Trends in the life-history styles of vertebrates: an introduction to the second ALHS volume

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A conference entitled 'Alternative Life History Styles of Fishes and Other Organisms' was held in Grahamstown, South Africa, in June 1987. The aim of the conference was to examine the way in which epigenesis (i.e. the interactions among gene products, cells, tissues, organs and the environment during the formation of an organism) shapes the life-history styles of plants and animals. In particular, we wished to examine the concept of alternative life-history styles (ALHS), i.e. that organisms may follow one or both of two trajectories, which are constantly created during their development, depending, for example, on whether the environment is relatively stable or unstable. The conference attracted scientists working on a wide range of organisms. The first volume of proceedings, entitled 'Alternative Life-History Styles of Animals' (Bruton 1989a), discusses ideas and presents case-histories of the ALHS displayed by insects, fishes, amphibians, reptiles, birds and mammals, including man. The second volume presented here is devoted entirely to fishes. A few additional papers on the ALHS of fishes, completed and submitted later as regular submissions to the journal, are also included in this second volume.

The term 'fishes' applies to cold-blooded aquatic vertebrates, and not to a distinct taxonomic grouping. Modern fishes are divided into at least four classes which are as distinct from one another as are the four classes of other vertebrates, the amphibians, reptiles, birds and mammals. In particular, the class Chondrichthyes has had a 400-million-year history distinct from that of the other main class of fishes, the Osteichthyes, and has reached a quite different evolutionary presence. Fishes are the most diverse group of vertebrates and also dis-

play the greatest range of different life-history styles. Their fecundity ranges from less than 10 to many millions of eggs and the extent of parental care ranges from none to extensive. They show indirect development with larvae and a full metamorphosis as well as direct development without larvae. Fishes inhabit a wide variety of habitats and they have highly flexible phenotypes which can expose different ecomorphological options to the constantly changing environment. They are therefore ideal subjects for the study of alternative life-history styles.

Typical textbook accounts of fish ontogenies are often biassed in favour of findings in northern hemisphere, temperate countries where fishes have a relatively narrow range of life-history styles. The general impression created is that all fishes have larvae and undergo indirect development. Studies in tropical environs, which are well represented in this volume, have demonstrated the wide range of ALHS in fishes, especially towards the precocial end of the spectrum.

The aim of this introductory note is to demonstrate some broad trends in the distribution of ALHS in vertebrates, and also to discuss some interesting issues, such as why there are no guarding chondrichthyians or live-bearing birds, whether the terms 'altricial' and 'precocial' can be applied equally to fishes and birds, and why the role of dispersers is reversed in the higher vertebrates.

The advantage of an aquatic habitat

Fishes are the most ancestral of all vertebrates and have also persisted in the environment in which

vertebrates first evolved - water. All vertebrates have a fluid-based metabolism which, in general, is not functional under conditions of desiccation. The embryos and other early developmental stages of vertebrates are particularly vulnerable to the effects of desiccation as they are relatively immobile of their own accord and have a high surface-to-volume ratio. These problems are largely overcome in aquatic environments where the animal is bathed in a life-giving fluid. As a result, most fishes have retained the habit of water-borne breeding and only species which, for instance, live in shallow pools that are subject to desiccation (e.g. *Nothobranchius* species) or in floodplains with fluctuating water levels (e.g. *Hepsetus odoe*) have opted to try out-of-water incubation. In contrast, land animals are constantly under threat from desiccation and they have had to evolve various mechanisms for the protection of their young. These include a relatively impervious egg shell in reptiles, birds and monotreme mammals, and various forms of internal bearing in marsupial and placental mammals.

If the proportions of different vertebrate groups in the non-guarding, guarding and bearing sections of Balon's (1975, 1981) reproductive guild categories are compared (Fig. 1), we find that there is a larger proportion of non-guarders among aquatic breeding animals and of guarders and bearers among the terrestrial breeding animals. The main reason for this pattern is probably the relative hospitability of the external milieu in the aquatic environment to early developmental stages. A few reptiles (e.g. the sea snake *Pelamis platurus*) and several mammals (cetaceans and sirenians) have returned to the sea and freshwaters to take advantage of this situation. On land, the majority of non-guarding taxa is found among the amphibians and reptiles, while all the homeotherms show intensive parental care, with the birds guarding and the mammals bearing their young (Fig. 2).

