4.13 Predation

4.13.1 Marine

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Introduction

Predation, the killing and consumption of animals for food, is of fundamental importance in controlling diversity and abundance of organisms in modern marine environments. Predation was probably also critical in shaping longer term trends in adaptation; Vermeij (1977, 1987) has documented an evolutionary 'arms race' between marine shelled organisms and their predators through Phanerozoic time. Co-evolution between organisms and their predators has led to an intensification of the struggle for existence and increased complexity of organisms through time, which Vermeij refers to as escalation.

Predators form the apex of the biomass pyramid in any given community, and are commonly designated as first, second, or third order, depending on whether they feed primarily on herbivores or on other carnivores.

Predator–prey interactions are normally considered to represent dependent coactions, and a considerable theory has been developed based on the assumption that population sizes of predator and prey are mutually dependent. Indeed, certain terrestrial community studies appear to document a dependency of predators on specific prey. However, it has also been argued that much predation, particularly amongst marine organisms, is of a non-specific and opportunistic nature. In this case, the impact of predation on a particular prey species, and vice versa, may be less significant.

Modes of predation

The act of predation involves several phases (Bishop 1975): search, capture, penetration, ingestion, digestion, and defecation. The penetration and ingestion phases can be combined under the heading of subjugation. Vermeij (1987) further subdivided the modes of subjugation employed by durophagous marine predators into five categories. Whole animal ingestion involves swallowing the entire body of the prey animal and generally leaves no distinct marks upon the prey skeleton. In the process of insertion and extraction, the predator penetrates the skeleton of the prey and removes flesh through the aperture, again without damaging the skeleton. These modes of predation are not generally reflected in the hard part morphology of predators and thus are not identifiable in the fossil record. Some predators kill their victims by grasping them and transporting them into environments in which they cannot survive, e.g. in the case of shore birds which commonly transport marine molluscs into subaerial environments where they feed upon them. The chances of detecting this mode of predation in the fossil record are slim.

Pre-ingestive breakage and drilling both leave direct trace fossil evidence in the form of bite or crush marks and circular to parabolic bore holes. Both of these modes of predation have been the subject of several recent studies (for reviews see Vermeij 1987). Many predators break or puncture the shells of their victims prior to ingestion, using a variety of tools. Several marine molluscs employ a form of forced entry to break or separate the valves or plates of their prey. For example, the gastropod Acanthina utilizes a sharp spine on its shell’s outer lip to break apart the plates of barnacles;whelks of the genus Busycon use the sharp outer lip of their shell to chip and pry at the valve margins of bivalves. Cephalopods also possess chitinous or calcified beaks for biting or crushing prey. A wide variety of marine vertebrates, both living and fossil, utilize blunt pavement teeth to crush hard-shelled prey; these include rays, pycnodonts, placodonts, and various marine sharks. Most sharks, as well as fossil mosasaurs, use sharp teeth to pierce or fracture the shells of their prey. In the process, they may leave distinctive bite marks, such as divots or rows of holes in those shells (Fig. 1A–D). Crustaceans use three distinct strategies to break the shells of their prey, and in the process also produce distinctive traces. The shells may be crushed between the opposed surfaces of claws. Peeling involves the piece by piece breakage of the outer margin of gastropod shells by crabs (Fig. 1C) until the flesh of the organism becomes accessible to the predator. Still other crustaceans, primarily stomatopods, crush the shells of their prey by pounding them with blunt, expanded segments of their maxillipeds.
Drilling is a specialized mode of predation, largely restricted to marine molluscs, including both gastropods and cephalopods. These organisms leave very distinctive drilling traces, referred to the ichnogenus Oichmus (Fig. 1G–I), that provide direct records of successful predation. The boring procedure involves secretion of unknown acids by an accessory boring organ and mechanical abrasion by the denticles of the radula. The entire process is relatively slow, requiring from 5 to 100 hours for completion. Consequently, normally only a single hole is drilled per shell, although rarely one or more incomplete holes may be observed and there are instances of holes being produced in unoccupied shells. As a whole,
gastropod predatory boreholes can be distinguished from other types of borings in that they are circular in outline, penetrate the prey shell perpendicular to the shell, are parabolic or cylindrical in cross-section, and normally range from about 0.5 mm to 3.0 mm in diameter. Hole size is generally related to the size of the gastropod predator. Modern drilling gastropods are rather highly prey selective, favouring certain species of bivalves. They also show preferential positioning of the bore hole, most commonly near the centre of the prey shell (Fig. 1E, F). However, some Polynices and many muricids actually drill shells along the commissure (Fig. 1I). Naticid drill holes tend to be regularly parabolic in cross-section and, when incomplete, display a raised boss in the centre of the floor (Fig. 1H). Muricid gastropods, on the other hand, produce holes that are cylindrical in outline, tend to be more randomly distributed on the shells, and do not show a raised boss when incomplete. A third group of gastropods, the cassids (helmet shells), produce circular holes in echinoderm tests.

