep have been followed by a further half an hour of this state. The change is to a new State variously known as REM (rapid eye movement) sleep or ‘paradoxical sleep’. The distinguishing features indicated by these terms include a rapid flickering of the eyeballs (easily observed even when the eyes are closed in most mammals) and the appearance of fast, low-voltage EEG patterns which would otherwise be characteristic of an awake and alert animal. Originally, the similarity of the EEG records in this phase to those of attentiveness led to the idea that REM sleep was ‘light’ (Kleitman, 1939; Oswald, 1962). But behavioural indications, such as how easy it is to wake someone up from REM sleep, and how long they take to show physical reactions to external stimuli, do not support this conclusion, and extensive experimentation with cats seems to have established that by most criteria, dreaming sleep is ‘deep’ (Jouvet, 1967). The term ‘paradoxical sleep’ is used precisely because
electroencephalographic brain waves are characteristic of attentiveness, but there is little reaction to the outside world. This is a vital point for theories of the biological function of paradoxical sleep, since Oswald (1962) and Ullman (1959) supposed that the attentiveness indicated by EEG records meant that this was a phase of greater external vigilance, and that REM sleep served a ‘sentinel’ function. If Jouvet is correct in the finding that REM sleep is not accompanied by any increase in sensitivity to external dangers, then the ‘sentinel’ theory must be dropped. This leaves the way clear for theories of the internal utility of REM sleep, most obviously for theories of the biological function of dreaming. People woken from REM sleep can almost always report vivid dreams, while those woken from other phases of sleep usually cannot, and therefore it is assumed that dreaming and REM sleep are closely related.

Animals, of course, do not give verbal accounts of dreams. But it is clear that in general the sleep of mammals can be divided into slow wave and paradoxical phases, on the basis of brain activity, in exactly the same way as this is done for human sleep. The anatomical and neurochemical aspects of the brain mechanisms which govern sleep and dreaming are almost certainly held in common by man and other mammals, and most of the experimental work on the brain mechanisms which control the sequence of sleep phases has been performed on cats (Jouvet, 1967, 1975). Certain brainstem centres, but not the cortex, must be intact if the normal cycle of sleep phases is to occur. Raphe nuclei in the pontine region of the brainstem, and especially their constituent neurons which contain the neurotransmitter serotonin (5-hydroxytryptamine or 5-HT) are important for the induction of slow-wave sleep. Destroying these neurons produces insomnia, and boosting them by drug treatments leads to a dramatic increase in both slow-wave sleep and succeeding phases of paradoxical sleep. Clearly, other brain circuits are involved as well—we know that stimulants such as caffeine or amphetamine (Benzedrine) may prevent sleep, and these are drugs which facilitate pathways which use the transmitter substance noradrenalin. The appearance of the paradoxical or REM phases of sleep seems to require yet another process which involves the neurotransmitter acetylcholine, since ‘anti-cholinergic’ drugs selectively prevent this phase while leaving slow-wave sleep undisturbed. ‘It is evident that the appearance of PS (paradoxical sleep) is protected by a delicate succession of biochemical mechanisms’ (Jouvet, 1975). The interactions between these mechanisms is not completely understood, but there is a further very important experimental fact. This is that the paradoxical lack of behavioural arousal during REM sleep may not be seen if another brainstem nucleus (the locus coerules) is lesioned. When this is done in cats, sleepwalking, or ‘pseudo-hallucinatory behaviour’ occurs during the REM sleep phases. They jump about, adopt aggressive postures and expressions and hiss and growl, or move their front paws as if playing with a mouse: all this with their eyes almost closed, and with frequent bumping into walls. This is powerful evidence for dream-like programming of instinctive behaviour patterns during paradoxical sleep, and supports the impression which one gets from watching
twitching and growling in ‘dreaming’ dogs and cats. Less obviously, it suggests that brain instructions for action are usually present during REM sleep, but are normally suppressed—behaviour itself is de-coupled

from brain representations of behaviour. This clutch mechanism between activity in brain circuits and motor implementation does not seem to apply to the eyes, since it is their extensive movements when other behaviour is lacking which typifies paradoxical sleep. It could be that eye movements are excluded from the de-coupling system simply because they do not matter—it makes very little difference to the sleeping animal whether eye movements occur or not, whereas sleepwalking can obviously lead to trouble.

