

Birds as habitat for parasites

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INTRODUCTION

Ecology is the study of the mutual relations between organisms and their environments or, as is appropriate in part II of this book, between a wide variety of parasites (Table 13.1) and the environment provided by their avian hosts (Table 13.2). The aims of this review are to introduce the diversity of bird–parasite interactions, to outline the variety of microhabitats for parasites provided by birds, and to identify features of the alimentary tract, the blood system, the skin, and the nest as examples of particular microhabitats.

One approach to understanding birds as habitat for parasites is to focus on the fact that most species are supremely adapted for powered flight. The morphology, structure, and physiology of most birds are geared for flight; birds show remarkably little external variation other than in size and colour (Webb *et al.* 1979). Most variation is to be found in the structure of the feeding apparatus and the morphology and physiology of the alimentary tract (Crompton 1985). These structures are the adaptations which have given birds remarkable dietary choice (Martin *et al.* 1951) and access to numerous sources of nutrients, energy, and infective stages of endoparasites. The feeding behaviour of birds has evolved to exploit a wide range of available diets, enhancing access to the infective stages of parasites. For the purpose of this review, a parasite (Table 13.1) is defined as one partner of a pair of interacting species that have ‘integrated’ their genomes so that the parasite is dependent on at least one gene of the other species, called the host (MacInnes 1974). This concept is useful because it draws attention to lineages of genes and the co-evolution of hosts and parasites (Dawkins and Krebs 1979). We must be careful, however, in the notion of what constitutes a species; viruses and many microorganisms do not easily conform to the established view of species (May 1992). We should also note that nutritional relationships are the hallmarks of most host–parasite systems; at some stage in its life history a parasite is likely to obtain nutrients and energy from the food, metabolites, or tissues of its host.

ASPECTS OF THE EXTENT OF BIRD–PARASITE RELATIONS

Estimates of numbers of birds and their parasites

The present inventory of free-living and parasitic organisms indicates that 1 820 000 forms have been described (Stork 1988), with perhaps as many as a further 10 000 000–

Table 13.1 Examples of the diversity of bird-parasite associations

Type of parasite	Status* Life history† activity‡	Feeding Microhabitat [§]	Host	References
Virus				
DHBV (duck hepatitis B virus)	En D?	I (hepatocytes)	<i>Anas platyrhynchos</i> (mallard/domestic duck)	Uchida <i>et al.</i> 1988
Duck plague virus	En D?	I (many cell types)	<i>Anas rubripes</i> (black duck)	Leibovitz 1969
Mycoplasmas				
<i>Mycoplasma cerogypsi</i>	En D	AM	<i>Coragyps atratus</i> (black vulture)	Panagala <i>et al.</i> 1993
Bacteria				
<i>Aegyptianella botuliformis</i>	En ID(V)	AM	<i>Numida meleagris</i> (guinea fowl)	Huchzermeyer <i>et al.</i> 1992
<i>Borrelia burgdorferi</i>	En D(V)	AM	<i>Catharus fuscescens</i> (veery)	Anderson <i>et al.</i> 1986
<i>Yersinia pseudotuberculosis</i>	En D	AM	Many species	Fiennes 1982
Fungus				
<i>Aspergillus fumigatus</i>	En D	AM	<i>Larus argentatus</i> (herring gull)	Pouling 1952
Protozoa				
Apicomplexa (coccidians and haematozoans)				
<i>Eimeria wobeseri</i>	En D	AM	<i>Larus argentatus</i> (herring gull)	Gajadhar and Leighton 1988
<i>Plasmodium relictum</i>	En D(V)	H	<i>Spheniscus magellanicus</i> (magellanic penguin)	Fix <i>et al.</i> 1988
<i>Sarcocystis rauschorum</i>	En ID	AM	<i>Nyctea scandiaca</i> (snowy owl)	Cawthorn and Brooks 1985