Cephalopods drill primarily for the purpose of paralysing their prey. The hole is generally oblique to the shell surface and tends to be conical, but is rather irregular in size and shape. Cephalopod boreholes are not yet known from the fossil record.

Fossil record of predation

Direct records of ancient predation are relatively rare in the fossil record; as Bishop (1975) noted, the evidence of predation is normally destroyed (literally eaten) in the process of its formation. However, several lines of evidence provide some insight into the evolutionary history of predation. The body fossil record of potential predators provides information on the general ranges of different carnivorous organisms. The predatory behaviour of fossil organisms may be inferred indirectly from morphological comparisons with living analogues known to have carnivorous habits, e.g. cephalopods and naticid gastropods. The fossil record commonly provides direct indications of a predaceous mode of life because the organs used in manipulation, biting, and ingestion of prey are typically heavily skeletonized and thus preservable. Such tools include the crushing claws of crustaceans, modified chelicerae of eurypterids, and a wide array of pavement and biting teeth in vertebrate groups.

Cephalopods with probable chitinous beaks are abundant from the Late Cambrian or Early Ordovician onward, but the direct fossil record of calcified beaks (rhytcholestes) does not begin until the Late Palaeozoic. Durophagous arthropods include mainly phyllocarids and eurypterids in the Palaeozoic; these had appeared by the Late Ordovician but attained maximum diversity in about the Middle Devonian. The decapod crustaceans in the Triassic evolved more efficient mechanisms of shell crushing by claws or maxillipeds. In the Jurassic, new groups of shell-crushing crustaceans evolved, including the stomatopods and brachyuran crabs.

A major increase in durophagous predators involved the abrupt appearance of varied jawed fishes in the Devonian Period, including the placoderms, ptyctodonts, hybodonts, and others (Fig. 2). Certain sharks, such as Helodus, with shell-crushing pavement teeth, have been implicated by Alexander (1981) as producers of distinct crush marks in Carboniferous brachiopods.

The large marine predators of the Mesozoic were dominated by reptiles within the subclass Diapsida: the placodonts (Placodontia), nothosaurs and plesiosaurs (Sauropterygia), ichthyosaurs (Ichthysauria), mosasours (Squamata; family Mosasauridae), and marine crocodyles (Crocodilia; family Metriorhynchidae, Teleosauridae). The evolution of large marine predator communities in the Mesozoic can be divided into four main periods of stability and slow diversification, separated by periods of reorganization or extinction (Massare 1987, 1988).

Sharks and large fish continued to diversify through the Late Cretaceous, and were the important marine predators in the Early Tertiary. Sharks probably reached their peak with the giants of the Miocene. Whales appeared in the Eocene, but early forms, the zuglodonts, were heterodont, long-bodied ambush predators more similar in body form to the Cretaceous mosasours than to modern whales. Seals, sea-lions, and modern whales appeared in the Late Oligocene and Miocene. Thus by the later epochs of the Tertiary, the marine predator communities had begun to take on a modern aspect.

Actual cases of predators in situ on prey, or of prey within stomach contents, provide compelling evidence for carnivory but are too rare to be of more than anecdotal interest. Notable examples include fossil asteroids (starfish) in situ on probable bivalve prey from the Devonian of New York and specimens of fish from various units, particularly the Cenozoic Green River Formation, with partially swallowed smaller fishes inside them (see p. 305). Certain late Palaeozoic sharks similarly display stomach contents, including fragments of brachiopods and crinoids.
4.13 Predation

A second source of data on ancient predation comes from the trace fossil record. Traces of successful or attempted predatory attacks include the distinctive marks made by biting and gnawing of predators on hard shells as well as drill holes of predatory molluscs (Fig. 1). Bite marks provide strong indications of predatory attack, although they usually cannot be linked to specific predators. Exceptions include several instances of circular punctures in Carboniferous ammonoids; the size and spacing of the holes implicates the associated cladosodontid shark *Symmorium* as the predator. Classic examples of bite marks are known from Cretaceous ammonoids, where the holes match the size and spacing of the teeth of associated mosasaurs (Fig. 1A).

