

Parasitism: what is a parasite?

1.1 Animal associations

The majority of animals live independently in their natural habitats, seeking their own food materials and utilising free water and oxygen for their metabolic processes. Between some animals, however, a variety of patterns of association have developed, and these may be broadly divided into two groups: homogenetic associations – those between individuals of the same genotype; and heterogenetic associations – those between individuals of different genotype.

Individuals of the same species may form loosely united communities, such as herds of cattle or flocks of sheep, while others, such as some species of ants or bees, may form elaborately organised communities in which individual members often exhibit considerable division of labour or specialisation.

Heterogenetic associations are in general much more complex and a number of terms have been developed to describe them. Like many terms used in biology, these are essentially operational words which are definable only within broad limits and not in absolute terms. They do, nevertheless, serve a useful role in enabling us to file data into convenient, though not water-tight, compartments. Terms such as *commensalism*, *phoresis*, *symbiosis*, *mutualism* and *parasitism* have been widely used for various types of heterogenetic association, and their definition – which has always been controversial – has been much discussed by early workers such as Baer (1952), Caullery (1952) and Read (1970) and more recently by modern workers such as Kreier & Baker (1987), MacInnis (1976), Trager (1986), Schmidt & Roberts (1989), Mehlhorn (1988) and Noble *et al.* (1989). These terms were developed in a period when little data on the possible physiological and/or mathematical basis of such an association were available. Within recent years, the situation has changed some-

what, and although information is still meagre, the general increase in knowledge of animal physiology, biochemistry and population dynamics enables these associations to be considered on a broader basis. In particular, it is increasingly recognised that Parasitology is essentially a branch of Ecology and the phenomenon of parasitism can be considered as an ecological relationship between two *populations* of different species; much attention has been paid to the quantitative aspects of this relationship (Anderson, 1982, 1987; Anderson & May, 1985; Cox, 1982; Crofton, 1971*a,b*; Esch *et al.*, 1989; Kennedy, 1975, 1976, 1983; Rollinson & Anderson, 1985; Schmid & Robinson, 1972).

An important conclusion which has emerged from such studies is that – instead of parasites being randomly distributed within the host population (as might be expected) – they tend to be overdispersed, i.e. a few hosts harbour large numbers of parasites and many hosts harbour only a few. That this type of frequency distribution is a major characteristic of parasitism was first postulated by Crofton (1971*a,b*) and has since been confirmed by numerous studies on many host–parasite systems, especially those involving helminths.

A negative binomial has proved to be a good empirical description of this pattern of infection and an example of this is shown in Fig. 1.1. This shows the distribution of the metacercaria of the trematode *Diplostomum spathaceum*, which commonly occurs in the eyes of fish throughout the world (p. 259, Fig. 17.6). The lenses of a few fish are found to be infected with enormous numbers of larvae (over 400 in one fish) but most only contain relatively few, and its distribution closely follows a negative binomial pattern (Pennycuik, 1971).

In some host–parasite systems, such as the plerocercoid of the cestode *Schistocephalus solidus*, also in the stickleback (p. 315, Figs 22.9, 22.15), dispersion is reduced because some fish may die and the larvae are

2 | 1 Parasitism: what is a parasite?

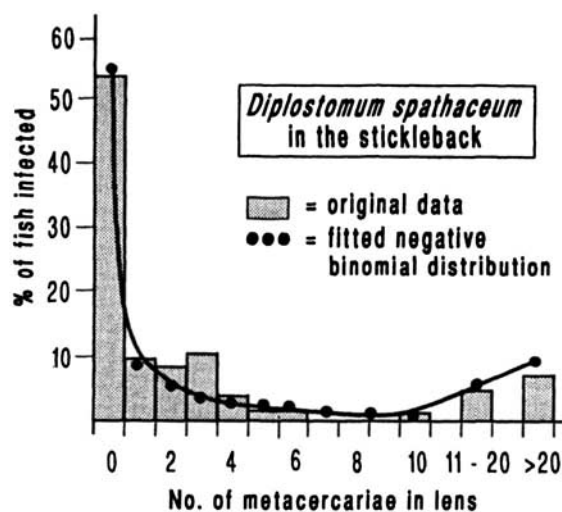


Fig. 1.1
 Frequency distribution of the metacercariae of the trematode *Diplostomum spathaceum* (p. 259) in the eye (lens) of the 3-spined stickleback, *Gasterosteus aculeatus*, compared with the negative binomial expected frequency. (Modified from Pennyquick, 1971.)

generally distributed as a log normal (Fig. 22.13) rather than a negative binomial pattern.

Further quantitative aspects of the frequency distribution of parasites are discussed in detail in the references quoted above and are not considered further here.

The relativity of any definition of parasitism must also be emphasised, for this will depend on the relative weight placed on certain aspects by a particular observer. Thus different workers have emphasised factors such as (a) the intimacy of the association, (b) its pathogenic effect, (c) its metabolic or physiological dependence, (d) whether or not the host 'recognises' the parasite as 'foreign', (e) the ability of the parasite to 'recognise' the host site as being a suitable ecological niche. These factors are not, of course, independent, and complex interactions between them may occur in any particular host-parasite situation.