Arthropoda									
Arachnida									
Metastigmata (ticks)									
<i>Argas robertsi</i>	Ec	D	B	S (skin)				Ardeola ibis (cattle egret)	McKillingan 1994
<i>Ixodes arboricola</i>	Ec	D	B	S (skin)				Muscicapa striata (spotted flycatcher)	Haarlov 1962
Mesostigmata (mites)									
<i>Neoschoengastia shiraii</i>	Ec	D	B	S (skin)				<i>Phasianus colchicus</i> (pheasant)	Fujisaki 1991
Prostigmata (mites)									
<i>Sternostoma tracheacolum</i>	En	D	B	D (lungs)				<i>Melospittacus undulatus</i> (budgerigar)	Fain and Hyland 1962
Astigmata (mites)									
<i>Geranophilus canadensis</i>	Ec	D	OS	S (feathers)				<i>Grus canadensis</i> (sandhill crane)	Atyeo and Windingstaad 1979
Insecta									
Phthiraptera (lice)									
<i>Columbicola columbae</i>	Ec	D	CF	S (feathers)				<i>Columba livia</i> (rock dove)	Clayton 1991
<i>Menacanthus eurysternus</i>	Ec	D	B,CF	S (skin)				<i>Pica pica</i> (common magpie)	Price 1975
Siphonaptera (fleas)									
<i>Ceratophyllus gallinae</i>	Ec	D	B	S (skin)				<i>Parus caeruleus</i> (blue tit)	Ash 1952
Diptera (flies)									
<i>Neotitophilum praestum</i>	Ec	D	B	S (skin)				<i>Acanthia canabina</i> (linnet)	Keilin 1924; Tate 1954
Hemiptera (true bugs)									
<i>Oectacus vicarius</i>	Ec	D	B	S (skin)				<i>Hirundo pyrrhonota</i> (cliff swallow)	George 1987

Crustacea

Pentastomida (tongue worms)

Reighardia sterna En D B L (air sacs) *Larus argentatus* (herring gull) Riley 1972

Aves (birds)

Cuculus cahorus Bp D Nest *Acrocephalus scirpaceus* (reed warbler) Davies and Brooke 1989

*Ec, ectoparasite; En, endoparasite; Bp, brood parasite.

†D, direct life history; ID, indirect life history; (V) vector involvement either as an intermediate or paratemic host.

‡AM, absorbing molecules; B, feeding on blood; CF, chewing feathers; H, haemoglobin; OS, oily secretions; T, tissues.

*I, intracellular site; In, interstitial site (tissues); L, luminal site (cavity); S, superficial site (surface); N, nest.

For access to more of the extensive relevant literature, see reviews by Coatsney and Roudabush (1949), Clayton *et al.* (1992), Dogiel (1964), Fain and Hyland (1962), Hoogstraal and Aeschlimann (1981), Hubalek (1994), Lapage (1961), McDonald (1969, 1974, 1981, Rausch (1983), and Wehr (1971).

11 000 000 still waiting to be discovered (Hammond 1992). Birds are currently reckoned to comprise 9672 species (Sibley and Monroe 1990) and, given their conspicuous nature and the appeal that they have to humans, it seems unlikely that many more new species of birds will be found. According to Hammond (1992), many of the future new species will be found amongst parasitic organisms.

Table 13.2 Some features of birds as habitat for parasites

Feature	Observation	Reference
Estimated global population	100 000 000 000	von Hartmann 1971
No. of described species*	9672	Sibley and Monroe 1990
Most numerous bird	<i>Quelea quelea</i> (red-billed dioch)	Flegg 1985
Largest bird	<i>Struthio camelus</i> 100–136 kg (red-necked ostrich)	Calder 1985
Smallest bird	<i>Calypte helenae</i> 1.6–3 g (bee hummingbird)	Calder 1985
Examples of longevity†	<i>Troglodytes aedon</i> 5 years (house wren) <i>Turdus migratorius</i> 10 years (American robin) <i>Numenius arquata</i> 31 years (curlew)	Dorst 1971
Body temperature	40 ± 1.5°C (resting) 43 ± 0.5°C (active)	Calder 1985
Example of skin temperature	Skin surface 39.5°C Core 41.5°C	Spearman and Hardy 1979
Skeleton mass	65 g/kg bird mass	Calder 1985
No. of contour feathers	4607 <i>Sturnella magna</i> eastern meadowlark) 25216 <i>Cygnus columbianus</i> whistling swan)	Markus 1985 Markus 1985
Blood volume	5–13% body mass	Jones and Johansen 1972
Erythrocyte (RBC) count	1.89–5.0 × 10 ⁶ /mm ³	Jones and Johansen 1972
Haematocrit (PCV)‡	39.5% (mean)	Jones and Johansen 1972
Erythrocyte half life	35–45 days (pigeons)	Jones and Johansen 1972
Haemoglobin concentration	9–21 g/100 ml blood	Jones and Johansen 1972
Leukocyte count	15–30 × 10 ³ mm ³	Jones and Johansen 1972