Sublethal, healed fractures and punctures are common in certain types of Palaeozoic brachiopods and bivalves (Fig. 1C, D). Alexander (1981, 1986) recognized lethal and sublethal (healed) shell damage in assemblages of Ordovician to Pennsylvanian brachiopods, and observed an increased proportion of lethal fractures in the later Palaeozoic. Together with the decline in frequency of repaired damage, this evidence suggests an increased intensity and effectiveness of predatory attack. Vermeij (1977) similarly documented trends in healed breakage amongst post-Palaeozoic molluscs, primarily gastropods. Distinctive scalloped fractures in the outer lips of the gastropod shells can be identified as having been made by peeling crustaceans (Fig. 1E). The oldest instances of this lip-peeling type of fracture are known from the Middle Ordovician, but case studies from the Ordovician and Silurian suggest that lip-peeling was exceedingly rare. In contrast, about 10–20% of individuals in some Devonian gastropod assemblages have suffered peeling, indicating levels of predation comparable to those of the Late Palaeozoic (Schindel *et al.* 1982) and Mesozoic (Vermeij 1977, 1987). Shell repair cannot be interpreted unambiguously because it monitors not only predatory attack, but also the ability of shells to resist attack.

In contrast, the boreholes of carnivores testify to lethal attacks. However, it is critical to distinguish between non-predatory, domiciliary borings and those produced by predators or parasites on live organisms. Carriker & Yochelson (1968) noted several diagnostic characteristics of the latter, including penetration through a single valve, few holes per shell, holes drilled perpendicular to shell surfaces, and evidence for prey and site selectivity.

The earliest evidence for drilling predation is derived from the Early Cambrian problematical, discoidal fossil *Mobergella* which displays minute drill holes in selective positions indicating probable predatory attack. Small cylindrical borings are also known through much of the Early Palaeozoic, although the affinities of these and the habits of their producers are not well understood. Many may have been produced by semiselective parasites living within the sediment. However, the first boreholes likely to have been made by gastropods occur in Devonian rocks. Circular–parabolic holes, closely resembling those produced by naticid gastropods, from the Middle Devonian of New York State, display a considerable degree of host and site selection (Fig. 1F), as well as the presence of a raised boss in the centre of incomplete holes, which is often considered diagnostic of the naticid gastropod mode of boring. Similar holes on related prey species are known from the Carboniferous. However, it appears that this early group of predaceous snails, probably a clade of archaeogastropods, became extinct at the end of the Palaeozoic. The drilling...
habit re-evolved during Middle—Late Triassic times, probably by a group of Mesogastropoda that became extinct before the end of the Triassic. Gastropod boreholes of both muricid and naticid affinity appear in the late Early Cretaceous (Albian). Throughout later Cretaceous and Cenozoic times gastropod drilling became an extremely potent mode of predation in marine communities. Relatively high percentages of molluscs in some faunas display predatory attacks by gastropods. These snails show a great deal of stereotypy in their mode of attack and position of boring on the shells of prey (Reymert 1971).

Coprolites (Section 4.12) provide another trace of predation and their fossil record has been systematically documented by Häntschel et al. (1968). However, coprolites are very scattered and only a few specimens have been attributed directly to particular host species; notable examples occur amongst Jurassic ichthyosaurs, whose coprolites commonly contain fragments of molluscan shells.

The third source of evidence for predation is a very indirect one, derived from apparent antipredation adaptations in probable prey species. Signor & Brett (1984) noted a coincidence between the rapid diversification of durophagous predator groups and various trends in the skeletal morphology of potential prey, starting in the Late Silurian to Devonian periods (Fig. 2). Aspects of skeletal morphology that were adaptive for resistance to predatory attack appeared rather abruptly in the Siluro-Devonian and increased toward the end of the Palaeozoic. Trends include the loss of umbilici in gastropods, and increased shell thickness and spinosity amongst brachiopods, gastropods, cephalopods, and crinoids (Fig. 2B).