If the *degree* of association is considered first, most workers would agree that the terms *commensalism* and *phoresis* represent only loose associations whereas the terms *symbiosis*, *mutualism* and *parasitism* represent intimate associations in which the metabolism of one species is dependent to some degree on permanent association with an individual of another species. The concept developed here is that it is the metabolic dependence of one species on another which separates these intimate kinds of association very markedly from those of the looser kind. As explained further on p. 6,

mutualism and symbiosis are here considered as special cases of parasitism in which mutual metabolic dependence occurs.

Although this text is concerned with the phenomenon of parasitism in particular, it is worth while to consider briefly the other types of heterogenetic associations in order to place parasitism in its true perspective.

1.2 Commensalism

The term literally means 'eating at the same table', and there are a number of often-quoted classical examples of this type of loose association between animals of different species. One of the best known is that between certain species of hermit crabs and sea-anemones, in which the anemone lives on the shell sheltering a hermit crab. The sea-anemone benefits directly, having access to the remains of food caught and scattered by the crab, whereas the crab benefits by the presence of the sea-anemone which assists in warding off undesirable predators. In many cases, although this type of association is beneficial to one or both organisms, it is not usually obligatory for their existence. An exception is the association between the hermit crab *Eupagurus prideauxi* and the anemone *Adamsia palliata*, in which neither of the partners is able to survive alone. The crab crawls into a shell which is too small for itself and uses the pedal disc of the anemone as cover for the unprotected portion of its body.

Commensalism may thus be considered a type of loose association in which two animals of different species live together *without either being metabolically dependent on the other*, although one or both organisms may receive some benefit from the association. It is important to stress the absence of *metabolic* dependence in this type of association, for it is the absence of this feature, in particular, which in the definition considered further below (p. 3) separates a commensal sharply from a parasite.

1.3 Phoresis

There appears to be no difference of opinion on this term, which is used for a particular type of association in which one organism merely provides shelter, support or transport for another organism of a different species.

The classical example is that of fishes belonging to the genus *Fierasfier*, which live within the respiratory trees of holo-

thurians, or occasionally in starfish. These fish are relatively helpless and are readily attacked and devoured by other species. The holothurians appear to be undisturbed by the presence of the fish.

○○○ 1.4 Parasitism

In the type of association which forms the subject matter of this book, contact between the individuals of two different species differs markedly from that already described in that it is intimate and continuous. Many parasites have free-living stages in their life cycles and only during the periods when they make contact with their hosts can they actually be considered to lead a parasitic existence.

○ 1.4.1 General considerations

Of all the types of animal associations, perhaps the term parasitism has been the most difficult to describe. This appears to be largely due to the failure to recognise that the term has only a relative meaning. It has also been complicated by the insistence of many authors that a parasite must *necessarily* be harmful to its host: Crofton (1971*a*) proposes further that the term parasite should be restricted to organisms which are *potentially* capable of *killing* their host. In the writer's opinion, emphasis on the harmful effects of a parasitic association, more than any other single factor, has somewhat bedevilled a broad, biological approach to considerations of the phenomenon. It must be recognised, however, that any worker is entitled to restrict his usage of any term in any way, provided that he clearly defines his understanding of the term.

In an earlier edition of this text, while recognising the relative basis of terminology in general, the writer stressed the physiological and metabolic relationship between host and parasites (Smyth, 1962). At that time, little was known concerning the interaction of host and parasite metabolisms, but since then this field of parasitology has expanded considerably and much more information is now available. This view has been further developed by a number of authors (see Lincicome, 1963; Read, 1970) but is only one of the various aspects of the whole complex phenomenon of parasitism. Intricate physiological or immunological interactions between host and parasite are also involved, especially during the infective and establishment processes (Rogers, 1962; Sprent, 1963). Many of these aspects

are discussed when the individual life cycles of different species are being considered; immunological reactions are dealt with in Chapters 32 and 33.

○ 1.4.2 Metabolic dependence

A parasite is thus considered here to be an organism which is not only in continuous, intimate association with another organism, the host (normally of a different species, but see below), but is also metabolically dependent, directly or indirectly, on it to some degree. The relative nature of this association is stressed and it is possible to draw up a list of parasite species which show an increasing degree of metabolic dependence on their hosts. At one end of this hypothetical scale (Fig. 1.2) is zero dependence, i.e. a free-living organism; at the other end is 100 per cent dependence or total parasitism. In between these two extremes lies a range of organisms which satisfy their metabolic requirements to a varying extent at the expense of the host.

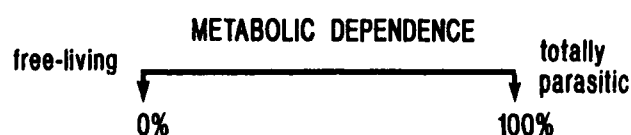


Fig. 1.2 Diagram illustrating the relative concept of parasitism based on the degree of metabolic dependence of a parasite on its host. A free-living organism shows zero dependence, whereas a blood-dwelling protozoan (e.g. *Plasmodium*) is 100 per cent dependent. All degrees between these two extremes are encountered.