* About half of these species are migrants (Fisher and Peterson 1964)

† These data and others quoted by Dorst (1971) come mainly from ringing wild birds. Under natural conditions, bird populations remain stable, so birth rate and death rate must be equal. Most species of bird experience high rates of mortality during the first year of life (Gibb 1961).

‡ PCV, packed cell volume.

It may be claimed that birds will be likely to support a minimum of at least 58 000 species of individual types of parasite. This conservative estimate is extrapolated from the fact that at least one virus, one bacterium, one fungus, one protozoan, one helminth, and one arthropod are specific parasites of *Homo sapiens*, which has been studied more thoroughly than any other species of host. If each bird species supports at least six host-specific taxa of parasitic organisms, the total is about 58 000 species of parasite for the known number of bird species. The number, however, is likely to be much greater than

58 000. Although the literature dealing with records of avian macroparasites, such as helminths, is vast (see Rausch 1983: Janovy, Chapter 15), much less is known about microparasites, such as viruses and bacteria (Nuttall, Chapter 14). Examination of wild birds for the presence of parasitic infections is often restricted to salvage specimens (McInnes *et al.* 1994; Munro *et al.* 1995) from which data on microparasites can be difficult to obtain. Contemporary parasitologists often find themselves examining the survivors of a parasite community in the occasional, solitary host (Dronen *et al.* 1988) as it is usually judged unacceptable to kill birds in sufficient numbers for extensive endoparasite surveys. The ectoparasitic fauna of wild birds is better studied, because birds can be sampled non-destructively and the parasites counted directly (Clayton and Walther, Appendix C).

Estimates suggest that the Earth supports a total bird population of the order of 10^{10} individuals (von Hartmann, 1971). Every one of these birds is infected with parasites, as a germ-free state can only be achieved in barrier protected isolators (Bradley *et al.* 1967). Roughly 283 000 000 birds, representing 185 species, spend the winter in the British Isles. However, those hosting the bulk of avian parasite biomass will be the 36 species responsible for over 90% (272 000 000) of the overwintering population. The starling, with 37 000 000 individuals, is the most abundant species in the British Isles, and the fieldfare, with about 1 000 000 individuals, is number 36 in the rank order of abundance.

Fieldfares are almost entirely winter visitors to the British Isles. We have virtually no direct knowledge about the impact of migration on the parasite fauna of a bird species or the role of host migration in the dispersal of parasites. Valhjunas (1984) was able to demonstrate that the annual migration of birds from the White Sea to the Baltic Sea influenced the transmission of blood parasites. Species of *Plasmodium*, *Haemoproteus*, and *Trypanosoma* (see Janovy, Chapter 15) are transmitted to birds during their stay in the relatively mild and warm Baltic winter, which presumably favours the vectors. Conversely, parasitic infection may affect migration. The greater yellowlegs spends the winter in South America and returns to the Arctic to breed. Recent work has shown that some birds are unable to undertake this northerly migration, due to a shortage of body fat, which in turn is associated with trematode burdens (McNeil *et al.* 1994).

MICROHABITATS FOR PARASITES PROVIDED BY BIRDS

Many observations have established that parasites occupy relatively precise sites or microhabitats in their hosts (Crompton 1973) and that the physiology of the parasites is sometimes specialized for the conditions prevailing in these microhabitats (see Crompton 1970; Kennedy 1976). However, our understanding of how parasites have become adapted to precise microhabitats in specific avian hosts is limited and merits investigation within a comparative phylogenetic framework (Brooks and McLennan 1991; Hoberg, Brooks, and Siegel-Causey, Chapter 11).

