Occurrence of ectoparasites on Great Cormorant chicks in Danish breeding colonies

M.Sc. Thesis

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by
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Preface and Acknowledgements

The present Master's thesis is the result of a project carried out in collaboration with three institutions: The Department of Population Biology, Institute of Biology, University of Copenhagen; the Department of Wildlife Ecology and Biodiversity, National Environmental Research Institute at Kalø; and the Department of Arctic Environment, National Environmental Research Institute in Roskilde.

The field work of the project was made in connection with the ringing of chicks and/or counting of nests by the Department of Wildlife Ecology and Biodiversity. A large part of the data analyses and subsequent writing took place at Kalø.

Two external supervisors have been connected with the project. The reason is that Mads Forchhammer changed his conditions of employment during the project from the University of Copenhagen to the National Environmental Research Institute in Roskilde and thus changed from being internal to external supervisor.

It would not have been possible for me to complete the project without help and support from many people.

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SYNOPSIS

1. Host-parasite interactions

Parasitism has during the last few decades gained increasing attention among ecologists and evolutionary biologists, and parasites are now considered to play an important part in line with predators, competitors, and resource limitation in affecting the growth of animal and plant populations (Anderson and May 1979; Dobson and Hudson 1986; Toft 1991). It is now generally accepted that parasites have a strong influence on the life history evolution, sexual selection, and population dynamics of their hosts (Ilmonen 2001).

Parasites are an extremely important group of organisms, both economically and numerically (Begon *et al.* 1996). It has been estimated that more than half of all animal species on the earth and much more than half of the individuals are parasites (Price 1980; Begon *et al.* 1996). All living organisms – even parasites themselves – can potentially serve as hosts for parasites. In this thesis the focus is on birds as hosts for parasites. The main emphasis is laid on ectoparasites, but birds are attacked by representatives from most of the well-known parasitic groups (Rothschild and Clay 1952).

Host and parasites can interact in various ways. In this chapter, I describe some general aspects.

Definitions

A *parasite* can be defined as an organism living in or on another living organism obtaining from it part or all of its organic nutrients, commonly exhibiting some degree of adaptive structural modification and causing some degree of damage to its host (Price 1980). The *transmission* of the parasite (the passing of a parasite from one host to another) can be *horizontal* (between unrelated hosts) or *vertical* (between parents and their offspring) and may be mediated by a *vector* (any host that transmits parasites) (Clayton and Moore 1997). The life cycle of a parasite can be *direct*, in which case the

parasite develops and reproduces in a single *definitive* host, or it can be *indirect* and requires one or more *intermediate* hosts for the parasite to complete part of its development (Clayton and Moore 1997). The parasites can be more or less attached to their host. *Permanent* parasites stay on the body of the host during their entire life cycle, whereas *temporary* parasites may leave the host for varying periods, including entire stages of their development (Clayton and Moore 1997).

Parasites can be divided into *endoparasites* that live inside the host, and *ectoparasites* which occur on the outside of the host, i. e. the skin and its outgrowths (Clayton and Moore 1997). Another classification that has been widely accepted is the distinction between microparasites and macroparasites made by Anderson and May (1979). *Microparasites* (viruses, bacteria, fungi, and protozoans) are small, have a short generation time and multiply directly within the host at extremely high rates. They often have an acute negative impact on the host and can induce acquired immunity that may last for the entire life of the host. *Macroparasites* (helminths and arthropods) often have a much longer generation time than microparasites and have indirect life cycles or more gradual direct multiplication. They often have a more chronic effect on the host, and the acquired immunity elicited by macroparasites depend in general on the number of parasites present in the host and tend to be of shorter duration (Anderson and May 1979; Clayton and Moore 1997).

The *load* of parasites can be expressed by various parameters, such as *prevalence*, the proportion of parasitized individuals in a population; *intensity*, the mean number of parasites per individual; and *density*, the mean number of parasites per infected individual (Choe and Kim 1987; Clayton and Moore 1997).

A special group of parasites among birds is *brood parasites*, which lay their eggs in the nests of other birds, either their own or other species, thus gaining the care of the foster parent whose nesting success usually is depressed (Payne 1997).

General aspects

The distribution of parasites within the host population is generally aggregated, with most individuals having a few or no parasites, and a few individuals exhibiting very

high infestations (Booth *et al.* 1993; Clayton *et al.* 1999). The aggregation is believed to reflect differences in host susceptibility to infestation due to genetic, behavioural or environmental factors (Begon *et al.* 1996). In such a distribution, which is characterized by a variance to mean ratio greater than 1, the intensity is relative high whereas the prevalence is relative low (Pacala and Dobson 1988; Begon *et al.* 1996). If the distribution is even or random, prevalence tend to be relatively high and intensity relative low. This type of distribution is more unusual and could arise, if for example high intensity of infestation kills the host (Begon *et al.* 1996).