The alternative view is that eye movements are present in paradoxical sleep for more positive reasons. It has been suggested that they are in some way necessary for ‘looking at the pictures’ in dreams (Oswald, 1962, pp. 128—34). There is also a theory that the single function of paradoxical sleep is to provide extra practice for conjugate eye movements, which are necessary for following objects or scanning the visual field with both eyes in parallel (conjugate eye movements are used by primates and to some extent by mammalian carnivores with front-facing eyes). This theory (Berger, 1969) may seem plausible if one assumes that paradoxical sleep occurs only in primates and mammalian carnivores, but it founders on the fact that the dreaming phase is prominent in many species which could have very little use for conjugate eye movements. There is extensive paradoxical sleep in the mole, which is quite blind (Allison and Van Twyer, 1970), and mammals with eyes that face to the side may exhibit the brain rhythms characteristic of human dreaming, notably the opossum (Van Twyer and Allison, 1970) and the rat (Jouvet, 1975).

Sleep and dreaming and mammalian habits

In order to assess general theories of the biological or psychological functions of sleep, it is clearly necessary to take into account species differences, and to compare sleep in the various vertebrate classes. It is probable that sleep is associated with many complex physiological cycles, but in the context of the cognitive aspects of brain function the most interesting theory is Jouvet’s idea that the distinctive dreaming phases of sleep (that is in the paradoxical, REM state) function as periods for the mental rehearsal of instinctive behaviours. I have noted above that when phylogenetic comparisons are considered, dreaming sleep appears to be paradoxical in more ways than one. It is curious that mammals, supposedly less governed by instinct than other vertebrate classes, should need special attention to instinctive behaviours. Also, if dreaming is specifically mammalian, it would be unusual as a mammalian speciality in appearing to survive the removal of the cerebral cortex. Conceivably, as the mammalian brain adopted a
heavy reliance on learning by experience, mediated by cortical memories, remaining instinctual programs require extensive rehearsal to fit in with the general plan. However, any universal principle applying to mammals as a whole needs to be modified in the light of the diversity of the habits of individual species.

It is sometimes claimed that ruminant herbivores, such as sheep, cows and goats, do not sleep at all, since sheep may not lie down during the night, and cows and goats, even when lying down, usually keep their head up and their eyes open, and continue to chew the cud, Careful observation and EEG recording suggests that these species may accomplish some sort of sleep, which includes brief periods of dreaming, even while chewing the cud with their eyes open (Oswald, 1962), but obviously they obtain fewer of the benefits that sleep may provide than rats, cats or monkeys. Similarly, marine mammals, including both whales and seals (the latter having the front-facing eyes of carnivores) usually sleep for brief periods under water, interrupted by the necessity of coming up for air. Breathing in these cases imposes special limits on sleeping patterns, and for ruminants the utility of nocturnal chewing and vigilance against predators may impose equally strong ecological pressures against prolonged somnolence (Allison, 1976). But within the limits set by ecological specialisations it is still conceivable that paradoxical sleep plays a distinctive part in mammalian brain function. Since human dreams provide such dear examples of mental experiences freed at least temporarily from external behavioural realities, the fact that similar brain processes to those involved in human dreaming can be observed in other mammals is certainly worth remembering.

Sleep and dreaming in non-mammals

From the point of view of progressive phylogeny, it would be convenient if dreaming were confined to mammals, since this would support a firm line of demarcation between thinking and dreaming vertebrates and reflexive lower forms. It is hardly surprising then, that in the absence of data to the contrary, the assumption has often been made that ‘the physiological state associated with dreaming is a very old and basic characteristic of mammalian life’ with the corollary that in all non-mammals this state is absent (Snyder, 1966). But we can now, with some confidence, eliminate this clear typology, and allow birds, at least, a dream life not very different from that of mammals. It may be that a firm distinction will eventually emerge between the higher, warm-blooded vertebrates, which dream, and the lower, cold-blooded animals, which do not, but the data on sleep in fish, amphibians and reptiles are at the moment very sketchy.