Enclosing the eggs and young in desiccation-resistant egg envelope(s) or in the body cavity reduces the number of young that can be cared for at one time, which means that land-based vertebrates cannot adopt, to the same extent as fishes, the survival strategy of producing a large number of
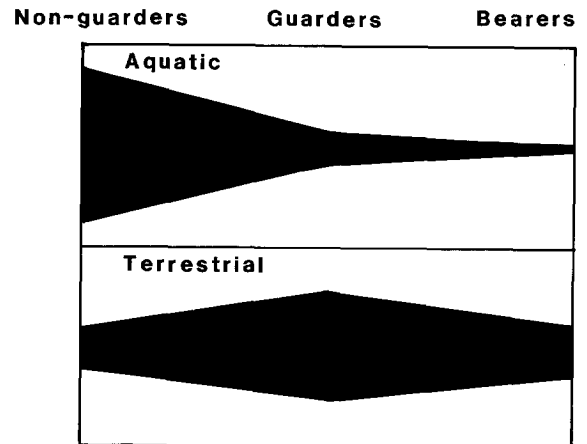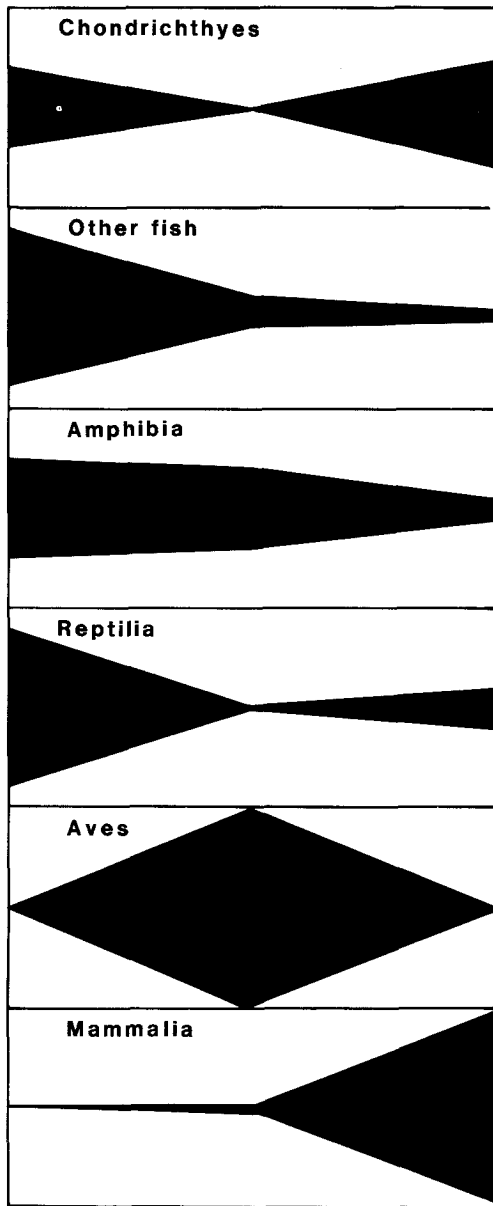

Fig. 1. Diagrammatic representation of the proportions of aquatic breeding and terrestrial breeding vertebrates in the different reproductive guild categories of Balon (1975, 1981, 1984).

small young in order to offset the impact of unpredictable environments. Bearing a relatively small number of young does, however, confer other advantages in that the individual young can be larger and more parental care can be given to each offspring, thus increasing the chances of survival of each individual.

An aquatic environment also confers other advantages due to its higher density and three-dimensionality, compared to most terrestrial environments. One of the primary functions of an early developmental state, once it has left the care (if any) of the parent, is to move away so as to avoid competition with the parent for space and food. In the aquatic environment, passive (and sometimes active) movement of the young in water currents is common, whereas such opportunities are not as readily afforded by air movements on land. As a result, the early developmental intervals of fishes are often prolonged so as to take advantage of this dispersion mechanism, whereas on land the early developmental intervals of vertebrates are often curtailed so that the animal can grow and quickly become capable of active movement in its own right (and for other reasons). These factors further favour the retention of relatively altricial breeding modes in aquatic environs and relatively precocial modes in terrestrial environs.