Evidence suggests that parasites may act in a density-dependent manner and thus are capable of regulating the size of the host population (Anderson and May 1979; Dobson and Hudson 1986). For macroparasites the effect on host population size depends on both the virulence of the parasite and the parasite's distribution within the host population (Hudson and Dobson 1991). Parasites with high virulence or pathogenicity kill the host when parasite intensity is low, resulting in low rates of transmission and an insignificant effect on the host population. Moderately pathogenic parasites tend to exert the highest degree of regulation on host population size, as it appears from Figure 1.1 (Hudson and Dobson 1991). A strong effect on host population dynamics can also be seen, if the parasite's effect on host reproduction is much greater than its effect on host mortality, which can generate cycles of the host population (Toft 1991).

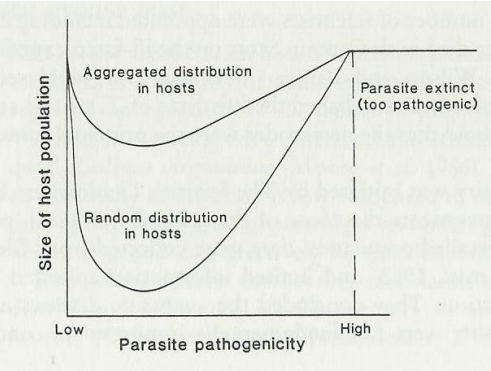

Figure 1.1 Effect of macroparasite pathogenicity and type of distribution on the size of host population (From Hudson and Dobson 1991).

As previously mentioned parasites may act in a density-dependent way to regulate the size of a population, which is also the case for competitors and predators. In fact a coarse comparison can be made between parasitism, competition, and predation that resembles the distinctions made between r- and K-selected species (Dobson and Hudson 1986) as summarized in Table 1.1.

Table 1.1 Comparison of some life history characteristics of micro- and macroparasites with those of other interspecific regulatory agents (From Dobson and Hudson 1986).

Life history characteristic	**Microparasite**	**Macroparasite**	**Parasitoid**[2)]	**Competitor**	**Predator**
Ratio of mean expected lifespan[1)]	<<1	<1	~1	~1	>1
Ratio of body sizes	Much smaller than hosts	Smaller than host	Mature stages similar	Similar size	Larger than prey
Intrinsic growth rate of population	Much faster than hosts	Faster than hosts	Comparable but slightly slower	Similar or almost identical	Usually slower than prey
Interaction with host individuals in natural populations	One host usually supports several populations of different species	One host supports a few to many individuals of different species	One host can support several individuals	Individuals reduce the proportion of available resources	Many prey items are needed to feed each predator
Effect of the interaction on the host individual	Mildly to fairly deleterious	Variable, can be intermediate	Eventually fatal	Not usually fatal	Usually immediately fatal
Ratio between number of species at the population level	Many species of parasite within each host individual	Many species of parasite from each host population	Most hosts harbour one or sometimes several parasitoids	Several species may utilize one common resource	Each predator uses several prey species
Degree of overlap of the two species ranges	Occur as diffuse foci throughout host's range	Occur as diffuse foci throughout host's range	Usually present throughout host's range	Ranges overlap but usually not entirely	Range is usually greater than prey's

[1)] All ratios expressed as exploiter/victim**.**

[2)] E.g. certain insects that lay their eggs in other insect larvae, in which the larvae develop and kill the host as they hatch.

The effects of parasites on host individuals and populations have generated an array of host defence mechanisms (Hart 1997; Moyer *et al.* 2002*b*). Thus parasites and their host have closely coevolved over time through the process of interactions, i.e. action, reaction, and counterreaction (Choe and Kim 1987).

Factors influencing parasite occurrence

The occurrence of parasites varies with a number of intrinsic and extrinsic factors. Different factors inherent to the host, such as age, sex, and behaviour, may influence the population size of parasites (Marshall 1981). Variations related to age and sex are presumably due to morphological, physiological, and behavioural factors of the host. Young birds tend to be more heavily infested than adults, most likely because of inadequate grooming and immune responses (Marshall 1981; Lehmann 1993). The biology and behaviour of the parasites may also account for age specific variations in parasite load (cf. the manuscript in the present thesis). Another factor that may influence parasite load is host sex. Fleas appear to occur more often on male birds than on females (Marshall 1981), and Blanco *et al.* (2001) found that the negative effect of chewing lice on the nutritional condition of Magpies (*Pica pica*) was more pronounced in males than in females. The condition of the host is often negatively related to the load of parasites, as has been reported for ticks on chicks of Yellow-legged Gull (*Larus michahellis*) (Bosch and Figuerola 1999). Not only the age of the host but also the age of the parents of the host seems to influence parasite occurrence. Daunt *et al.* (2001) found for European Shags (*Phalacrocorax aristotelis*) that broods raised by young pairs were more infested by lice than broods raised by older pairs. Furthermore, time of breeding of the host might also influence population dynamics of parasites. Evidence indicates that some ectoparasites such as lice are able to synchronize their peak reproduction to the nesting period of the host (Foster 1969).