Vermeij (1977) documented a great acceleration in the intensity of predation beginning in later Triassic and Jurassic times, which he termed the Mesozoic marine revolution. He noted the abrupt rise of durophagous groups such as crabs, stomatopods, and various shell crushing vertebrates, and documented several apparent antipredatory trends in molluscan groups. These include a tendency toward the evolution of thicker shells with narrow, toothed apertures, and the development of ribs and spines in several groups. Probable coevolution of predators and their prey may have promoted an increased diversity of defensive adaptations on the part of potential prey organisms. It would appear that the intensity of predation in marine systems has increased rather steadily at least from Late Cretaceous times to the present day, and may be responsible in part for the relatively higher species richnesses of many modern marine communities, as well as for many peculiar morphological adaptations of molluscan prey groups.

References


4.13 Predation

4.13.2 Terrestrial

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Arthropods

The first partially terrestrial animals, myriapods of Early Silurian (Llandoveryan) age, apparently were predaceous and fed upon small aquatic animals (Niklas 1986). Later Palaeozoic terrestrial arthropods (colembolans, insects, mites) were primarily herbivorous; however, in the Carboniferous certain large insects of the Order Protodonata, as well as spiders, specialized as predators on other insects. During the Mesozoic and Cenozoic a number of terrestrial arthropod groups (e.g., spiders, many beetles) became specialized as predators.

Tetrapods

The first terrestrial vertebrates, early labyrinthodont tetrapods, were probably entirely predaceous, feeding on fish and other aquatic animals, as well as smaller amphibians. These predators, beginning with the ichthyostegids in the Late Devonian, possessed sharp, spike-like, and undifferentiated teeth for impaling prey. Maximum usable prey size was limited by the size of the mouth gape. Later, the evolution of shearing-type teeth in the pelycosaur permitted active slicing, and thus consumption of larger bodied prey animals. Herbivorous land vertebrates do not appear in the fossil record until the Late Carboniferous and carnivores continued to outnumber herbivores until at least the Middle Triassic. The shift toward increased numbers of herbivores is associated with the origin of therapsids in the Middle Permian. This transition may have been related, in turn, to the desiccation of coal swamps and concomitant loss of the palaeo-dictyopteran insect fauna (Niklas 1986).

Bakker (1977, 1986) subdivided terrestrial tetrapod communities into four great groupings or mega-dynasties, based on dominant herbivore and carnivore types; he stressed increasingly complex predator–prey interactions and, to a large extent, decreasing predator-prey ratios through time. Bakker used ratios of estimated biomass of predators to that of potential prey species, in particular, based on well preserved local fossil assemblages, to make inferences regarding metabolism and lifestyle of carnivorous tetrapods.

Megadynasty I. Early terrestrial ecosystems of Megadynasty I (Carboniferous–Early Permian) were dominated by primitive reptiles and amphibians. The top predator was the synapsid reptile Dimetrodon, which was almost certainly ectothermic (cold-blooded), as evidenced by bone microstructure. Predator:prey ratios in these terrestrial ecosystems were characteristic high: large biomasses of predators were supported by small populations of moderate sized herbivores.

Megadynasty II. Megadynasty II (Early Permian–Middle Triassic) is referred to as the time of protomammals, indicating dominance by the mammal-like therapsid reptiles (Fig. 1A). A variety of osteological and morphological evidence indicates that therapsids were endothermic (warm-blooded) (see Bakker 1977; Benton 1979). Therapsids include diverse carnivorous, insectivorous, and herbivorous species. In populations from the Karoo beds of South Africa, predator:prey ratios average about seven per cent, only slightly higher than modern mammalian systems. The age of protomammals involved three waves of diversification (dynasties) and lasted approximately 15–20 Ma before giving way to Megadynasty III in Late Triassic times.

The Middle Permian (Kazanian) witnessed an explosive adaptive radiation of predatory therapsids, the largest of which were bear-sized, dome-headed anteosaurs. These predators were substantially more diverse than those of the Early Permian, including five families, as opposed to the single Sphenacodontidae which had previously occupied the role of large predator. The Kazanian therapsid fauna was decimated by a mass extinction and replaced in Late Permian (Tartarian) time by newly evolved groups of therapsids dominated by predatory, sabre-toothed dicynodonts; low predator:prey ratios (5–12%) prevailed. In turn, the Tartarian fauna underwent a mass extinction at the end of the Permian and elimination of all top predators enabled two new groups to expand into that role during Early Triassic (Scythian) time: the dog-like cynodont therapsids and, more significantly, archosauromorphs belonging to the Erythrosuchidae (Fig. 1B). The latter are forerunners of the thecodonts, including the crocodile-like phytosaurs and proterochampsids, which occupied roles of both top- and medium-to-small sized predators during the Middle–Late Triassic. Coevolution of prey defences is indicated by the appearance of heavily armoured aetosaurs.