Four avian microhabitats have been chosen for detailed discussion below; the alimentary tract, the blood system, the skin and its features, and the nest. The skin supports a highly specialized fauna of ectoparasites (see Zimmermann 1988; Loye and Zuk 1991). Blood is a major source of food for both parasites which live directly in it and for many ectoparasites living on the skin. Blood also conveys the agents of the host's

immunological surveillance and effector mechanisms, which parasites must withstand if they are to survive (Wakelin and Apanius, Chapter 3). Nests are important to consider, because they are essentially an extension of the bird that serves as a refuge for numerous ectoparasites.

Alimentary tract as a habitat for parasites

Crompton and Nesheim (1976) reviewed interactions between parasites and the alimentary physiology and nutrition of domesticated birds. There are numerous variations in the alimentary tracts of the different major taxa of birds (Figs 13.1–13.20; Crompton 1985) attributable to the wide variety of food habits and diets. Nevertheless, knowledge of alimentary physiology obtained from studying chickens has general application throughout the class Aves. In all birds, the proventriculus is secretory and the ventriculus is responsible for mechanical grinding. The post-pyloric intestine, or small intestine, which begins at the pyloric sphincter where chyme leaves the ventriculus, is the main site for enzymic digestion and the absorption of digestion products (Fig. 13.1). There is usually a pair of caeca (Figs 13.12–13.14), which join the intestine posteriorly near the cloacal region. Not all birds have caeca and some have just one (Fig. 13.17). The caeca support a large microflora (10^{11} cells/g) and so probably contribute to the digestion of cellulose, lignin, and other products. Chickens fed on commercial rations grow well without caeca, but red grouse would probably not survive on their natural diet without these organs (Moss and Parkinson 1972). The avian alimentary tract is a remarkably plastic tissue, which responds to seasonal dietary changes (Pendergast and Boag 1973) and to food habits (Leopold 1953). There are also marked alterations in the relative proportions of different parts of the alimentary tract during growth (Crompton and Walters 1979), reflecting differing nutritional needs during development.

In all birds, there is likely to be a gradient of movement along the gut, with peristalsis being stronger anteriorly than posteriorly (Crompton and Nesheim 1976).

Figs. 13.1–13.20 Aspects of the morphology of the avian alimentary tract. In all figures the scale bar represents ~ 20 mm and the solid arrows show the usual direction of intestinal flow. Abbreviations: b.b., brush border; b.v. blood vessel; c., caecum; cl., cloaca; co., colon; d., duodenum; e.c., epithelial cell; g.c., gland cell; i., ileum; l., lumen; l.p., lamina propria; m., mucosa; sm., submucosa; mu., muscularis; p., pancreas; pv., proventriculus; s., serosa; u., ureter; v., ventriculus. (13.1) Stomach and intestine of a domestic fowl (*Gallus gallus*). (13.2) Gall-bladder and bile ducts of a domestic fowl. (13.3) Cloaca of a domestic fowl. (13.4) Crop of hooded vulture (*Necrosyrtes monachus*). (13.5) Extensible oesophagus of red tailed hawk (*Buteo jamaicensis*). (13.6) Crop of bobwhite quail (*Colinus virginianus*). (13.7) Oesophagus of ruby-throated hummingbird (*Archilochus colubris*). (13.8) Crop of rock dove (*Columba livia*). (13.9) Stomach region of double-crested cormorant (*Phalacrocorax auritus*). (13.10) Stomach region of American woodcock (*Scolopax minor*). (13.11) Stomach region of pink-footed goose (*Anser brachyrhynchos*). (13.12) Caeca of yellow-billed cuckoo (*Coccyzus americanus*). (13.13) Caeca of coot (*Fulica atra*). (13.14) Caeca of great horned owl (*Bubo virginianus*). (13.15) Rudimentary caeca of chestnut sided warbler (*Dendroica pensylvanica*). (13.16) Caeca of snipe (*Gallinago gallinago*). (13.17) Caecum of heron (*Ardea cinerea*). (13.18) Caeca of great black-backed gull (*Larus marinus*). (13.19) Transverse section of part of the ileum. (13.20) Detail of the structure of a villus from the ileum (see inset on Fig. 13.19). (From Crompton 1985).