Host defence which includes behavioural responses and immune reactions is believed to be an important and central factor in regulating parasite populations and will be described in the last section of this chapter. Habitat selection by host is also believed to influence parasite occurrence, as illustrated by a study made by Gregoire *et al.* (2002), who observed that the prevalence of tick infestations of Common Blackbirds (*Turdus merula*) was significantly higher for birds living in rural habitats compared to urban habitats. Also differences in host behaviour can contribute to variations in parasite load. For example may differences in foraging behaviour between Thick-billed Murre (*Uria lomvia*) and Black-legged Kittiwake (*Rissa tridactyla*) be one cause of a higher species richness in ectoparasite communities found on kittiwakes compared to murres (Choe

and Kim 1987). Murres dive to forage in contrast to kittiwakes, thus ectoparasites not adapted to an underwater situation could not survive on murres.

The transmission of parasites is increased among colonial birds and thus considered a major cost of living in colonies (e.g., Brown and Brown 1986; Duffy 1991; Rózsa *et al.* 1996). Characteristics of the colony such as age, size, and density of nest may influence the parasite occurrence. For instance, the tick prevalence in kittiwake colonies was observed to increase significantly with the length of time that the colony site had been occupied (Danchin 1992). However, colony age is mainly believed to be important for parasites overwintering at the breeding site like bugs, ticks, and mites (Hoi *et al.* 1998). Parasite load has been found to increase with colony size (Brown and Brown 1986; Hoi *et al.* 1998) and nest density (Brown and Brown 1986; Duffy and Campos de Duffy 1986). Among seabirds the nesting habits of hosts also appear to influence parasite occurrence. In one study Common Puffin (*Fratercula arctica*), a burrow nester with relatively little contact with conspecifics, showed low prevalence and low intensity of chewing lice, whereas Common Murre (*Uria aalge*) and Thick-billed Murre, both ledge nesters with frequent contact between individuals were highly infested (Eveleigh and Threlfall 1975).

Intrinsic factors of the host may interact with extrinsic factors such as season and climate to regulate parasite abundance. For example unsuitable temperatures and humidities are major causes of mortality in ectoparasitic insects (Marshall 1981). Furthermore, for many ectoparasites increasing temperature up to a certain level shortens the duration of the life cycle significantly and thus increases the intrinsic growth rate of the population (Marshall 1981). Parasites like lice that are closely associated with the host's body throughout their life cycles depend generally more on the microclimate of the host and are much less affected by season and climate than parasites which spend much of the time off the host (Marshall 1981). However, low ambient humidity can cause reductions in the abundance of lice on birds, and birds in arid regions have been shown to harbour much fewer lice than conspecifics in humid regions (Moyer *et al.* 2002*a*; Calvete *et al.* 2003).

Characteristics of the nest such as nest substrate and type of nest are important for the occurrence of many nest associated parasites. For instance colonies of kittiwakes on buildings and Cliff Swallows (*Hirundo pyrrhonata*) on bridges were fund to harbour

much smaller populations of ticks and bugs respectively than similar colonies located on cliffs. Compared to cliffs buildings and bridges may lack cracks and crevices that are suitable for refuge and thus may impede overwinter survival of the parasites (Loye and Carroll 1991; Danchin 1992). Also the nest climate might influence parasite occurrence; for example carnids and hippoboscid flies are more frequently found in sheltered birds' nest than in exposed nests (Capelle and Whitworth 1973; Marshall 1981).

Other species than the host may also influence parasite abundance. Interspecific competition between parasites can lead to exclusion or shifts in site preference or abundance (Marshall 1981). For instance auks (Alcidae) harbouring many Ixodid ticks seldom have any chewing lice (Marshall 1981). Also predators act to regulate parasite populations; ants are in this way suggested to reduce tick parasitism on nesting seabirds (Duffy 1991).

A crucial factor for parasite occurrence is the possibility of transmission to new hosts. Thus factors influencing the rate of transmission such as the density of hosts and the presence of suitable vectors are important for population dynamics of many parasites (Simberloff and Moore 1997). The problem of reaching new hosts has furthermore been met in most parasites through the production of enormous numbers of eggs or other developmental stages (Ruppert and Barnes 1994).

Effects on host

The effects of parasites on wild birds under natural conditions can be difficult to measure (Nuttall 1997), and many observations on parasite effects come from domestic animals or laboratory studies. Since several field studies have suggested that interactions between parasite load and factors such as climate, food shortage, and predators are important (Lehmann 1993), results from domestic animals and laboratory studies should be considered with caution. However, the impact of parasites on birds seems to vary a lot. Some parasites may have detrimental effects resulting in reduced fitness and survival of the host (Brown and Brown 1986; Bosch and Figuerola 1999). Others have apparently no discernible effects (Rogers *et al.* 1991; Dawson and Bortolotti 1997). Some may even be beneficial to their avian hosts, like some feather

mites that are suggested to control the growth of fungi or bacteria on feathers (Proctor and Owens 2000).