MacInnis (1976) neatly proposes a similar fundamental concept of parasitism by defining it as an association in which '*one partner, the parasite, of a pair of interacting species, is dependent upon a minimum of one gene or its products from the other interacting species, defined as the host, for its survival.*

We must make clear here what we mean by 'metabolic dependence'. Although at first sight it would appear that most parasites are only dependent on their hosts for food materials, a closer examination shows that the situation is more complex than this. Examples can be given of parasites which are dependent on their hosts for one or more of the following: (a) developmental stimuli; (b) nutritional materials; (c) digestive enzymes; (d) control of maturation and (more rarely) mitosis.

Each of these can now be considered in some further detail.

4 | 1 Parasitism: what is a parasite?

(a) **Developmental stimuli.** Stimuli of this nature may be defined as those which stimulate or 'trigger' the parasite to enter into its next phase of development. Thus, parasites have evolved devices whereby they can automatically 'recognise' that they are in the particular host environment suitable for establishment and subsequent development. This is achieved by responding to a particular parameter, or combination of parameters, of that environment. A wide variety of factors can be utilised by parasites, the only stipulation being that each host environment contains a unique combination of parameters; this is essential to ensure that the recognition and trigger for development only occurs at the appropriate site. Thus many parasites in an encysted state (e.g. the metacercarial cysts of trematodes p. 195, the oocysts of coccidia p. 95) or in a suspended state (e.g. the infective larvae of many nematodes, such as *Haemonchus contortus*, p. 416), utilise mainly the high $p\text{CO}_2$ of the intestine as a 'signal' for excystment or ensheathment; moreover, this process is often enhanced by other factors such as a low E_h or the presence of bile. In contrast, many cestodes utilise bile as a signal; this normally stimulates the evagination of the scolex so that attachment can occur. In at least one species, *Echinococcus granulosus*, the evaginated scolex must further make contact with a suitable surface, i.e. the gut mucosa or a suitable surface *in vitro* (p. 515). Again several cestodes of birds (body temperature, 40 °C) with larval stages in fish (body temperature, 10–15 °C) utilise the sudden change in temperature from fish to bird host as the stimulus to trigger the plerocercoid larva to undergo maturation (p. 509) in the bird host.

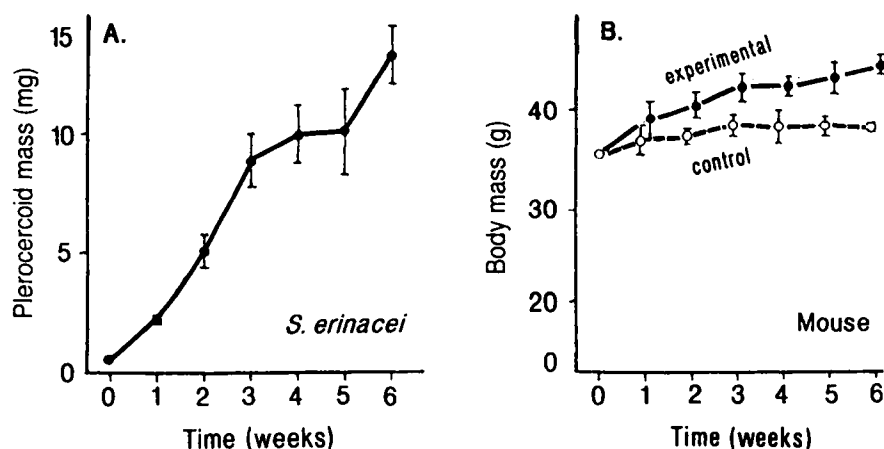
How these triggers act in physiological or biochemical terms has been one of the major problems in parasitology and is discussed when the developmental biology of the various groups is considered.

(b) **Nutritional dependence.** It is self-evident that this is undoubtedly the commonest form of metabolic dependence. A range of levels occurs and parasites may be dependent for nutritional supplies on (a) the food of the host either before or after digestion; (b) the tissues of the host; or (c) secretions of the host. In most parasites, all the nutritional requirements are satisfied by the host but some parasites may obtain additional materials from extraneous sources. Consider, for example, the case of a monogenetic trematode (p. 169) parasitic on the gills of a fish. This parasite feeds on the blood vessels of the gills, but is able to digest the engorged

blood by means of its own enzymes and utilise the breakdown products obtained. Owing to the close contact with sea water, however, it almost certainly has access to extraneous oxygen by diffusion. Thus, in the synthesis of the parasite tissue, some of the oxygen molecules utilised for synthetic or energy purposes will have been derived from non-host sources. Nutritional dependence on the host can thus not be said to be complete.

In contrast, species of blood flukes, e.g. *Schistosoma haematobium* (p. 237) in the mesenteric veins of man are 100 per cent dependent on the host for all nutritional supplies including oxygen. Thus, in the synthesis of parasite tissue the percentage of atoms of host origin which are metabolically involved could be used as a means of estimating the nutritional dependence on the host.