The vast majority of birds, although early risers, are strongly diurnal, needing the clear light of day to make use of their excellent visual sense. On the hypothesis that a sleep instinct exists to ensure
nocturnal quietude (Meddis, 1975), birds would have as much need of it as mammals. There are nocturnal birds of course, such as owls and nightjars, and one cave-dwelling species has apparently evolved a sonic system similar to that of bats for dark flying, but these species usually doze off during the day. Many perching birds sleep standing up, on one or both legs, and might be thought therefore to sleep lightly, especially as a sick or anaesthetised bird will quickly fall off its perch. However, successful perching during sleep is brought about partly by an anatomical arrangement of muscles in which the grip is tightest when the main muscles are relaxed. Lack of muscle tension in the neck is quite apparent from the habit of dropping the head and tucking it under a wing. Non-perching birds such as ducks, and birds which sleep in burrows or nests, can adopt even more restful postures for sleep. None of this, of course, implies the existence of dreaming or paradoxical sleep, and initially EEG recordings were taken to suggest that although birds showed evidence of the REM sleep state, they were in it for a negligible amount of time—less than 1 per cent of the total sleep periods (Klein, et al., 1964; Tradardi, 1966). More extensive observations have now established that, in the limited number of bird species studied, the total duration of sleeping, and the proportion of sleeping time spent in the paradoxical phase, are both comparable to the figures for mammals. Up to 50 per cent of the day is taken up by sleep, and about to per cent of sleep is occupied by the paradoxical state: this is for the pigeon (Goodman, 1974), and for two birds of prey (Rojas-Ramirez and Tauber, 1970). An interesting test case for the hypothesis that paradoxical sleep exists for the purpose of producing eye movements arises in owls, whose tubular eyes are so firmly fixed in their sockets that no movements can occur in any circumstances.

Berger and Walker (1972) duly reported that there are no rapid eye movements during sleep in the burrowing owl, but EEG recordings made it plain that desynchronised brain rhythms are present in this species nevertheless.

Since the birds so far studied show mammalian amounts of paradoxical, ‘REM’ sleep, by the criterion of electroencephalographic measurements, even if eye movements are limited, or absent altogether, we may safely conclude that the electrical brain rhythms characteristic of dreaming are not a mammalian preserve. Any generalisations about sleep in lower vertebrates would be very much less safe. The simplest assertion is that lower vertebrates do not sleep at all, and that if they have periods of ‘behavioural rest’ there is no brain state which corresponds to the paradoxical phase in birds and mammals (Allison, 1972; J. M. Walker and Berger, 1973). Let us look first at the question of sleep/wakefulness cycles, leaving aside the division of sleep into paradoxical and other phases. The main difficulty with amphibians and reptiles is that so much time is spent in behavioural torpidity that whether this should be regarded as sleep or ‘just resting’ is largely a matter of opinion. (Consider the problem of an awake, but resting, tortoise.) Even those who have devised
electroencephalographic methods which give some indication of brain states for reptilian sleep and wakefulness are forced to admit that there are long periods of time which have to remain unclassified by these methods (Flanigan, et al., 1974). However, many reptile species have very definite diurnal cycles of behaviour. Crocodilians typically spend most of the night in water, emerging for an early-morning bask in the sun (Lang, 1976), and many lizards seek out favourable locations in trees or stonework for their nocturnal state, whatever this may be. In these species, behavioural signs of sleep, such as marked attenuation of reactions to external stimuli, closing of the eyes, and muscular relaxation, are relatively unambiguous.