Parasites may influence various features of host life history. Studies of reproductive traits (reviewed in Møller 1997) have shown that parasites can cause delayed reproduction, reduced clutch and brood size, smaller offspring, and a smaller number of clutches per year. Also the survival and growth of chicks may be negatively affected by parasites (Richner *et al.* 1993; Fitze *et al.* 2004). The adverse effects on current reproduction may lead to increased parental effort in order to compensate, which in turn can result in a decrease in future reproduction success and adult fitness (Møller 1993; Fitze *et al.* 2004). Parasite infection may also make hosts more susceptible to predation (Begon *et al.* 1996) and to other parasites, and parasites may influence the outcome of competitive interactions (Price 1980). Furthermore, the spatial distribution of the host can be affected by parasites through the promotion of host dispersal from heavily infested habitats (Boulinier *et al.* 2001).

It has generally been thought that well-adapted parasites evolve to have minor or no impact on host fitness, since the fitness of the parasites depends on that of their host (Rogers *et al.* 1991; Toft 1991; Clayton and Tompkins 1994). However, studies on ectoparasites have shown that virulence may be linked to type of transmission and degree of dependence on the host (Lehmann 1991; Clayton and Tompkins 1994, 1995). Ectoparasites with a lower mobility such as lice that are highly dependent on their host, and are mainly transmitted vertically from parents to offspring tend to be of low virulence. In contrast, horizontally transmitted ectoparasites are relatively independent of host reproduction; they may move between hosts and are capable of escaping a dead host. These ectoparasites may pay a minor price for killing their host and thus may be extremely virulent, i.e. like some species of mites and ticks (Lehmann 1991; Clayton and Tompkins 1994, 1995).

The detrimental effects of parasites may be small most of the time, but during food shortage, harsh climate, disease, and other adverse or stressful conditions the impact on host may be severe (Allander 1998; Wesołowski 2001). Furthermore, the prevalence of parasites may vary from year to year according to environmental factors including winter temperatures and diseases of the parasites, and may not impact hosts every year (Hart 1997).

Although information indicates that microparasitic infections can affect wild bird populations by causing premature death or reducing breeding performance, most microparasites have little apparent effect on wild birds in contrast to domesticated birds (Nuttall 1997). Most often serological data may show an antibody reaction to infection but without associated records of disease (Nuttall 1997). Also many species of helminths appear to have little or no effect on their bird host (Rothschild and Clay 1952), although some, like the caecal nematode *Trichostrongylus tenuis* in Red Grouse (*Lagopus lagopus scotius*), have been suggested to cause a reduction in reproduction and survival of the host (Hudson and Dobson 1991).

The effects of ectoparasites on birds have been more documented than the effects of helminths and microparasites (Janovy Jr. 1997). It is generally accepted that relatively small numbers of ectoparasites do not affect the host, but ectoparasites present in large numbers have the potential to severely reduce fitness of the host (Duffy 1983; Brown and Brown 1986; Hoi *et al.* 1998). Direct effects of ectoparasites include blood consumption, tissue damage, and immune reactions or irritation (Allander 1998). Also nest desertion (Feare 1976; King *et al.* 1977), adverse effects on host condition/fitness and survival (e.g. Loye and Carroll 1991, 1995; Brown and Brown 2002) and reduced reproductive success (Møller 1993; Richner 1993; Fitze *et al.* 2004) have been associated with ectoparasite occurrence. Furthermore, ectoparasites may act as vectors of microbial, protozoan, or helminth infections (Janovy Jr. 1997). As mentioned in the previous section young birds are often more affected by ectoparasites than adults (Lehmann 1993; Bosch and Figuerola 1999), presumably because of inefficient grooming behaviour and immune defence, and because they have a higher ratio of surface to body volume (Lehmann 1993) and are more closely associated with the nest than adults (Marshall 1981). Only a few studies have found an adverse effect of ectoparasites on adult survival (Booth *et al.* 1993; Brown *et al.* 1995; Wesołowski 2001).

Other effects of parasites on host that are more subtle and may result in reduced host fitness are the costs associated with host defence as described in the following section.

Host defence

The pervasiveness and the potential harmful effects of parasites have selected for a wide variety of defences in animal hosts, despite the fact that host defences can be quite costly both in time and energy (Lehmann 1993; Blanco *et al.* 2001; Moyer *et al.* 2002*b*). Thus host defence represents a trade-off between the costs of susceptibility and the costs of resistance (Begon *et al.* 1996). Some of the defence mechanisms believed to act against parasites include behavioural responses and physiological responses such as immune reactions (Moyer *et al.* 2002*b*).