(c) **Digestive enzymes.** Dependence of a parasite on the host for its food materials is of little value unless it can utilise the food thus obtained. There is increasing evidence that the majority of trematodes and nematodes possess the digestive enzymes necessary to hydrolyse complex molecules. Many parasites, like the monogenetic trematode quoted above, can digest blood and tissue. The larva of *Diplostomum phoxini* (p. 504), for example, can digest an egg-albumen mixture *in vitro* and utilise the breakdown products for the processes of growth and differentiation. Such organisms are therefore not dependent on the host for digestive enzymes. On the other hand, adult tapeworms can probably only utilise molecules small enough to be taken in through their tegument (p. 284) and are therefore largely dependent on their host's ability to break down carbohydrates, fats and proteins enzymatically. There is some evidence, however, that larval cestodes (e.g. cysticerci) can take in large molecules by pinocytosis (p. 284) but the situation in adult worms is equivocal (p. 284). A process of *membrane* (= contact) digestion may also occur in cestodes (Fig. 24.1). Some parasites have lost the enzyme systems involved in certain fundamental processes. For example, cestodes have lost their capacity for *de novo* synthesis of lipids and have become entirely dependent on the host for the provision of these (Frayha & Smyth, 1983). However, it is important to note that the host may also utilise metabolic products from the parasite, so the process of exchange may sometimes be a two-way one (Lincicome, 1963). Striking examples of this are the plerocercoids (spargana) of the cestodes *Spirometra mansonioides* and *S. erinacei* (p. 310) which release a

**Fig. 1.3**

(A) Growth of plerocercoids ('spargana') of the cestode *Spirometra erinacei* (p. 310) in the tissues of mice, and (B) their effect on the body mass of their hosts. (After Shiwaku *et al.*, 1982.)

Table 1.1. *Spirometra mansonioides*; comparison of some molecular activities of the human growth hormone (hGH) with those of the plerocercoid growth factor (PGF)

	hGh	PGF†
Relative molecular mass	22000	22000
Isoelectric point	4.9	4.7
Reacts with hGH-specific monoclonal antibody (%)	100	61

Source: Data modified from Phares (1987).

substance (the *plerocercoid growth factor*) which induces increased growth weight (Fig. 1.3) in infected mice (Mueller, 1974; Odening, 1979; Shiwaku *et al.*, 1982). This factor has been shown to have physiological and biochemical characteristics similar to the human growth factor (Table 1.1) and Phares (1987) has put forward the intriguing hypothesis that the plerocercoid growth factor is produced by a human growth factor gene which has been 'stolen' by the parasite from the human host, a situation which has been referred to as 'genetic theft'!

(d) **Control of maturation.** A number of species have been shown to be dependent on the host for the control of their maturation processes. Such examples represent a remarkable stage in the evolution of parasitism, whereby an endocrine system developed to stimulate metabolic processes in one animal is utilised by another of a different species. This results in the

synchronisation of the reproductive phases of host and parasite, an effect which has considerable survival value for the parasite. For example, the blood protozoan *Leucocytozoon* (p. 138) undergoes a multiplication phase resulting in a rapid increase in the number of its gamete-producing cells (gametocytes) only during the breeding season of its duck host, a time which corresponds to the natural occurrence of its vectors (blackflies).

Other parasites whose life cycles are influenced by the hormonal activity of the host are certain parasites of the frog – the protozoa *Opalina ranarum* (p. 146) and *Nyctotherus cordiformis* (p. 152), and the monogenean *Polystoma integerrimum* (p. 163). The life cycles of these organisms are beautifully synchronised with that of the amphibian host and involve release of cysts or eggs at a time when the frog is breeding in water, i.e. when potential tadpole hosts are assured. It has been shown experimentally that maturation of the parasites is related to the levels of sex hormones in the host and may be induced experimentally by injecting suitable hormones into the host (Mofty & Smyth, 1964).

As astonishing example of host–parasite synchronisation also occurs in a monogenetic trematode, *Pseudodiplorchis americanus*, parasitic in the spadefoot toad, *Schaphiopus couchii*, in the USA (Tinsley, 1982–1990; Tinsley & Jackson, 1986, 1988). This toad is entirely desert-adapted and enters the water to spawn only for a few hours in 1–3 nights during the summer rains (Figs 11.8–11.11). The uteri of the parasites contain over 200 fully developed larvae, which are encapsulated. When the toads enter the water the larvae are released

6 | 1 Parasitism: what is a parasite?

within seconds of their deposition, the escaping oncomiracidia invading the nostrils of adult toads. Unlike *Polystoma*, however, the trigger for the egg release does not appear to be hormonal and its nature, at present, is unknown. The life cycle of *Pseudodiplorchis* is discussed further on p. 167.

A further remarkable example of synchronisation of host and parasite metabolic activities has been demonstrated by Wikgren *et al.* (1970) who showed that the mitotic activity pattern of plerocercoids of the cestode *Diphyllobothrium dendriticum* followed the same circadian rhythm as the comparable cycle of the host. Many other examples of circadian rhythms in parasites are known (Hawking, 1975).