In fish, on the other hand, and especially in sharks, which need to keep moving to maintain buoyancy, the difficulty is in finding a sufficient lack of activity to qualify even as resting. But it has been claimed that, in teleost fish at least, periods of active swimming may alternate with periods of floating which are passive enough to suggest sleep (e.g. Shapiro and Hepburn, 1976; Tauber and Weitzman, 1969, say eye movements may be observed during the periods of behavioural inactivity in some species). Even with sharks, it is possible that phases of lowered sensory alertness could occur during mechanical

and automatic continuation of swimming. It is not possible to say, therefore, that sleep, as behavioural quiescence, is absent in lower vertebrates, although it is not unreasonable to speculate that the brain-states which control sleep in higher vertebrates are different from those which govern cycles of behavioural activity in other classes.

Some have sought to support the distinction between brain mechanisms controlling sleep on anatomical grounds. The brainstem nuclei associated with the reticular system, which have been firmly implicated in the control of sleep cycles in mammals, in particular the raphe nuclei and the locus coeruleus, are very similar in birds and mammals, and appear to be identifiable in reptiles, but have been presumed to be absent in fish and amphibians (Kappers et al., 1936; Allison, 1972). It would be unwise, however, to place too much emphasis on this aspect of brainstem anatomy, since cell areas in the reticular system of sharks and frogs have been labelled as raphe nuclei in more recent reports (Smeets and Nieuwenhuys, 1976; Opdam et al., 1976). But we can note in passing that this is a case where the evolution of the hindbrain, as opposed to the forebrain, assumes considerable theoretical importance, even for a cognitive process (dreaming).

Although the brainstem structures which are required for paradoxical sleep in mammals are present in reptiles, the electroencephalographic evidence concerning this type of sleep in reptiles is extremely sparse. There is a report of behaviourally observed rapid eye movements during the sleep of chameleons, which is theoretically important, if it is reliable (Tauber et al., 1966). These arboreal lizards adopt a resting posture along a branch as dusk approaches, and close their eyes (and retract their eyeballs) when it gets dark. After this the grip of the feet relaxes and,
especially during the first half of the night, there are periods, about 5 minutes in length, when the eyes can be observed in rapid movement. Tauber et al. (1966) could not differentiate between the eye-movement periods and other periods of sleep on the basis of EEG recordings, but these were clearly different in sleep and waking, showing distinctive irregularly spaced spikes during sleep, and rapid low-voltage saw-tooth patterns during waking. Spikes, or ‘sharp-waves’ have also been recorded during behavioural sleep in tortoises (J. M. Walker and Berger, 1973), iguanid lizards (Flanigan, 1973) and crocodilians. In the iguanids, ‘behavioural sleep’ is identifiable by a flat-out posture, and greatly reduced reactivity (Flanigan, 1973; Tauber et al., 1968). Such behavioural indications of sleep must be Less obvious in tortoises, but in these animals there is

pharmacological evidence that EEG spiking is analogous to EEG slow-waves: the same drug, atropine sulphate, increases both slow-wave sleep in mammals and spiking sleep in tortoises (Hartse and Rechtschaffen, 1974). In iguanids, sleep deprivation amplifies the spikes recorded in subsequent sleep (Flanigan, 1973).

It thus appears that while reptiles may have periods of inactivity and reduced alertness which are accompanied by characteristic EEG patterns and which therefore appear to correspond in some degree to the slow-wave sleep periods seen in mammals and birds, there is little to suggest that reptiles typically exhibit anything which corresponds to paradoxical sleep. It is therefore tempting to assume that this dreaming state has evolved only in the higher vertebrates. The simplest interpretation of this would be that paradoxical sleep began as a device for ensuring a modicum of metabolic activity in warm-blooded animals undergoing energy-conserving quiescence (Zepelin and Rechtschaffen, 1974). A word is thus in order about forms of behavioural arrest other than sleep. Physiologically, anaesthesia shows some similarity to slow-wave sleep, and as a rule, a drug which anaesthetises one vertebrate will also put out all others. At any rate, some sort of temporary brain shut-down, leading to a collapse of the sensory and motor systems, can be induced in all vertebrates by chemical interference with brain activity (or by a sufficiently vigorous knock on the head). A more specialised self-induced slowing down of body and brain activities occurs in hibernation, which is used in several orders of mammals (most commonly in rodents), one order of birds (caprimulgiformes), one order of reptiles (chelonians) and in isolated amphibian species (Mrosovsky, 1971). It is assumed that brainstem mechanisms are involved in the programming of hibernation, and the clearly apparent metabolic functions here suggested comparisons with sleep. A less obviously functional phenomenon is the so-called ‘animal hypnosis’ (preferably, ‘tonic immobility: Maser and Gallup, 1977) which may be induced in species in all vertebrate classes by certain forms of physical restraint.