Behavioural responses

Behavioural responses represent a first line of defence against parasites (Hart 1997). They can be divided into the following four categories (adapted from Hart 1997): (1) removing ectoparasites from body and plumage, (2) avoiding and controlling nest-borne parasites, (3) avoiding flying insects, and (4) sexual selection.

Removing ectoparasites from body and plumage

The most obvious behaviour in order to remove ectoparasites is grooming. In birds grooming consists of preening with the bill and foot scratching, the later apparently controlling ectoparasites on regions inaccessible to preening, such as the head (Clayton 1991*a*). Besides being important in maintenance of the plumage preening seems to be effective in removing ectoparasites. Previous studies have shown that birds with naturally or manipulated deformed bills had significant higher numbers of chewing lice than birds with normal bills (Ash 1960; Clayton 1990, 1991). Preening thus normally keeps the number of ectoparasites like lice and mites down (Hart 1997) in addition to maintaining the plumage, and birds seem to spend considerably time on this activity. As it appears from the appendix in the present thesis preening was observed to comprise up to 20% of the observed activities of Great Cormorant chicks; the amount of preening increasing with increasing age of the chicks. The time spent on preening, which has been shown to depend on parasite load (Clayton 1991*a*), is one of the costs of this anti-parasitic behaviour. Preening also reduces the vigilance of the bird, thus making it more susceptible to predators (Hart 1997). Furthermore, the preening behaviour of birds has

selected for avoidance mechanisms in ectoparasites such as lice. The eggs of lice tend to be mostly found around the head and other areas the birds cannot preen (Hart 1997), and studies suggests that lice have evolved complex avoidance behaviour and small body size that may facilitate their escape from preening (Clayton 1991*a*; Clayton *et al.* 1999).

Another behaviour which long has been suspected to serve the purpose of removing ectoparasites is anting. This behaviour has been reported in more than 200 species of birds (Hart 1997). The birds either dab ants over their feathers with their beaks or lie on an ant hill and let the ants swarm over their bodies spraying formic acid and/or terpenoids on the feathers. The function of anting has been much discussed and recent data show that anting has no effect on feather mites and lice (Hart 1997). Another theory suggests that anting may reduce bacterial and fungal growth on skin and feathers of birds via antibiotic secretions from the metaplural glands of the ants (Hart 1997).

Other types of behaviour such as dust bathing and sunning have been suggested to play a role in controlling ectoparasites. Dust bathing desiccates the plumage, and since it has been shown that low humidity reduces the number of lice (Moyer *et al.* 2002*a*) one of the purposes of dust bathing may be a reduction of parasites. Also sunning can act to desiccate the plumage and Moyer and Wagenbach (1995) showed for sunning Black Noddies (*Anous minutus*) that feathers were heated to a temperature that killed chewing lice.

Avoiding and controlling nest-borne parasites

Birds' nests are a habitat for a variety of ectoparasites so not surprisingly birds seem to have evolved several behavioural defences against nest-borne parasites. Many studies have shown that birds tend to avoid using old nests that they detect have a high number of ectoparasites (Hart 1997; Chapman and George 1991; Loye and Carroll 1991). Removing of old nest material before building a new nest may also be of importance. Pacejka et al. (1998) found that the removal of old nest material by male House Wrens (*Troglodytes aedon*) prior to building reduced mite numbers significantly. As mentioned in the previous section birds may also desert heavily infested nests during breeding at the cost of subsequent mortality of nestlings (Hart 1997). Several examples of this have been observed for seabirds in tick-infested colonies (Feare 1976; King *et al.* 1977;

Duffy 1983). Nesting early in the spring may also be a way of controlling parasite load as parasite populations tend to accumulate during the breeding season (Duffy 1991). Another behaviour that has been suggested to act as a defence against nest parasites is nest fumigation, the insertion of fresh plant material containing active insecticides in nests. However, the purpose of nest fumigation has been much discussed (reviewed by Dawson 2004) and further studies are needed to clarify whether the behaviour is an adaptation against parasitism.

Besides ectoparasites the nest is also a source of microparasites like bacteria and many bird species engage in nest sanitation behaviour by means of avoiding to defecate in the nest and removing faecal sacs deposited by chicks from the nest (Hart 1997).

Avoiding flying insects

Flying insects such as mosquitoes are potential vectors of pathogens and birds exert different types of behaviour to avoid them. Defensive movements like foot stamping, head shaking, bill snapping, and wing flapping are known to reduce bites by mosquitoes quite effectively (Scott and Edman 1991; Hart 1997). During sleeping or resting many birds hide their head and one leg in the plumage and thus reduce the exposed surface area (Scott and Edman 1991). Also grouping has been suggested to protect against flying insects by dilution effect (Hart 1997).

