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The spectrum of animal–animal associations

Intra-specific associations

With the possible exception of the castaway sitting with his eight records on that mythical desert island, we all rely to a greater or lesser extent on other people. We have associations with them. These personal relationships vary from the remote, the people who provide services that we only notice when they are withdrawn because of industrial (in)action; through the casual, the person we try to ignore on the bus; to the intimate, our immediate family and close friends.

Similar associations occur between animals of the same species (**intra-specific associations**). The range of these associations is enormous and attempts to categorise them are fraught with difficulty as there are so many exceptions. It is, however, possible to offer a number of illustrative examples. These are presented in order of increasing permanence and dependence between the partners.

Herd/flock associations

A herd or flock is generally a loosely knit community which individual animals are free to join or leave. While the size of the herd makes it conspicuous and may attract the attention of predators it is generally the sick and young animals that are vulnerable. Increased numbers provide protection, as some individuals can be on watch while others feed, so that there is continuous vigilance for the group as a whole and greater protection for the majority. When predators

Table 1.1. *Relationship between female fecundity and parental care in a number of teleost fish species*

	Number of eggs in batch	Parental care
Cod (*Gadus morhua*)	4,000,000	None
Herring (*Clupea harengus*)	35,000	None
Gunnel, Butterfish (*Pholis gunnellus*)	400	Parents guard egg mass on shore
Siamese fighting fish (*Betta splendens*)	150	Male guards bubble nest
Stickleback (*Gasterosteus aculeatus*)	75	Male guards nest
Sea horse (*Hippocampus*)	55	Male brood pouch
Tilapia	35	Female broods in mouth

do strike they tend to attack individual, outlying animals and there is often a movement of individuals towards the centre of the group where protection is greatest. Interestingly this protection is not only from macropredators but also from biting flies and other **ectoparasites**. Individual animals in larger groups have fewer flies on them and those in the centre of the group have fewer than those at the periphery. Herds, flocks, shoals and swarms also provide advantages in mate location and breeding, indeed some species only aggregate during the breeding season. These associations are thus generally beneficial but not obligatory and many species are largely solitary except for short periods of mating.

Parental care

The amount of effort devoted to parental care by different species varies greatly and seems to be inversely proportional to the number of offspring produced (Table 1.1).

At one extreme are those animals that shed their gametes into the environment and take no further interest in their development or well-being. Seasonality, shoaling, aggregation and communal habits all tend to encourage the union of gametes, but the wastage of zygotes is enormous. In human terms this may appear profligate and irresponsible, but the larval stages of, for example, marine invertebrates provide much of the animal plankton that is so important to marine food webs.

At the other extreme are the higher mammals with internal fertilisation and development and the birth of a small number of relatively well developed offspring. In the case of the primates birth may be followed by several years of more or less continuous attention until the young are fully capable of leading an independent existence. In some cases, e.g. elephants, care of the young is shared by different members of a larger family group so that the biological parents do not have sole responsibility for raising their young. This is, of course, another advantage of living in a group of the same species.

Between these two extremes are many intermediate stages. There are many examples of marine annelids, crustaceans, molluscs, fish and other species that brood their eggs in burrows or nests or about their bodies. Parental care is not necessarily the responsibility of both parents or even of the mother. It is male Siamese fighting fish (*Betta splendens*) and three-spined sticklebacks (*Gasterosteus aculeatus*) that build nests, entice their females to them and then guard the fertilised eggs until they hatch. Male sea horses (*Hippocampus*) have a brood pouch beneath the tail and eggs are transferred to this during mating. Here they remain until they have hatched and the fry are able to fend for themselves. In the case of the midwife toad (*Pipa*) it is the female that provides the brooding protection. The eggs are not laid in water as they are for other amphibians, but are deposited under flaps of skin on the back of the female. Here they hatch and metamorphose so that small toads emerge from their mothers. Once the young have left the parent there is often little effort to provide long-term protection, and indeed in some cases an unwary offspring may provide a tasty mouthful for a hungry parent!