Periods of stasis occur in the crop (Fig. 13.6) or the gullet of piscivorous birds (Fig. 13.9), in the caeca (Fig. 13.13), and, to some extent, in the ventriculus and the posterior part of the intestine. Stasis favours the build-up of the microfloral population, which is involved in the breakdown of plant products, in the synthesis of vitamins, in the metabolism of bile salts (see Coates 1973), and which serves as a major component of the food of alimentary parasites (Lee and Atkinson 1976). Experiments have shown that some types of parasite do not flourish in germ-free chickens (Johnson and Reid 1973).

Parasites (Table 13.1) occupying the oesophagus and anterior small intestine, where motility is strong, must possess attachment devices for adhering to host cell surfaces, as in the case of microparasites (Fuller 1973) such as *Lactobacillus* spp., or gripping the mucosa, as in the case of macroparasites (Nickol 1969) such as *Mediorhynchus* spp. Alternatively, parasites may avoid the problem of intestinal motility by using the intracellular habitat, as do the coccidia, or by burrowing into gut tissues, as do many species of nematode. Invasion of enterocytes and other epithelial cells by protozoan parasites, and browsing on these cells by digenean trematodes, are other good examples of alimentary microhabitat specialization.

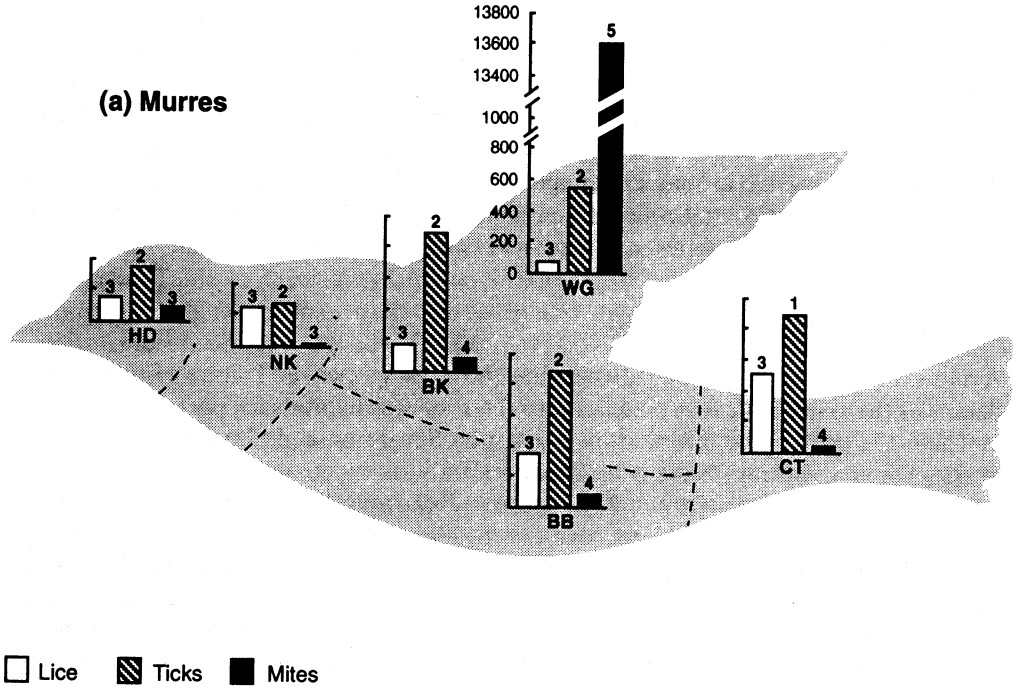
Many species of bird regurgitate pellets of digestive waste or food when feeding their young. Although this reverse peristalsis, which can be forcible, may threaten some parasites living in the anterior part of the gut, it has also become a specialized transmission mechanism. Apparently, both adult and fourth stage larvae of the nematode *Cosmocephalus obvelatus* are transmitted to young gulls in regurgitated food from their infected parents (Wong and Anderson 1982).

Blood system as a habitat for parasites

A large number of parasites utilize bird blood and the circulatory system as a microhabitat (Table 13.1). The blood is a fluid, connective tissue consisting of circulating cells and a liquid matrix, known as the plasma. Blood serves every tissue; it distributes heat, gases, nutrients, immunological agents, hormones, and waste, and it carries chemosensitive information necessary for the regulation of osmotic pressure and hydrogen ion concentration (see Weiss 1977). Some basic features of avian blood are given in Table 13.2.