Sexual selection

Another way for birds to counteract the impact of parasites on themselves and their offspring is to select mates that are less susceptible to parasites. Hamilton and Zuk proposed in 1982 a hypothesis of sexual selection that has been the object of much research and discussion. The hypothesis suggested that secondary sexual characters such as colours, ornamentations and singing are fully expressed only by males who are resistant to parasites. Females choose mates on the basis of these characters in order to obtain resistant males and thus resistance genes for their offspring (Hamilton and Zuk 1982). Besides the inheritance of resistance to offspring females might choose unparasitized males in order to protect themselves and/or their offspring from direct parasite transmission (Clayton 1991*b*). Møller (1991) found evidence that female Barn Swallows (*Hirundo rustica*) were choosing mates on the basis of their parasite load,

since unmated males more often had parasites and more parasites than mated males. Likewise Clayton (1990) demonstrated a significant preference of female Rock Doves (*Columba livia*) for unparasitized males compared to males with experimentally increased loads of chewing lice.

Physiological responses

Immune reactions

Immunological and other physiological responses take action when sufficient numbers of parasites penetrate the behavioural defences (Hart 1997). Like mammals birds have highly specialized immune systems of both innate/natural immunity and acquired immunity that can counteract parasitic infections and maintain the integrity of the body (Wakelin and Apanius 1997). Furthermore, specific antibodies from acquired immunity against certain parasites have been shown to be transferred from females to chicks via the egg (Gasparini *et al.* 2002). Various physiological factors of the host such as hydrochloric acid and proteases in the stomach, a low level of oxygen in the gut contents, and the high body temperature of birds may also represent barriers to parasitism (Ruppert and Barnes 1994).

The maintenance and production of the immune system have energetic and nutritional cost for the host (Blanco et al. 2001; Ilmonen 2001) and the fitness cost imposed on host by parasites may be reflected in the host's investment in immunity (Blanco et al. 2001).

Moult

In addition to replacing worn feathers the shedding of the host's exterior, moulting, has traditionally been associated with a considerable reduction in ectoparasite abundance, particularly lice (Marshall 1981). However, Moyer *et al.* (2002*b*) found that feather moult in Rock Doves had no effect on louse numbers and that lice actively seek refuge inside the sheath encasing developing feathers. Thus further studies are needed to clarify the effect of feather moult on ectoparasites.

2. Types of bird parasites

Birds are hosts to a wide variety of both micro- and macroparasites (Janovy 1997; Nuttall 1997). Many different viruses have been isolated from birds or avian blood-feeding ectoparasites, e.g. paramyxovirus like Newcastle disease virus, and orthomyxovirus like influenza virus (Nuttall 1997). Also many bacteria are known to infect birds, e. g. bacteria of the genera *Borrelia*, *Salmonella*, *Yersinia*, and *Pasteurella* (Nuttall 1997). Other types of microparasites in birds include fungi like *Aspergillus*, and protozoa of which the haematozoan genera *Plasmodium*, *Haemoproteus* and *Leucocytozoon* appear to be widespread (Janovy 1997; Nuttall 1997).

Avian macroparasites include helminths (worms) and arthropods (Janovy 1997). The groups of helminths that occur in birds are trematodes (flukes), cestodes (tapeworms), nematodes (roundworms), acanthocephalans (thorny-headed worms), and annelids (leeches) (Janovy 1997). Most helminths are intestinal parasites, but some species infect other regions of the birds, such as the air sacs, kidneys, eyes, subcutaneous tissues, and the vascular system. The route of transmission of helminths is either direct by ingestion of eggs or larvae, or indirect through ingestion of an infected intermediate host (Janovy 1997).

The arthropods of birds are mostly ectoparasites, including mites and ticks (Acari), flies (Diptera), true bugs (Hemiptera), chewing lice (Mallophaga), and fleas (Siphonaptera) (Clayton 1991*a*; Janovy 1997). The different groups feed on the bird in various stages of their development and show different degrees of attachment to the bird or its nest. Permanent ectoparasites like chewing lice and some mites, such as quill and feather mites, stay on the host during the entire life cycle (Janovy 1997). Quill mites live inside the quills of flight feathers, whereas feather mites live on the surface of feathers along the barbs often in very specific niches (Janovy 1997). Other groups of mites infest the skin, subcutaneous tissue, nasal cavities, trachea, lungs, and air sacs. Some mites are temporary parasites and occur in birds' nests, from which they visit the host briefly to feed (Janovy 1997). Many other types of ectoparasites such as ticks, true bugs of the family Cimicidae, and fleas are also temporary parasites and live on birds

during periods of feeding and reproduction, but spend time off the host, usually in the nest. This behaviour also applies to the dipteran families of blow flies (Calliphoridae), louse flies (Hippoboscidae), carnid flies (Carnidae), botflies (Muscidae), flesh flies (Sarcophagidae), and neottiophilid flies (Neottiophilidae). Other families of Diptera are not attached to the nest and occur only on the birds as blood-feeding parasites during ephemeral visits. These include mosquitoes (Culicidae), black flies (Simuliidae), biting midges (Ceratopogonidae), and horse and deer flies (Tabanidae) (Janovy 1997). It is assumed, that nest ectoparasites and ´field´ ectoparasites have not reduced their consumption rate, but only reduced the risk associated with remaining on the host compared to permanent ectoparasites (Lehmann 1993).