From the above examples, it is clear that the physiological or metabolic dependence of a parasite on its host is a most complex matter involving much more than just nutritional factors and that each host–parasite system must be analysed individually before the full extent of this dependence can be evaluated.

○ 1.4.3 Mutualism and symbiosis

An association in which both associates benefit has long been referred to as *mutualism* by some authors and *symbiosis* by others. The literature on the definition of these words is confused. Mutualism is derived from the Latin *mutuus* (= exchanged), whereas symbiosis comes from the Greek *symbioun* (= to live together). The term *symbiosis* could thus broadly be used to include all the different kinds of relationship that exist in nature. By usage, however, it has come to be restricted to associations of a special kind in which the participating species are dependent on each other for existence. In cases of mutualism, on the other hand, the association is not obligatory for existence.

On the metabolic view put forward above, both mutualism and symbiosis are merely recognised as special cases of parasitism in which some metabolic by-products of the parasite are of value to the host. There are several well-known examples of the phenomenon. The association between wood-eating termites and hyperflagellates in their intestine is of the symbiotic type of parasitism. The termites are entirely dependent on the flagellates for certain nutritional requirements, notably the supply of nitrogen and carbohydrates obtained by the breakdown of wood. The flagellates are similarly dependent on the host for nutriment and the physical environment in which they live. The depen-

dence of the host on the flagellates may be readily demonstrated by raising the termites to a temperature which is lethal to the protozoans, thus defaunating them. Under such conditions, the termites fail to survive, as they lack the enzyme systems necessary to digest a wood diet.

The association between intestinal ciliates and their ruminant hosts (discussed on p. 154) is of a similar nature. Several genera of ruminant-dwelling protozoans produce the enzymes cellulase and cellobiase, thus enabling them to split cellulose and utilise the breakdown products for their metabolism. The rate of fission of these ciliates is extremely rapid, and they soon die. On disintegration, they provide the host with about one-fifth of its total nitrogen requirements.

An example of an association which could be considered to be mutualistic is that between the coelenterate *Hydra viridis* and the alga *Zoochlorella* which lives within its endodermal cells. The alga produces oxygen which *Hydra* utilises, and *Zoochlorella* makes use of the nitrogenous waste products of *Hydra* for its synthetic processes. It is possible that a mutualistic association exists in many cases of parasitism, but sufficient physiological studies have not been made to reveal their existence.

○ 1.4.4 Types of parasite

Once the relative connotation of the term ‘parasite’ is accepted, parasites can be classified in other ways according to their life cycles, position in or on the host, or other features. It is common practice, for example, to speak of *ectoparasites* and *endoparasites*. *Ectoparasites* are organisms (e.g. fleas, lice, ticks) that live on the outside of their hosts, usually attached to the skin, feathers, hair, gills, etc.; such forms can never lead a completely parasitic existence, but utilise oxygen from outside the host. Many maintain only periodic contacts with their hosts and, according to the definition given earlier, cannot be considered parasites but essentially special kinds of predators. *Endoparasites* are parasites living within their hosts, in the gut, body cavity, lungs or other tissues; such forms nearly always live a completely parasitic existence. Certain parasites fall into both these groupings. The itch mite (*Sarcoptes scabiei*), for example, burrows in tunnels in the skin and could satisfy the criteria of either an ectoparasite or an endoparasite. Again then, these terms cannot always be accurately defined, but they are convenient general terms. Parasitologists also speak of *facultative* parasites, organisms