Apart from relatively large, regularly replaced, nucleated red blood cells (RBCs), the blood contains four main types of leukocyte (lymphocytes, monocytes and their derivatives, polymorphonuclear granulocytes, and thrombocytes), which, in birds, have a clotting function analogous to that of platelets in mammals (Cox 1976). In birds, microparasites have been particularly successful at surviving within RBCs. Occupation of the RBC provides the individual parasite with a food supply, controlled physico-chemical conditions, and possible seclusion from some immunological factors (Cohen, 1982). Populations of some intracellular microparasites probably benefit from the fact that their pathogenicity is minimal, since they damage cells which are expendable (Table 13.2). For example, although malarial parasites, such as *Plasmodium relictum* (Table 13.1), destroy RBCs, the impact of this destruction is limited, because these cells have a short lifespan and are regularly removed from circulation by the spleen.

(a) Murres



(b) Kittiwakes

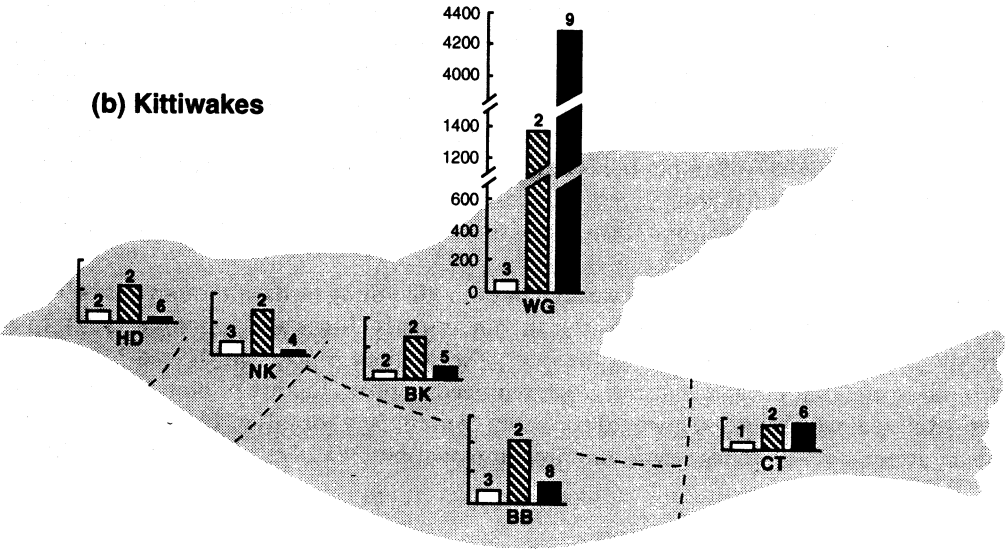


Fig. 13.21 Relative abundance of lice, ticks, and mites on different body regions of (a) murres (b) kittiwakes: HD, head; NK, neck; BK, back; BB, breast and belly; CT, crissum and tail; WG, wings. The number above each bar denotes the number of species in each ectoparasite group. The vertical scale is the same for all regions. Reproduced with permission of the publishers from the *Canadian Journal of Zoology* from Choe and Kim (1988).

It is usual to find that microparasites from the blood system are vectored by haematophagous invertebrates (Lehane 1991), which may even be ectoparasites of the same host species. Microparasites such as *Trypanosoma avium* and macroparasites such as *Austroilharzia terrigalensis* (Table 13.1) live freely in the plasma in blood vessels and are exposed to all the host's immunological agents. It is not known how these and other parasites survive in immunocompetent birds (Rose 1981), but perhaps antigenic variation (Turner 1984) and concomitant immunity (Hagan *et al.* 1993) serve to protect blood-dwelling microparasites and macroparasites, respectively.

Skin as a habitat for parasites

Avian skin includes the feathers, which are the most specialized feature of birds. Some details of the skin and feathers, relevant to their roles as habitats for parasites, are listed in Table 13.2, and more information is given by Spearman and Hardy (1985), Markus (1985), Choe and Kim (1988), and Clayton (1991).