General trends of ALHS among plants and animals

Non-guarders   Guarders   Bearers

Chondrichthyes

Other fish

Amphibia

Reptilia

Aves

Mammalia

[10%

Fig. 2. Diagrammatic representation of the proportions of the different vertebrate classes in the reproductive guild categories of Balon (1975, 1981, 1984).

The ancestral groups of land plants (Bryophytes, Pteridophytes and Gymnosperms) are relatively altricial as they reproduce by releasing spores or seeds which are poorly endowed with nutrients, whereas the more advanced groups (the Angiosperms) are more precocial as they typically surround the embryo with stored food and a protective coat.

Although most invertebrates are relatively altricial non-guarders, there is a good representation of precocial guarders and bearers. Indirect development is clearly shown by the various holometabolous insects whereas the hemimetabolous insects have direct development. Numerous diplopods, arachnids and insects make nests, and passive defence of the young occurs in many annelids, arachnids, insects and crustaceans. Parental care is most highly developed in the insects. Active defence of the young is known in species of Hemiptera, Coleoptera, Orthoptera, Dermaptera, Embioptera and other groups, whereas the social Hymenoptera (ants, bees and wasps) and Isoptera (termites) have highly structured communities for the provision of food, heat and sanitation to the young.

Viewing the vertebrates as a whole, it is interesting to note that the bony fishes, and to a lesser extent the Amphibia and Reptilia, have representatives in all the sections of reproductive guilds, i.e. non-guarders, guarders and bearers (sensu Balon 1975, 1981). About 80% of the approximately 21 000 species of extant bony fishes (Cohen 1970, Nelson 1984) are non-guarders, in the sense that they carry out no parental care on the fertilised eggs and early developmental stages, and about 15% are guarders and 5% are bearers (Breder & Rosen 1966, Balon 1975, 1981) (Fig. 2). Interestingly, the majority of bearers among the fishes as a whole are found in relatively ancient taxa, such as the Chondrichthyes, Chimaeriformes and Coelacanthiformes as well as in relatively derived taxa within the Euteleostei, such as the Siluriformes, Atheriniformes and Perciformes. Advanced breeding modes are rare in the more plesiomorphic groups such as the Elopiformes, Anguilliformes, Clupeiformes and in some Euteleostei (Breder & Rosen 1966, Balon 1975, Compagno 1990). The

Amphibia show nearly the same range of breeding guilds as fishes, with open substratum spawners, brood hiders, nest guarders and external and internal bearers (Duellman 1985, 1989). The Reptilia also have non-guarders, guarders and bearers, but with a higher proportion of bearers than either the bony fishes or the Amphibia (Branch 1989) (Fig. 2). The birds are all guarders and have no non-guarders or bearers, whereas the mammals are all internal bearers with the exception of the monotremes, which are guarders, and the marsupials, which are a combination of internal and external bearers. Furthermore, none of the amniotes (reptiles, birds and mammals) have a marked metamorphosis with indirect development. There is thus, in general, a progression from predominantly non-guarding, more altricial forms among the lower vertebrates to a greater proportion of more precocial guarders and bearers in the higher vertebrates. There are, however, two exceptions to this rule - the Chondrichthyes, which have no guarders but many bearers, and the birds, which have no bearers but many guarders. Why is this?

Why are there so many viviparous chondrichthyians?

In contrast to the bony fishes, in which about 5% (1050 species) are viviparous, the cartilaginous fishes have about 57% livebearers (about 515 species) (Compagno 1990, and personal communication). The other 43% (about 390 species) are all non-guarders which lay large cased eggs, although further study may reveal that there are facultative internal bearers among them, and there are no guarders, as far as we know (Fig. 2). Some of the non-guarders are brood hiders (e.g. a bullhead shark). Interestingly, all the Rajiformes are non-guarders and all the Myliobatiformes are bearers, whereas both non-guarders and bearers are found among the various orders of sharks and chimaeras. It is, however, difficult to classify the reproductive sections of cartilaginous fishes using the rules established for bony fishes. Sharks are an ancient group with a long history of independent evolution, and it is not surprising that they have found different

solutions to the problems posed by reproduction. There is thus a fine gradation between non-guarding, oviparous sharks and rays which retain their eggs for long periods, e.g. the whale shark, *Rhincodon typus,* and facultative internal bearers and obligate lecithotrophic livebearers. Compagno (1990) has estimated that as many as 27% of all chondrichthyians are obligate lecithotrophic livebearers (formerly called ovoviviparous) (Balon 1985).