Birds, of course, take greater care of their progeny and will feed and care for them until they are relatively well developed, able to fly and to feed independently. This, in the case of some of the larger species, may take a year or more and thus reduces the reproductive potential of the parents. A balance is thus achieved between the number of progeny and the effort that the parents put into raising their young.

Pairing

The reproductive imperative is strong in all species but the outward signs of intimacy vary enormously. **Hermaphrodite** organisms which contain both male and female organs may appear to have overcome the difficulties of locating a suitable mate, but for many of these species cross-fertilisation is the rule so they face similar problems to **dioecious** species.

Many species show no appreciation of the opposite sex and gamete production and release appear to be governed more by environmental factors than by association. Other species go to considerable lengths to attract a mate even though for most of the time they are solitary. The **pheromone** attractants produced by some female moths are legendary, being able to attract males from several kilometres away. Yet other species only come into breeding condition when in more or less permanent relationship with a mate, and mate attraction becomes even more important for these. In many cases, once the partners have paired and mated the association is terminated and many males go off to seek other females, but for other species the pair may remain together for a time after mating. If parental care is to be provided by both parents then the relationship between them must last for at least the time needed to raise their young.

Some species, e.g. swans, are **monogamous** and mate for life, but each member of the pair is capable of an independent existence. There are species where one of the members, usually the male, gives up its independence to remain permanently with the female. Thus the diminutive males of some deep sea angler fish remain permanently attached to their much larger partners and share a blood supply. It is assumed that this unusual mode of life is in response to the extreme environments of the fish and the difficulties of locating a mate in the abyssal depths. Probably the most extreme example of togetherness is illustrated by *Trichosomoides crassicauda*, a nematode parasite of the bladder of rodents in which the male spends his life within the uterus of the female. It is difficult to conceive of a more intimate association.

Colonial life

Not all colonial animals exhibit co-operation between individuals, indeed there may be competition between individuals, especially among juvenile stages for advantageous sites. Thus barnacles and mussels live in aggregations of individuals brought together by ecological and environmental factors and are probably better considered more like herds than true colonies. However, the most intimate and interdependent of intra-specific relationships are exhibited by animals that live colonially. The interrelationships between morphologically and physiologically different individuals with consequent division of labour in an ant or bee colony are well known. In some cases the colony may behave in such a co-ordinated way that it acts virtually as a single enormous individual. Even amongst colonial animals there is a gradation in levels of intimacy and interdependence. A single worker bee may be considered as an individual (it can sting you) as well as part of the greater whole, the colony. This is not true for the constituent polyps of the colonial coelenterates (Siphonophora). The Portuguese man-of-war (*Physalia*) and by-the-wind-sailor (*Velella*) drift on the ocean currents and may be seen on the shores of Britain during the summer. While these appear to be and are often considered individual organisms they in fact consist of a number of polyps, each with a specialised function for buoyancy, feeding, defence, reproduction, etc., much as the worker, soldier and queen ants have their own specialised functions within an ant colony. The only real difference is that the individual coelenterate polyps are no longer capable of individual locomotion.

Intriguing as these intra-specific associations are they are more the province of the animal behaviourist than the parasitologist, and the remainder of this text is concerned with associations between animals of different species (**inter-specific associations**).

Inter-specific associations

Emerson (1803–1882) once said '*He shall be as a god to me, who can rightly divide and define*', and there have been many attempts to achieve such division and definition of the vast range of inter-specific associations that have evolved. None of these attempts has been wholly successful and different authors have provided terminology to suit their own purposes. The present author is no exception and some definitions will be offered below. However, he is making no claims for deification and is well aware of the inadequacies of some of the definitions offered. Evolution has provided an infinity of variations around the theme. One concept that may be helpful is to consider the range of relationships not as a series of discretely defined entities but more as a continuum, with one type of association merging into the next rather in the way that the individual colours of the light spectrum merge almost imperceptibly from one to the next.