Obviously, the suspension of normal behavioural reactivity can occur in varying circumstances and for various purposes, and the basic diurnal cycle of sleep and rest is at once too complicated and
too simple to be given explanations in terms of psychological utility. Yet the dreaming phase of sleep stands out as a special case. The subjective intensity of human dreaming has always provided a pointer to the separation of mental experience from external reality. The opportunity to rehearse and elaborate internal schemata in the absence of external necessities may or may not be a crucial requirement for higher vertebrate adaptability, but the bare fact of the existence, during paradoxical sleep, of electrical indices characteristic of waking brain states without neural input and output in the sensory and motor systems, suggests that brain representations of external events have attained independence from the external events themselves. Since this fact applies to higher vertebrates, but not to lower vertebrates, it deserves a great deal of attention in theories of mental evolution.

Vertebrate life and vertebrate brain powers —conclusions

The review in this chapter of various natural categories of behaviour which stand in need of control by the brain does not reveal a single condition of life or psychological requirement as a pressure towards successive improvements in brain capacity. Any account of the anatomical evolution of the vertebrate brain must allude to greater physical size of the brains of higher vertebrates, in which the forebrain appears to have been most subject to evolutionary changes. But it is not clear that in terms of biological functions the brain of one vertebrate class serves a set of purposes which are radically different from those achieved by brains in any other class. The problem is that most behavioural programming needs, such as the reception of visual information, the selection of feeding strategies, and the control of social interactions necessary for reproduction, span the entire panorama of vertebrate species. Presumably the answer is that the same behavioural tasks can be accomplished in different ways, but this means that we cannot simply say that a brain of one type is necessary for predatory habits while a brain of another type must evolve for any fruit-eating species; or that migration absolutely requires any particular form of brain organisation; or that a social species has to be more intelligent than a solitary species. In this sense phylogenetic status, with all its theoretical faults as a concept, may be a more reliable guide to the psychological capacities of a species than its ecological niche. Primates are intelligent because they are primates, not just because they live in trees, eat fruit, and form social groups. Clearly this brings back anagenesis, or ‘evolution above the species level’ with a vengeance, since we are left with the vague notion that a phylogenetic progression in brain capacity exists regardless of the specialisations of individual species. And in terms of the behavioural categories selected here,
there is not so much a progression as a simple dichotomy between higher vertebrates and lower vertebrates: in most cases where it is possible to suggest a form of mammalian superiority, the mammalian characteristic is seen in birds as well. This applies to such varied features as the importance of parental care, elaborate vocalisation, complex social organisation, flexibility in innate behaviour patterns, learning by individual experience and learning by imitation. It applies also in two cases where aspects of brain functioning can be examined directly: sensitivity to the emotionally rewarding or punishing consequences of motor responses is studied by allowing animals to turn on or off small electrical currents delivered to certain forebrain structures—this works for both mammals and birds but has not as yet been demonstrated in other classes; the changes in electrical brain rhythms which occur during human sleep can be found in mammals and birds but not in lower vertebrates. Results such as these confirm the traditional opinion that the brains of mammals support forms of learning and cognition which are superior to those found in reptiles but do little to strengthen the assumption that there is a clear psychological separation between mammals and birds. However, it is on the whole remarkably difficult to infer psychological capacities from the natural behaviours required of particular species or groups of species. An alternative source of evidence is laboratory testing of psychological capacities, and it is the results of such experimentation that I shall turn to in the remaining chapters.