All extant chondrichthyians have internal fertilisation via paired intromittent organs which deliver sperm into the female's vent, whereas most bony fishes have external fertilisation. In contrast to bony fishes, functional hermaphroditism and sex reversal are unknown in chondrichthyians (Breder & Rosen 1966, Wourms 1977). Both non-guarding and bearing cartilaginous fishes have a low fecundity and produce large young with direct development; their young are thus relatively precocial and well-developed when they are first exposed to the outside world (Compagno 1990).

The lack of guarders among cartilaginous fishes is probably explained by the high mobility and predatory habits of most species. Guarding may also be impractical in the open sea and on the continental shelf environments that are frequented by many cartilaginous fishes. The high incidence of livebearers among the Chondrichthyes may also be a consequence of their predatory habits as well as the need to produce precocial young in a highly competitive environment (Wourms 1977, Compagno 1990). Chondrichthyians appear to have adopted a relatively precocial mode of breeding early in their evolution, and the success of the group over millenia, while many other groups of vertebrates have come and gone, is evidence of the appropriateness of this life-history style. Viviparity also arose at an early time in the evolution of bony fishes, as shown by its presence in a coelacanth, *Holophagus,* from the Jurassic (Watson 1927, Balon et al. 1988); but the most speciose exponents of precociality today are probably the oviparous cichlid fishes of Africa and South America.

Why are there no live-bearing birds?

Viviparity is a highly successful mode of reproduction that has evolved independently in most classes of vertebrates. Only the birds are completely committed to egg-laying despite having the two prerequisites for vivipary, i.e. internal fertilisation and a vascularised chamber for the incubation of the developing eggs. Many reasons have been advanced for this anomaly in life-history evolution. An obvious consideration is that egg retention increases body weight and wing loading, which is an important consideration for small flying birds but not necessarily for large flying or flightless birds. Egg retention may also have the effect of reducing the clutch size, increasing maternal mortality risk and/ or reducing paternal investment (Blackburn & Evans 1986, Anderson et al. 1987). Gas exchange during egg retention may also be problematic (Lewin 1988). Another reason that has been advanced is that birds have not experienced selection for the intermediate evolutionary step of egg retention (Blackburn & Evans 1986). On the other hand, egg retention may offer some benefits, for example to birds which have to fly long distances between nest sites and food resources, such as many pelagic marine species (Ricklefs 1983). These seabirds regularly carry prey items 14 to 18% of the adult body mass, which suggests that retained eggs (3 to 6.6% body mass) would be a relatively minor impediment (Anderson et al. 1987). Reduction in the rate of predation on and parasitism of the adult may also be a benefit of reduced nest sitting. It also seems reasonable that livebearing would be a more efficient method of breeding in very cold climates, and it is surprising therefore that various large-bodied flightless polar birds, such as penguins, have not adopted this breeding mode.

Anderson et al. (1987) suggest that some kinds of birds may experience selection for egg retention, especially large-bodied species which typically lay one egg per clutch, such as members of the Procellariiformes, Pelecaniformes and Charadriiformes, but they suggest that the avian uterine environment is unfavourable for egg retention. The resting body temperature of most birds lies between 40 and 41°C regardless of body size (Calder & King 1974).

This temperature is at least 1°C higher than that of mammals and is a consequence of the metabolic demands of flight. Developing vertebrate embryos are known to be highly susceptible to elevated temperatures, and egg retention for longer than 24 h following ovulation and fertilisation may be harmful to the developing embryo. Anderson et al. (1987) also note that the rate of passage of the fertilised egg through the oviduct is remarkably similar in birds (usually 24 to 26 h) and that a possible barrier to the evolutionary extension of passage time is the 'exhaustion of genetic variance in egg-passage rate by past selection for rapid oviposition; the rate of evolutionary adjustment would then be limited by the appearance of novel mutations'. Birds typically incubate their eggs at temperatures between 34° and 38°C and experimental manipulation has revealed that eggs incubated above 40°C suffer high mortality and morbidity. Conversely it can also be concluded that the absence of egg retention has allowed birds to take advantage of body temperatures higher than those of other vertebrates, and to fly.