According to Clayton (1991), 2619 species of chewing lice (Phthiraptera) occur on birds, where they feed on feathers, skin debris, blood, and living tissue associated with feather development. Chewing lice are permanent parasites, which complete their entire life cycle on the body of the host. Some lice act as intermediate hosts for filarioid nematodes and these insects presumably must eat enough host tissue to acquire the living microfilariae (Clayton 1990; Anderson, R. C. and Bartlett 1994). Lice are often host specific (Clayton *et al.* 1992) and site specific (Clayton 1991) on their hosts (Fig. 13.21); neither phenomenon has been explained satisfactorily.

Many other types of ectoparasites (Table 13.1) live on birds during periods of feeding and reproduction, but spend time off the host, usually in the nest or breeding site (Marshall 1981). Bird blood, which is highly nutritious and contains many free molecules requiring no further digestion, also contains immunological agents, which will be produced in response to antigens released by the feeding ectoparasites (see Brossard *et al.* 1991). Ixodid ticks ought to be particularly vulnerable to the host response, since their feeding process may last for days. In marked contrast, mechanical preening and other behaviours form the basis of resistance to most ectoparasites (Hart, Chapter 4).

Blood lost to ectoparasites can weaken or even kill young birds, although it is believed that birds can tolerate blood loss better than mammals (Jones and Johansen 1972). In a study of the feeding behaviour of the leech *Theromyzon cooperi* on the red-billed teal, Fourie *et al.* (1986) found that one leech removed approx. 150 mg of blood when it fed! An adult teal weighing 500 g would probably contain 50 g (or ml) of blood (Table 13.2), so an attack by 10 leeches would rapidly remove about 3% of the bird's blood volume.

Nest as a habitat for parasites

Nearly all species of birds rely on nests (Collias and Collias 1984). Brood parasites are notable exceptions to the investment in nest building, but not to nest use (Payne, Chapter 16). In general, birds that spend more time building nests in secretive locations have offspring which spend more time in the nest being fed by their parents. Ground-dwelling birds usually have simple nests and precocious offspring, which rapidly learn to feed

themselves. The type of nest, the duration of time spent there by nestlings, and the food habits of the supportive parents are important factors in the establishment and persistence of bird-parasite associations.

Birds' nests are a habitat for a diverse invertebrate fauna. A single nest of a screech owl was found to harbour 22 991 arthropods of 61 species; the nest of an American kestrel harboured 26 553 invertebrates of 93 species (Phillips and Dindal 1990). The nest fauna includes various stages of ectoparasitic, blood-feeding arthropods representing the insect orders Hemiptera, Diptera, Siphonaptera, and Phthiraptera, as well as mites and ticks (Table 13.1; Janovy, Chapter 15). Thus, there are costs associated with nests (Hansell 1993); blood lost to ectoparasites and endoparasites acquired from ectoparasitic vectors are good examples. The presence of blood parasites is another possible cost of occupying a nest, as discussed by Payne (Chapter 16).

Birds show a variety of adaptations for avoiding these nest based parasite costs. Female cliff swallows preferentially select nests with low burdens of ectoparasitic arthropods, which reduces the risk of parasite-induced morbidity for their offspring (Brown and Brown 1991). Starlings have been observed to incorporate into their nests vegetation from plants which synthesize molecules that tend to inhibit the growth of arthropods and microorganisms (Clark and Mason 1985; Clayton and Wolfe 1993). Further work by Fauth *et al.* (1991) has suggested that the green elements in the nest may also enhance pair bonding in the starling, rather than merely functioning as a form of nest fumigation. Female bell miners and nest attendants of the same species have been observed to remove ectoparasite arthropods from nests containing nestlings (Clarke and Robertson 1994). Nestling survival was found to be greater with ectoparasite removal. Screech owls regularly bring live blind snakes (other prey is delivered dead) to their nestlings. Most of these snakes slither into the nest and feed on the arthropod fauna. Gehlbach and Baldrige (1987) observed that nestlings grow faster and experience less mortality if snakes are present than same season nestlings living in nests without snakes. Thus, snakes may significantly reduce the number of detrimental ectoparasites (Tate 1954; Brown and Brown 1986; Lehmann 1993; Clayton and Tompkins 1994; McKilligan 1994).

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