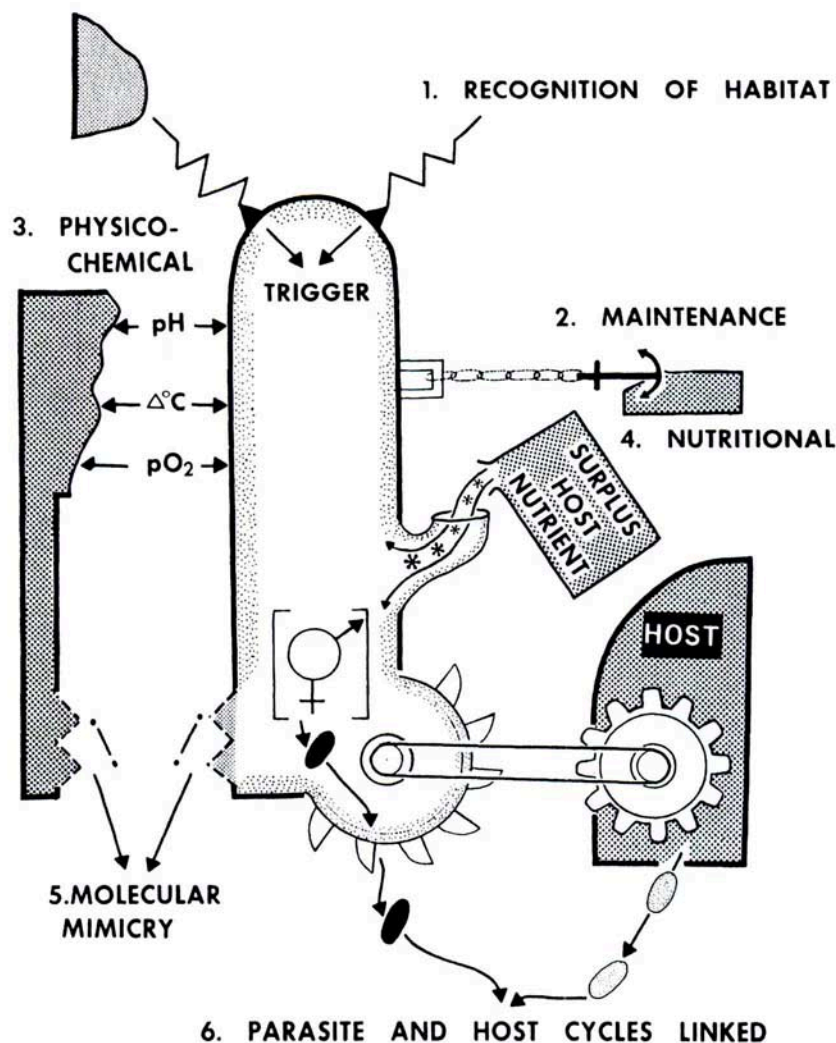


Fig. 1.4

A cartoon-like representation of an 'ideal parasite' which: (1) 'recognises' a host site suitable for establishment; (2) maintains its position there; (3) is adapted to the physico-chemical conditions of the host; (4) utilises host nutrient in a manner compatible with host

survival; (5) presents a surface with a molecular configuration such that the host immune response is absent or minimised (see p. 000); (6) has a life cycle synchronised with that of the host. (After Smyth, 1972.)

which can live either a parasitic or non-parasitic existence, and *obligate* parasites, which are obliged to live a parasitic existence and are incapable of surviving outside the host environment. In the latter definition the emphasis must be on a 'naturally occurring' environment, for many 'obligate' parasites can now be cultured in artificial environments of a complex nature (Chapters 33, 34).

To invade the body of another species of animal, and to live and multiply in or on it, could not have been achieved without considerable morphological, physiological, biochemical and immunological adaptations by the parasite. Some of these adaptations have been discussed here and are covered more fully in the text. It

is not intended, however, to discuss the morphological adaptations of parasites to their way of life. These have been discussed in detail by numerous authors, especially Baer (1952) and Caullery (1952), and a considerable literature exists on this aspect of parasitism.

Much more information is now also available on the biochemical and physiological adaptations of parasites, especially protozoa (Coombs & North, 1991; Englund & Sher, 1988; Gutteridge & Coombs, 1977; Kreier & Baker, 1987) and helminths (Barrett, 1981; Bennett, Behm & Bryant, 1989; Trager, 1986; Smyth & Halton, 1983; Bryant & Behm, 1989; Smyth & McManus, 1989).

8 | 1 Parasitism: what is a parasite?

A coherent picture of the processes underlying parasitism will only emerge when all aspects of the phenomena are fully understood. Fig. 1.4 is a cartoon-like representation of the 'ideal parasite' which serves to underline some of the problems involved.

○○○ References

(References of general interest have been included in this list, in addition to those quoted in the text.)