Bakker (1986) argued that the evolutionary re-
placement of therapsid predators by thecodonts is consistent with osteological evidence for endothermy in these archosaurs. Conversely, Benton (1979) contended that the increasingly arid climates of the Triassic favoured archosaurs because they were ectothermic; he noted that ectotherms need to eat less and can conserve water better than endotherms.

**Megadynasty III.** Megadynasty III (Late Triassic–Cretaceous) was the age of dinosaurs. Bakker documented low predator:prey ratios within dinosaur dominated communities, suggesting high metabolic rates among theropod dinosaurs, resembling those seen in modern predaceous mammals. This appears to corroborate other osteological and physiological evidence which indicates that dinosaurs were warm-blooded and active social creatures (but see Benton 1979).

Bakker (1986) documented a Mesozoic ‘arms race’ between dinosauromorph predators and prey. Early predators included the Late Triassic coelurosauroids: slender, agile, and bipedal predators with teeth specialized for forming long slashing wounds. Later predatory carnosaurs displayed an enormous increase in size from two-ton Allosaurus to five-ton Tyrannosaurus. Early theropods (e.g. Ceratosaurus) had a flexible lower jaw enabling them to gulp large chunks of flesh. Later, jaw flexibility was sacrificed in favour of a firm, strong bite. Even the large Tyrannosaurus had extremely well developed hind limbs and feet capable of sustained, relatively
high running speeds. Other lineages of saurischian dinosaurs evolved different mechanisms for killing prey. A spectacular example is the Cretaceous species Deinonychus which possessed huge, curved, sabre-like claws for impaling and slashing prey. Baryonyx, from the Lower Cretaceous of the U.K. possessed extremely large claws on the front limbs, which it apparently used to hook prey much in the way that grizzly bears utilize their claws to catch salmon.

In turn, Mesozoic herbivorous dinosaurs responded to the increasingly efficient and large predators by evolving a variety of defences. The sauropods took refuge in their large size. Bakker (1986) argued that they were also capable of some evasive action and perhaps could ward off attacks by swinging their large tails and battering their predators. Evidence from trackways suggests herding behaviour in brontosaurs which presumably was a defensive social strategy in response to predation pressure on the young. Juvenile dinosaurs were maintained near the centres of migrating herds to be protected by adults, much in the fashion of herds of large ungulate mammals today. Other dinosaurs, particularly Ornithischia, evolved more spectacular defense strategies. Stegosaurus not only had large bony plates on the vertebral column, but also possessed a tail armed with sharp spikes which was clearly a formidable defensive weapon. Ankylosaurs evolved extremely rigid armour plating over much of the body, and in some cases (e.g. Ankylosaurus) possessed a huge bone-crushing club at the end of the tail. Perhaps the most spectacular of the defensive weaponry was that of the ceratopsian dinosaurs (e.g. Triceratops). The massive heads of these Cretaceous dinosaurs were armoured with a heavy shield and adorned with one to five sharp horns, which could impale enemies.

Dinosaurian predators of the Mesozoic were joined by a variety of other predatory vertebrates. From Triassic times onward, crocodiles were important predators in freshwater bodies. The early birds, from the Jurassic Archaeopteryx to the end of the Cretaceous, were entirely carnivorous and apparently evolved directly from small predatory coelurosaurids dinosaurs. In addition, pterosaurs occupied many predatory niches presently occupied by numerous birds.

Megadynasty IV. Although mammals, including insectivorous species, originated in the Triassic approximately contemporaneously with dinosaurs, and their diversity exceeded that of archosaurs by

the Late Cretaceous, mammalian predators remained small with no large predatory species until the Early Palaeogene. The rise of the larger mammals of Megadynasty IV is a spectacular case of ecological replacement following on from the extinction of the dinosaurs.