The ectoparasites most frequently found within the family of cormorants and shags (Phalacrocoracidae) according to previous studies appear to be chewing lice and ticks (see the introduction of the manuscript in this thesis for references). In the following sections of this chapter I describe in further details the biology and population dynamics of chewing lice, carnids, and ticks, the three types of parasites found in my study on cormorant chicks.

Chewing lice

The taxonomy of lice has been much discussed, but in more resent work they have been placed within the single order Phthiraptera, divided into four suborders: the Anoplura or sucking lice (parasites of mammals), the Amblycera (parasites of birds and mammals), the Ischnocera (parasites of birds and mammals), and the Rhynchophthirina (parasites of elephants and warthogs) (Marshall 1981). The paraphyletic group Mallophaga or chewing lice consists of the suborders Amblycera, Ischnocera, and Rhynchophthirina.

Chewing lice are a very ancient group (Rothschild and Clay 1952). It is believed that they are derived from free-living ancestors, which lived in the bark of trees, feeding on organic debris. They gradually began to feed on the skin debris of reptiles, and when these reptiles, the ancestors of birds, began to develop feathers, a new source of food

and shelter became available to the parasites. It is believed that they subsequently spread to mammals (Davis *et al.* 1971).

Chewing lice are permanent ectoparasites ranging from 1 to 10 mm in size (Rothschild and Clay 1952). They are wingless, typically flat-bodied insects with six relatively short legs modified for clinging to the feathers or fur of the host. The entire life cycle, which lasts about 30-36 days and differs according to the species, is spent on the host (Davis *et al.* 1971). The eggs are fixed to the feathers or fur with a cement-like substance, and as chewing lice have no metamorphosis the nymphs emerging from the eggs resemble the adults in habits and general body form (Rothschild and Clay 1952). They shed their skin three times before reaching the adult state.

Avian chewing lice are as previous mentioned divided into the suborders Amblycera and Ischnocera (Fig. 2.1). Ischnocera feeds exclusively on feathers, which they metabolize with the aid of symbiotic bacteria (Marshall 1981). They are highly specialized for locomotion on feathers and do not go on the skin of the host. Amblycera, in contrast, are more agile and occur on the skin as well as on feathers. They feed on blood and dermal debris of the host in addition to feathers (Ash 1960; Marshall 1981).

Chewing lice, particularly Ischnocera, are extremely host-specific, and different species are restricted to specific areas on the host (Ash 1960). The dispersal is first and foremost by direct contact, mainly by vertical transmission from parent to offspring (Marshall 1981). Dispersal can also occur among hosts that use the same nest site or resting place, or by phoresis, in which the chewing lice are transported passively to a new host by other insects, most often hippoboscid flies (Marshall 1981). Amblycera are more active and move faster than Ischnocera, and they are capable of leaving a dead host and thus less dependent than Ischnocera on direct contact between hosts (Marshall 1981).

Chewing lice populations tend to fluctuate seasonally with a peak in early spring followed by a fall in population caused by the spring moult of the host (Marshall 1981). Also the transmission of lice from parents to offspring may cause a decrease in populations on adults (Marshall 1981) and an increase in the number on offspring (cf. the manuscript in this thesis). Furthermore, studies made by Foster (1969) suggest that the timing of breeding in some blood-feeding species of chewing lice is controlled by the reproductive hormones of their host. Thus the peak breeding in louse populations

coincides with the timing of breeding in the host, resulting in sufficient numbers of lice for transfer to the nestlings (Foster 1969).

As mentioned in chapter 1, host anti-parasite behaviour like preening normally keeps the number of lice down (Hart 1997), so usually the negative impact on host is low (Ash 1960; Blanco *et al.* 2001). However, members from both suborders have the potential to reduce fitness of the host when present in larger numbers. Ischnocera can cause extensive plumage damage resulting in reduced insulation, increased energetic cost and reduced winter survival of wild hosts (Booth *et al.* 1993; Clayton *et al.* 1999). Amblycera can cause dermatitis and scratching and reductions in egg production of poultry (Marshall 1981). Furthermore, Amblycera may act as intermediate hosts for endoparasites and virus (Clayton 1990).

(a) (b) (c)

Figure 2.1 Chewing lice (Mallophaga). (a) Amblycera: *Eidmanniella* sp.; (b) Ischnocera: *Pectinopygus* sp.; (c) *Pectinopygus gyricornis* on Great Cormorant chick. Reprinted from www.sid.zoology.gla.ac.uk (a) and www.darwin.zoology.gla.ac.uk (b); image by Kim Aaen (c).

Carnids

About 65 species of 4 genera from the family Carnidae (Diptera) have been described thus far, but there are probably numerous species not yet described (Papp 1998).