- Anderson, R. M. 1982. *Population Dynamics of Infectious Diseases: Theory and Applications*. Chapman & Hall, London.
- Anderson, R. M. 1987. The role of mathematical models in helminth population biology. *International Journal for Parasitology*, 17: 519–29.
- Anderson, R. M. & May, R. M. 1985. Helminth infections of human: population dynamics and control. *Advances in Parasitology*, 24: 1–101.
- Baer, J. G. 1952. *Ecology of Animal Parasites*. University of Illinois Press, Urbana.
- Barrett, J. 1981. *Biochemistry of Parasitic Helminths*. The Macmillan Press, London.
- Bennett, E.-M., Behm, C. & Bryant, C. 1989. *The Comparative Biochemistry of Parasitic Helminths*. Chapman & Hall, London. ISBN 0 412 32730 9.
- Bryant, C. & Behm, C. 1989. *Biochemical Adaptation in Parasites*. Chapman & Hall, London.
- Caulley, M. 1952. *Parasitism and Symbiosis*. Sidgwick & Jackson, London.
- Coombs, G. H. & North, N. J. (eds) 1991. *Biochemical Protozoology*. Taylor & Francis, London.
- Cox, F. E. G. 1982. *Modern Parasitology*. Blackwell Scientific Publications, Oxford.
- Crofton, H. D. 1971a. A quantitative approach to parasitism. *Parasitology*, 62: 179–93.
- Crofton, H. D. 1971b. A model of host-parasite relationships. *Parasitology*, 63: 343–64.
- Englund, P. T. & Sher, A. 1988. *The Biology of Parasitism: a Molecular and Immunological Approach*. Alan R. Liss, New York.
- Esch, G. W., Bush, A. O. & Aho, J. M. 1989. *Parasite Communities*. Chapman & Hall, London. ISBN 0 412 33540 9.
- Frayha, G. & Smyth, J. D. 1983. Lipid metabolism in parasitic helminths. *Advances in Parasitology*, 22: 309–87.
- Gutteridge, W. E. A. & Coombs, G. H. 1977. *Biochemistry of Parasitic Protozoa*. The Macmillan Press, London.
- Hawking, F. 1975. Circadian and other rhythms of parasites. *Advances in Parasitology*, 13: 123–82.
- Kennedy, C. R. 1975. *Ecological Animal Parasitology*. Blackwell Scientific Publications, Oxford.
- Kennedy, C. R. (ed.) 1976. *Ecological Aspects of Parasitology*. North-Holland, Amsterdam.
- Kennedy, C. R. 1983. General ecology. In: *Biology of the Eucestoda*, Vol. 1 (ed. C. Arme & P. W. Pappas), pp. 27–80. Academic Press, London.
- Kreier, J. P. & Baker, J. R. 1987. *Parasitic Protozoa*. Allen & Unwin, Massachusetts.
- Lincicome, D. R. 1963. Chemical basis of parasitism. *Annals of the New York Academy of Sciences*, 113: 36–380.
- MacInnis, A. J. 1976. How parasites find their hosts: some thoughts on the inception of host–parasite integration. In: *Ecological Aspects of Parasitology* (ed. C. R. Kennedy), pp. 3–20. North-Holland, Amsterdam.
- Mehlhorn, H. 1988. *Parasitology in Focus*. Springer-Verlag, Berlin. ISBN 3 540 17838 4.
- Mofty, M. M. El & Smyth, J. D. 1964. Endocrine control of encystation in *Opalina ranarum* parasitic in *Rana temporaria*. *Experimental Parasitology*, 15: 185–99.
- Mueller, J. F. 1974. The biology of *Spirometra*. *Journal of Parasitology*, 60: 3–14.
- Noble, E. R., Noble, G. A., Schad, G. & MacInnis, A. J. 1989. *Parasitology. The Biology of Animal Parasites*. Lea & Febiger, Philadelphia.
- Odening, K. 1979. Zum Erforschungsstand des 'Sparganum Growth Factor' von *Spirometra*. *Angewandte Parasitologie*, 20: 185–92.
- Phares, C. K. 1987. Plerocercoid growth factor: a homologue of human growth hormone. *Parasitology Today*, 3: 346–9.
- Pennycuik, L. 1971. Frequency distribution of parasites in a population of three-spined sticklebacks, *Gasterosteus aculeatus* L., with particular reference to the negative binomial distribution. *Parasitology*, 63: 389–406.
- Read, C. P. 1970. *Parasitism and Symbiology. An Introductory Text*. Ronair Press, New York.
- Rogers, W. P. 1962. *The Nature of Parasitism*. Academic Press, New York.
- Rollinson, D. & Anderson, R. M. 1985. *Ecology and Genetics of Host–Parasite Interactions*. Academic Press, London. ISBN 0 125 93690 7.
- Schmid, W. D. & Robinson, E. J. 1972. The pattern of a host–parasite distribution. *Journal of Parasitology*, 58: 907–10.
- Schmidt, G. D. & Roberts, L. S. 1989. *Foundations of Parasitology*. 4th Edition. Times Mirror/Mosby College Publishing, St Louis.
- Shiwaku, K., Hirai, K., & Torii, M. 1982. Growth-promoting effect of *Spirometra erinacei* (Rudolph, 1819) plerocercoids in mature mice: relationships between number of infected plerocercoids and growth-promoting effect. *Japanese Journal of Parasitology*, 31: 353–60.
- Smyth, J. D. 1962. *An Introduction to Animal Parasitology*. 1st Edition. English Universities Press, London.
- Smyth, J. D. 1972. *Parasites as Models in Cellular Differentiation*. Inaugural Lectures, Vol. 9, pp. 55–66. Imperial College, University of London.
- Smyth, J. D. & Halton, D. W. 1983. *The Physiology of Trematodes*. 2nd Edition. Cambridge University Press.
- Smyth, J. D. & McManus, D. P. 1989. *The Physiology and Biochemistry of Cestodes*. Cambridge University Press.
- Sprent, J. F. 1963. *Parasitism*. University of Queensland Press, Brisbane.