The earliest eutherian mammalian predators of the Tertiary, the arctocyonids, had five spreading clawed digits, short highly flexed limbs, and thick muscular tails. They were probably capable of climbing, digging, holding prey, and running over uneven or vegetated terrain. Generalized in locomotor and feeding adaptations, these forms gave rise to both the early carnivores and herbivores. The middle and late Palaeocene mesonychids improved upon the primitive form with stiffer, more elongate limbs as adaptations for a more cursorial mode of life. The second wave of mammalian predators, the Creodonta, evolved advanced dental adaptations for meat eating — carnassial teeth. Hyaenodonts were the main cursorial predators and the stocky, more heavily built ocyanids were the ambush predators. True carnivores (Order Carnivora), the third wave of mammalian predator diversification, appeared in the Late Eocene, and coexisted for a while with the creodonts (Bakker in Fatuym & Slatkin 1983). The earliest true carnivores were small weasel-sized vipers and myacids. The predator communities of the White River Badlands U.S.A. provide a glimpse of a Middle Tertiary community. Such Oligocene communities were a mixture of archaic and modern carnivores. The predators were predominantly small-sized (less than 60 kg). Locomotor adaptations suggest that there was an emphasis on climbing ability or short-distance ambush predation, but there were cursorial predators as well. The fauna lacked bone-crushing carnivores comparable to modern hyenas (Stanley et al. in Fatuym & Slatkin 1983).

In the Late Oligocene and Early Miocene, predator communities began to take on a more modern aspect. Dogs, some bear-dogs (amphicyonids), and, later in the Miocene, the hyenas independently evolved the long-limbed, fleet-footed adaptations of running predators. From the Oligocene onward members of the cat family filled most of the ambush predator niches. The sabre-tooth cat lineage included heavily built forms that specialized in preying on large, relatively slow-moving ungulates. Their demise was probably related to the extinction of most of their large, herbivore prey species at the end of the Pleistocene. The second lineage of cat evolution, which survives today, included generally
smaller species that were built for greater agility. They specialized in faster, smaller prey. Thus the evolution of predators in the Northern Hemisphere was a series of radiations, each beginning with fairly unspecialized forms, often as primitive or more so than the pre-existing predator groups. Successive radiations evolved better cursorial and dental adaptations, climaxing in the predator faunas of the Late Pleistocene.

The predator faunas of the island continents in the Tertiary were quite different. Giant birds occupied the cursorial predator niches in South America until the Pliocene, when the Central American land bridge allowed North American predators to invade South America. The South American ambush predators were cat-like marsupials that show striking parallels with the true cats of the northern hemisphere. In Australia, a variety of wolf-like marsupials filled the terrestrial cursorial predator niches.

Study of Cenozoic and Recent mammalian predator guilds indicates that predator diversity is tightly correlated with prey richness (Van Valkenburgh 1988). Furthermore, the basic array of predator feeding types has remained relatively constant for at least 32 million years, despite great taxonomic turnover. Van Valkenburgh concluded than competition has played a key role in the maintenance of this diversity.

Although mammals clearly dominated the large predator guilds during Cenozoic time, other vertebrates have become highly successful in the roles of smaller to medium sized predators. Lissamphibia (e.g. frogs, toads) have become specialized at insect capture. The rise of these amphibians, together with small rodents, has also triggered a major adaptive radiation of snakes, specializing in whole-prey ingestion as a result of highly flexible jaw articulations. The rise of passerine birds tracks the adaptive explosion of their insect prey; a number of raptorial predatory birds also appeared in the Cenozoic.

References


4.14 Parasitism

S. CONWAY MORRIS

Introduction

Parasitism is a symbiotic association whereby an individual derives nutritional benefit at the detrimental expense of another, by means of a long-term association. Usually such individuals concerned are separate species, but intraspecific parasitism, such as that typified by the stunted male fused to the female cestoid larval angler fish of the deep sea, is not unknown. Clearly, this definition of parasitism may grade into other types of symbiosis (e.g. commensalism), as well as the protracted predatory activity that is typical of many bloodsuckers (e.g. ticks, lampreys). In addition, the concept of parasitism may be expanded to include species with a parasitic stage at some point in their life cycle, usually juvenile. These so-called parasitoids characterize many phytophagous insects, and indeed if parasites and parasitoids are taken together they probably outnumber free-living species on the planet today.

However, despite the abundance of parasitic species in all habitats, and the fact that there are representatives in the majority of metazoan phyla