The interesting interruption in the evolutionary sequence of vertebrates from predominantly non-guarding to predominantly bearing guilds is thus a consequence of the method whereby birds have created a unique niche for themselves in competition with other terrestrial animals through being able to fly. The kiwis are the only living birds with all the characteristics that favour egg retention, and there is evidence that they retain their eggs longer than other birds (Calder & Rowe 1977). Were there perhaps some truly viviparous, flightless birds on islands before these habitats were invaded by mammalian carnivores?

If birds have an evolutionary constraint towards the development of vivipary, how can they be so successful, especially in highly competitive, saturated environments such as rain forests where high parental investment in a few young would be hypothesized to be the more appropriate breeding mode? The answer must be that birds have achieved most of the advantages that potentially accrue from vivipary through other specialisations, such as endothermy, egg incubation using feathers, nest construction, calcified egg shells and intensive

parental care. It is nevertheless interesting that an entire class of higher vertebrates has not found it advantageous to adopt the most advanced mode of breeding.

Do the terms altricial and precocial apply equally to fish and birds?

The terms 'altricial' and 'precocial', which are now widely applied to many groups of animals (vide Bruton 1989a), were earlier applied, for example, by Portmann (1938) and Nice (1962) to birds. Nice distinguished between altricial, semi-altricial, semi-precocial and precocial birds which she characterised mainly on the basis of the behavioural characteristics of the parents (the amount of care) and the young (the stage at which the nest was left, initiation of feeding). As Nice (1962) and Balon (1989b) have indicated, these terms are derived from *altrix*, which means a nurse, from *alere*, to nourish, and from *praecox*, which means ripened beforehand. The first term refers to the necessity for feeding and the second to the state of development of the young at hatching.

There has been some confusion in the use of these terms. 'Altricial' has been applied to nidicolous birds which hatch during an early interval of development and remain in the nest where they are fed by the parents, as well as to fish which also hatch during an early developmental interval but are not subject to any parental care. Precocial fishes, on the other hand, are subject to parental care, either in a nest or by being borne in an external or internal body cavity of the parent. The reason why Balon (1979, 1981) has chosen to use the words altricial and precocial for fishes [and they are also now being adopted for amphibians (Duellman 1989), reptiles (Branch 1989), and mammals (Perrin 1989)], is that an altricial bird hatchling and a fish larva are comparable states in development in respect to feeding (Balon 1986a) although they are subject to different levels of parental care. Both require exogenous food in order to transform from a less developed state into a definitive phenotype. The definitive phenotype of the altricial form is arrived at via a slow differentiation and remod-

elling (metamorphosis) of a temporary nutrient-gathering interval (the hoppers of locusts, caterpillar, larva, tadpole), whereas the definitive phenotype of the precocial form differentiates directly using mainly the endogenous or mixed food supply (Balon 1985). Precocial birds and fish, which undergo direct development, are capable of relatively independent existence at the end of 'incubation' due to the availability of a large endogenous food supply. The definition of the two life-history options is therefore based on epigenetic attributes and not on behavioural criteria alone (Balon 1985, 1989b).

The parental care which is afforded to more precocial fish embryos (e.g. by mouthbrooding cichlids) is mainly for the purpose of protecting the early developmental stages from predation, whereas the parental care effected by birds on altricial young is mainly for the purpose of feeding. Likewise, a monotreme or marsupial mammal is more altricial than a placental mammal as the young are at an earlier developmental interval at the end of 'incubation' and require exogenous feeding from the parent in order to complete their development to the definitive phenotype. The dependence of the young of altricial birds on their parents is therefore related to feeding whereas that of precocial fishes is related more to their vulnerability to predation. This vulnerability is partly a result of the reduced mobility of fish embryos which are carrying a large yolksac; in precocial birds the contents of the yolksac has been absorbed by the time of the final emergence from the egg into the outside world.