- Tinsley, R. C.** 1982. The reproductive strategy of a polystomatid monogenean in a desert environment. *Parasitology*, **85**: XV.
- Tinsley, R. C.** 1988. The effects of host sex on transmission success. *Parasitology Today*, **5**: 190–5.
- Tinsley, R. C.** 1990. Host behaviour and opportunism in parasite life cycles. In: *Parasitism and Host Behaviour* (ed. C. J. Barnard & J. M. Behnke), pp. 158–92. Taylor & Francis, London.
- Tinsley, R. C. & Earle, C. M.** 1983. Invasion of vertebrate lungs by the polystomatid monogeneans *Pseudodiplorchis americanus* and *Neodiplorchis scaphiopodis*. *Parasitology*, **86**: 501–17.
- Tinsley, R. C. & Jackson, H. C.** 1986. Intestinal migration in the life-cycle of *Pseudodiplorchis americanus* (Monogenea). *Parasitology*, **93**: 451–69.
- Tinsley, R. C. & Jackson, H. C.** 1988. Pulsed transmission of *Pseudodiplorchis americanus* between desert hosts (*Scaphiophus couchii*). *Parasitology*, **97**: 437–53.
- Trager, W.** 1986. *The Biology of Animal Parasitism*. Plenum Press, New York.
- Wikgren, B.-J. P., Knuts, G. M. & Gustafsson, M. K. S.** 1970. Circadian rhythm of mitotic activity in the adult gull-tapeworm *Diphyllobothrium dendriticum* (Cestoda). *Zeitschrift für Parasitenkunde*, **34**: 242–50.

2

Niches, habitats and environments

○○○ 2.1 Niches

Definition. As already emphasised, Parasitology is essentially a branch of Ecology in which the habitat and environment of an organism (the parasite) is provided by another organism (the host). Hence many of the principles which apply to free-living organisms can also be applied to parasites. One of the most important of these – and perhaps one of the most neglected – is the concept of the *niche*.

All living organisms can be said to occupy a biological *niche*, but few terms in biology have been so misunderstood and yet it is a term of great significance to parasitologists. It essentially refers to an (abstract) 'space' in the biotic environment in which life is possible. Some workers confuse the term with 'habitat', the latter being only the environmental component of the niche. The habitat is sometimes referred to as an 'environmental niche' of which the alimentary canal or the gills of fishes could be considered common examples. It is possible, for example, for two different species of parasites to occupy the same *habitat* (e.g. the intestine) while occupying different *niches*, because one utilises glucose as a nutritional substance, whereas the other utilises fructose; they thus occupy different (nutritional) niches.

These considerations have given rise to the concept of a *fundamental niche* as 'That unique combination of environmental factors, biotic and abiotic, which are capable of supporting life'. Since there are an unlimited number of both biotic and abiotic factors to be considered, the (abstract) concept of a fundamental or ecological niche is sometimes referred to as an *n-dimensional hypervolume*.

The question can be asked, what happens when two populations of the same species attempt to occupy the same niche? This problem was first considered by the Russian biologist Gause (1934), who postulated – what is now known as Gause's Law (Hypothesis) – that 'No two forms can occupy that same

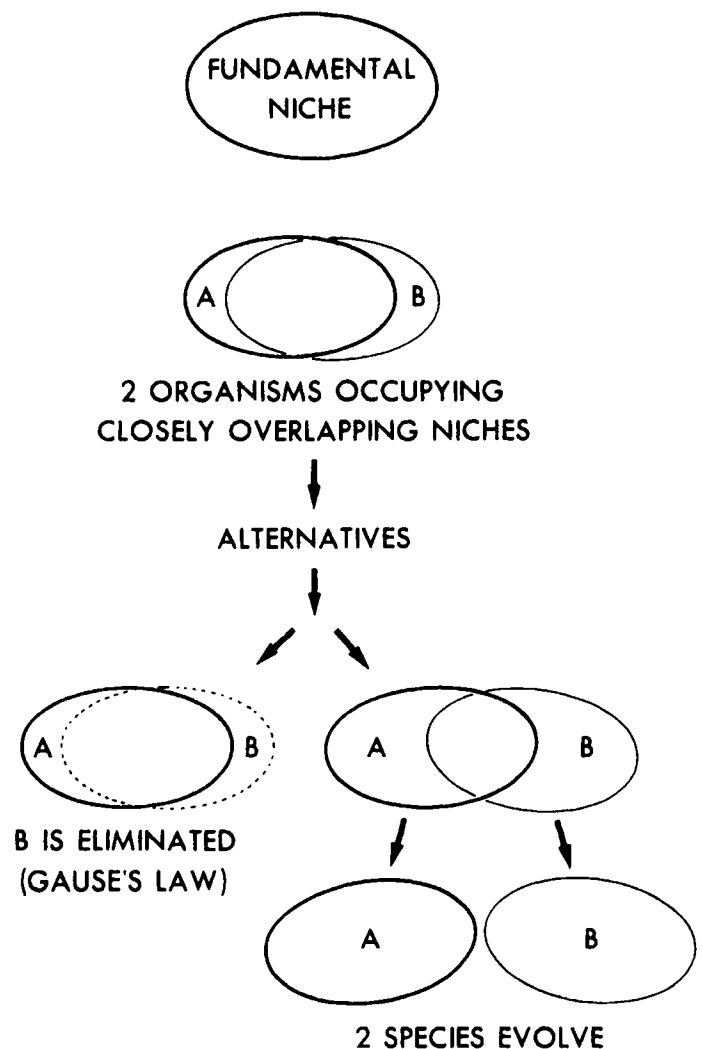


Fig. 2.1

Gause's Law. If two species attempt to occupy the same niche, for any length of time, either one will replace the other, or each species will evolve in such a way that their niches no longer overlap. (After Smyth, 1987.)