The extremes of such a sequence are relatively easy to recognise. No one would question that a hunting lion is a predator and the wildebeest its prey, or, on a different scale, that the spider is the predator and the fly trapped in its web the prey. The situation becomes more complicated with different relative sizes of predator and prey. A spider may trap an insect much larger than itself, stun it and over a period of time remove its body fluids as food. The prey is

Fig. 1.1 Female mosquito feeding on human skin. Depending on context she may be regarded as a micropredator or an ectoparasite. In addition she is likely to be a vector capable of carrying a range of disease-causing organisms from one host to another.

killed but not immediately, and the relationship is still recognisably predator/prey. But what if the insect had not been killed? This situation occurs when a mosquito takes a blood meal from a human (Fig. 1.1) or a leech attaches to a fish to suck its blood. The 'prey' item is not killed and, in many cases, except for a certain amount of nuisance, suffers little or no appreciable harm. The principle of attacking a larger animal and removing some of its body fluid is common to the spider, the mosquito and the leech, and some authors have used the term **micropredator** to cover all of these situations. Some 'micropredators', e.g. ticks and mites, may spend an appreciable proportion of their life on another animal and, because of their reproductive potential and blood feeding behaviour, cause extensive direct damage. Others, e.g. mosquitoes and Tsetse flies, may transmit disease-causing organisms. Many micropredators are often referred to as **ectoparasites**, (literally *ecto* – outside, *para* – beside, *sitos* – food) but again the principle of removing some of the host's body fluids is the same in each case. To add further to the confusion there are species, usually but not exclusively insects, which spend their larval stages within another species, again usually an insect, that they kill when they emerge as adults. These **parasitoids** have some of the attributes of a predator in that they eventually kill their host and some of the features of a para-

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site as they live part of their lives within it without killing it. Thus, even setting the first point in our spectrum is not as simple as might at first appear.

At the opposite end of the range are the mutualists. These are animals that are so interdependent that neither of the partners is able to maintain an independent existence, and removal of one results in the death of the other. Between the two limits of predator/prey relationships on the one hand and mutualists on the other there is a vast array of more or less intimate and more or less obligatory inter-specific relationships. The general term **symbiosis** (literally *sym* – together, *bios* – life) is often used to cover all categories of intimate inter-specific associations, but even here a word of caution is needed as some authors use the term symbiosis to cover a much more restricted set of non-obligatory, mutually beneficial associations.

Under the umbrella term symbiosis it is possible to recognise a number of sub-divisions that may be more or less clearly defined. In order of increasing intimacy and dependence these are commensalism, parasitism and mutualism, but as we will see there may be further sub-divisions within these.

Commensalism

Commensalism (literally *co* – together, *mensa* – table) is the least intimate and least obligatory of the generally recognised inter-specific associations. Both partners are able to lead independent lives but one or both may gain advantage from the association when they are together. Commensalism is widespread throughout the animal kingdom and a number of classes of commensalism have been recognised based on the biological nature of the bond between the partners. It should be noted that the associations recognised in the different divisions of commensalism are not exclusive to inter-specific associates; cleaning, protection, transport, etc. may be practised by partners in intra-specific relationships as well.

Cleaning commensalism Possibly the best-known and best-studied examples of commensalism come from the relationships between larger fish and small fish and shrimps which remove fungi and other ectoparasites from their bodies. The large fish encourage feeding by approaching specific, prominent 'cleaning sites' on the reef and taking up characteristic postures that indicate their non-aggressive intent. The cleaners then approach, remove and eat offending ectoparasites. This cleaning relationship has recently been investigated as a possible control measure against ectoparasitic sea lice on farmed Atlantic salmon kept in sea cages off Scotland and Norway. Initial experiments introducing wrasse (*Ctenolabrus* and *Labrus*) into the cages have been encouraging and may provide an environmentally friendly way of controlling a major problem.