Altricial animals thus produce a small amount of yolk which is insufficient in itself to produce the definitive phenotype (juvenile and adult) and have to pass through an interval of external feeding in order to accumulate sufficient nutrients for this development (Balon 1986a). The larva as a 'feeding machine' (Wassersug 1984) is thus a key element in the altricial life style. Examples of altricial animals include most species with a metamorphosis, nidiculous birds that produce naked young (passerines such as doves, robins, weavers and starlings, some birds of prey, egrets, albatrosses, etc.), mammals that produce naked young (e.g. rabbits), etc. The young stages of altricial animals often have temporary larval structures, such as the flat beak of fledg-

ling birds and the adhesive organs and vertical fin folds of young fish. Precocial animals, on the other hand, are characterised by direct development from an embryo to a juvenile, which feeds exogenously. Examples of precocial animals are most species with no metamorphosis, nidifugous birds that produce large eggs with a dense yolk (chicken, duck, ostrich, most waterfowl, megapodes, any bird that hatches and runs immediately), mammals that produce furred young with open eyes and soon run with the parents (e.g. hares, antelopes), megaherbivores, etc. (Bruton 1989b).

As with most biological phenomena, sheer maximisation may be counterproductive: the more offspring an animal produces, the less parental care can be given to each offspring and the more likely it is that a high proportion will not reach maturity. Eggs or young which are guarded or fed by the parents cannot be as numerous as those that are released and not guarded (taking allometric scaling effects into account). As a result, altricial fishes generally produce more eggs than precocial ones (Balon 1975, 1985), whereas the opposite applies to birds (Nice 1962). Precocial fishes and birds make a greater direct investment in each individual young but the total parental investment, which also takes into account indirect investment through guarding and feeding, is likely to be more comparable between the two life-history styles. These costs have not as yet been quantified, but the highest figure will probably be obtained for precocial fishes which guard or bear their young.

Reversal of priorities through mental competence (RPMC)

The same sets of variables that characterise the life-history styles of invertebrates and lower vertebrates – states Balon (1985, p. 250) – do not necessarily apply to higher vertebrates, especially placental mammals. The ultimate reproductive specialisation – placental viviparity – has enabled the central nervous system to develop to an unprecedented degree and become an innovation powerful enough to change earlier priorities in energy allocation and use (named the reversal of priorities

through mental competence, RPMC, by Balon 1983, 1989b). In most vertebrates the precocial forms are more competitive and inhabit the centre of the optimal resource range for the species, whereas the altricial forms are forced to the periphery and live in a more capricious environment (Geist 1971). In accordance with Geist's (1978, 1989) theory of health, the dispersers in placental mammals are large, robust, well-nutritioned during early development, well stimulated and able to express their full physical, physiological and mental potential. As a result, they are able to use a wider range of resources, exploit opportunities more efficiently, benefit from experience and are generally more flexible in their behaviour. In lower vertebrates the weaker forms or younger life-history intervals (especially the larvae) are normally the dispersers. Geist's (1971, 1989) non-dispersers or maintenance phenotypes are feeble and do not reach their full potential due to poor nutrition and low levels of stimulation, and are barely able to maintain themselves. They are therefore relatively sedentary even when resources decline. RPMC may also apply to birds but probably to a lesser extent due to their more stereotyped behaviour.

Are alternative life-history styles relevant?

Consciousness of the importance of alternative life-history styles initially grew out of the debate over the importance of density-dependent and density-independent control of populations (Andrewartha & Birch 1954, Lack 1954). The resolution of this debate made it clear that there are two extremes in life-history styles that are common in nature, the one suited to marginal environments that are subject to unpredictable perturbations, and the other to more equable environments that are subject to more predictable perturbations and in which plant and animal populations are likely to reach some sort of equilibrium (Colinvaux 1986, Bruton 1989b). Various patterns of responses to these different kinds of environments have been described, e.g. r- and K-selection (reviewed by Bruton 1989b), maintenance and dispersal phenotypes (Geist 1971), paedomorphs and peramorphs (Al-

berch et al. 1979), generalists and specialists (e.g. Allen 1976), profligate and prudential strategists (Hutchinson 1978), dominant and isolated forms (Løvtrup 1987) and altricial and precocial states (Nice 1962, Ricklefs 1979, Balon 1979, 1981, 1989b), but none describes the underlying mechanism. The epigenetic mechanism for the adoption of these options is suggested by the 'alprehost theory' of Balon (1988, 1989b) based on his life-history model and the theory of saltatory ontogeny (Balon 1985, 1986b, Flegler-Balon 1989). Thus altricial and precocial forms (and other pairs) may represent the pattern, alprehost the mechanism and the predictable or unpredictable environment the 'crucible' in which the process takes place, allowing one or the other or both forms to survive (Bruton 1989b). But is this explanation too simplistic?

With increased realisation of the importance of autopoiesis and of chaos in nature, it appears that natural patterns may be less clearcut. Rather than equilibria being the mode in nature, we may find that non-equilibrium states may be more universal. 'Equilibrium is the equivalent of stagnation and death' (Prigogine 1980) whereas non-equilibrium states that are maintained by self-organising processes are characterised by a continuous and continuously changing exchange of matter, energy and information between organisms and the co-evolving environment, and the constant introduction of variation. Maybe alternative life-history styles are too simple an explanation for the options which organisms are able to offer to the ever-changing environment. Perhaps natural events do not occur in simple triangles, circles and dichotomies? If so, we need to look for a less symmetrical arrangement which is more typical of untidy but dynamic and creative nature. The harmonious 'bifurcations' of the Tao favour the symmetrical arrangement (Balon 1989a) and must be falsified before the less symmetrical arrangement can be accepted.

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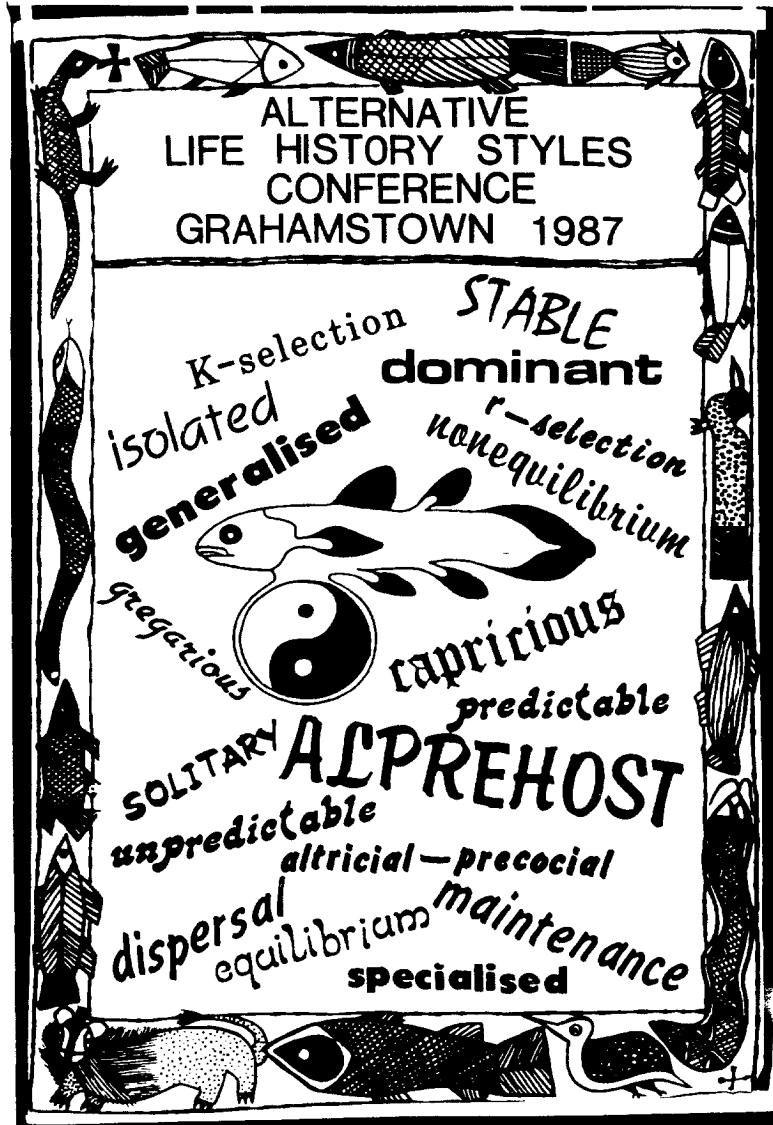
The design depicted on the shoulder bag used by the delegates to the 'Alternative Life-History Styles' conference held in Grahamstown, June 1987. The design shows the conference logo (a coelacanth fetus with a yin and yang yolksac) surrounded by various pairs of terms which have been used to name alternative life-history styles or the environments associated with them. Design by Dave Voorvelt of the J.L.B. Smith Institute of Ichthyology.