Cleaning commensalism is not restricted to aquatic environments. There are, among others land crabs that remove ectoparasitic ticks from sun bathing Galapagos iguanas; Egyptian plovers (*Pluvianus aegyptius*), which were known to Herodatus (*c.* 480–*c.* 425 BC) as crocodile birds because of their habit of entering the mouths of Nile crocodiles to feed; and cattle egrets (*Bubulcus ibis*) which remove ectoparasites from a wide range of African mammals. Red billed oxpeckers (*Buphagus erythrorhynchus*) spend much of their lives on large African savannah mammals feeding on ectoparasitic arthropods, especially ticks. They may also give their partners advance warning of approaching predators so that both partners gain advantage from the association. However, the ticks that are removed contain some blood. The birds may gain a taste for blood to such an extent that they take it directly from unhealed lesions in the skin. They do not directly damage intact skin themselves but do delay the healing of existing wounds and may increase the chance of secondary bacterial infection. The balance of the relationship has thus been tilted slightly in favour of one of the partners, the oxpecker, to the detriment of the other.

The kea (*Nestor notabilis*) is a New Zealand parrot. During the summer it feeds mainly on fruit and insects but in the winter when such food is scarce it moves on to sheep and feeds on ectoparasites. When these run out it will attack the sheep directly, clinging to the wool near the tail and digging a deep hole with its powerful beak to feed on the fat around the kidneys. The relationship between the sheep and the kea thus changes during the year and, from being mutually beneficial becomes something much more sinister. This again illustrates the difficulty in presenting a rigorous definition for any association: the relationship may change as circumstances change.

Protective commensalism The hermit crab (*Eupagurus bernhardus*) lives in the discarded shells of the edible whelk (*Buccinum undatum*). Often the whelk shell has one or more sea anemones (*Calliactis parasitica*) attached to it. The crab transports the otherwise sessile anemones and it is probable that the anemones also gain extra food particles from the feeding of the crab. Whether the crab gains anything from the association is problematical. However the Mediterranean hermit crab (*Dardanus arrosor*), which lives in rather more fragile shells, actively transfers anemones on to its shell, and it has been shown that crabs with anemones are less liable to predation from octopus. Thus both partners benefit from their association but are able to live independently.

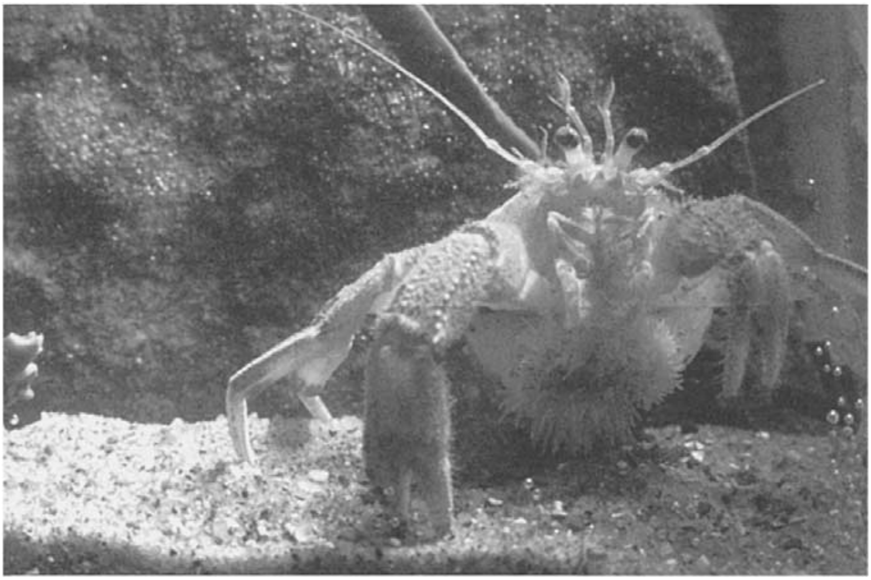

Fig. 1.2 Protective commensalism. The cloak anemone, *Adamsia palliata*, on a hermit crab, *Eupagurus prideauxi*. It is doubtful if the anemone provides much protection to the crab and this may be more an example of phoresis, but other crab/anemone associations have been shown to provide positive protective benefits.

The anemone (*Adamsia palliata*) which lives around shells occupied by the smaller hermit crab (*Eupagurus prideauxi*) (Fig. 1.2) is more commonly found on British shores. Normally when a hermit crab grows it moves to a larger shell, but *Adamsia* secretes a horny substance that effectively extends the shell making a move unnecessary. The anemone has a vested interest in maintaining the relationship as the crab is able to seek a new shell but a discarded anemone dies. This association, once established, is thus obligatory on one side but not the other.

Transport commensalism (phoresis) Transport commensalism or **phoresis** (literally transmission), as the name suggests, is an association based on transportation.

Dung pats in pasture constitute a rich habitat for many species of animal but they are temporary and liable to dry out or disintegrate and be washed away, depending on the prevailing weather. Their temporary nature is no problem to many of their inhabitants that are actively motile and can migrate to a fresh pat. For less active species the loss of habitat may be more serious and they may have to rely on haphazard contamination of the surrounding

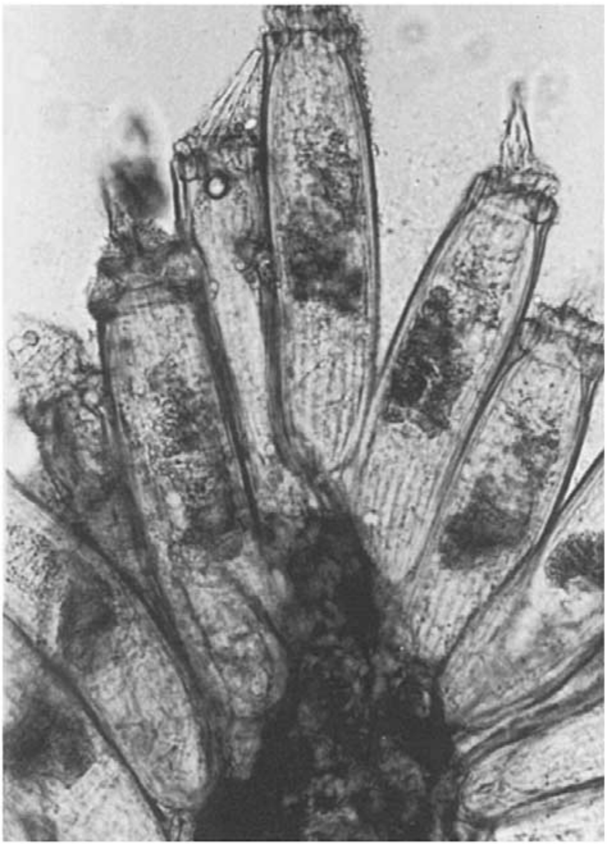

Fig. 1.3 Phoresis. Resistant dauer larva of the nematode *Pelodera coarctata*. The nematodes live on bacteria in faecal pats. As the habitat deteriorates they enter this resistant dormant state and attach to the cuticle of dung beetles for transport to fresh faeces.

pasture to effect transmission. The free-living nematode *Pelodera coarctata* solves the problem of transfer by 'hitching a lift' on another inhabitant of the dung pat, the dung beetle, *Aphodius fimentarius*. Normally the nematodes live and breed in the dung, feeding on the plentiful supply of bacteria there. As the dung begins to dry out they produce special desiccation resistant stages known as the **dauer larvae** (Fig. 1.3). These attach to the body of the beetle and are transported to a new site. As both nematode and beetle have a common aim in reaching fresh dung the partnership works well; there is no physiological connection between them and the association is only temporary.

Lice are wingless ectoparasitic insects that feed on blood, tissue debris and feathers of their hosts. Transmission of lice from host to host depends on