Members of the genus Carnus with 6 species are ectoparasites on birds (Grimaldi 1997). *C. hemapterus* is a c. 2 mm long black fly that parasites nestlings (Walter and Hudde 1987). Although it appears to be widespread, it is still uncovered in most areas (Grimaldi 1997) and little is known about its ecology and dispersive behaviour.

C. hemapterus shows no host specificity and has been reported from a broad range of bird species, especially raptors and cavity-nesting birds (Capelle and Withworth 1973; Cannings 1986; Dawson and Bortolotti 1997; Grimaldi 1997). It avoids host species which nest on the ground or in damp locations, and has a preference for hole nests or nests with a protective canopy (Capelle and Withworth 1973; Marshall 1981; Papp 1998). However, it has been found in ground nests of Great Cormorant (cf. the manuscript in this thesis).

The feeding of adult flies has been much discussed. It has been argued that the proboscis appeared too weak to penetrate the skin (Marshall 1981), but the presence of avian blood cells in smears of fly abdominal contents has indicated blood feeding (Kirkpatrick and Colvin 1989). So it is now generally accepted that the adults feed on blood of nestlings and maybe also on skin debris and secretions (Grimaldi 1997; Papp 1998). The larvae live in nests where they feed on dead organic matter and where they usually overwinter as pupae (Papp 1998). The adults emerge fully winged in the spring and when they have located a suitable new host the wings break off (Walter and Hudde 1987). Neither the adults nor the larvae have been found on adult birds, so flies are assumed to colonise new hosts actively during the winged phase of their life cycle (Grimaldi 1997). All females lose their wings, whereas one third of males retain them, suggesting that males may disperse further during mating (Capelle and Withworth 1973). After reaching a host the abdomen of the female swells to double size (Fig. 2.2), before deposit of the eggs in the nest (Marshall 1981).

The carnids seem to parasite only on young nestlings (Kirkpatrick and Colvin 1989; Dawson and Bortolotti 1997; Liker *et al.* 2001). They produce several generations, and the population size increases from the hatching of nestlings until half the nestling period and nestlings are free of parasites close to fledging (Roulin 1998; Roulin *et al.* 2003). Thus by the end of the summer only pupae can be found in the nest (Marshall 1981). The length of the period of parasite activity is found to be linked with the length of the nestling-development period of the host species (Liker *et al.* 2001).

Most studies have failed to show any detrimental effects from *C. hemapterus* on nestlings (see Valera *et al.* 2003 for references), although Cannings (1986) suggested that *C. hemapterus* infestation had a negative impact on the survival of Northern Saw-whet Owl nestlings (*Aegolius acadicus*).

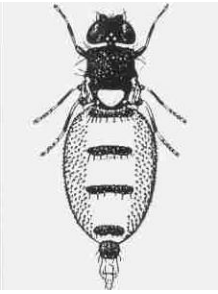

Figure 2.2 Carnus hemapterus, an engorged female. Reprinted from www.laus-miller.de.

Ticks

Ticks (Ixodida) are a group of mites (Arachnida: Acari) with approximately 850 known species in 19 genera in three families: Ixodidae, Argasidae, and Nuttalliellidae (Sonenshine 1991). They are geographically widely distributed as haematophagous ectoparasites on mammals, reptiles, and birds. The biology and life cycles of the two major families Ixodidae (hard ticks) and Argasidae (soft ticks) differ in many aspects as described below (details from Sonenshine 1991).

Ixodid ticks have four distinct life stages: an egg, a six-legged larva, a nymph, and finally the adult (Fig. 2.3). During each stage one blood meal is taken. The female enhances its size considerably during feeding, occasionally more than 100 times their unfed body weight (Fig. 2.4). After feeding the adult female lays up to several thousand eggs and dies. The entire life cycle may last from less than a year to more than three years, depending on the climate. Most ixodid ticks have three hosts, one for each stage

of the life cycle, but some species have only one or two hosts and spend two or more life cycle stages on the same host. Ixodid ticks can stay on the host for days or weeks to feed. In contrast, Argasid ticks feed for only a matter of minutes or hours on their host. They lack a hard dorsal scutum and after the egg and larva stages they often go through multiple nymphal stages before the adult stage. Argasid ticks feed many times during each life stage and often lay only a few hundred eggs. The duration of the life cycle is generally much longer than for Ixodid ticks and they have been observed to live for many years and resist long periods of starvation (Sonenshine 1991).

Figure 2.3 Stages of *Ixodes* ticks. From left a larva, two nymphs and an adult tick. Reprinted from www.danmarksinsekter.dk.

Most Argasid ticks are nest parasites and will retreat to a refuge in or near the nest after having fed on the host, whereas Ixodid ticks tend not to be so nestbound and can climb on to birds as they brush against vegetation during foraging or resting (Proctor and Owens 2000). Transmission of ticks between hosts is mainly horizontal and takes place through direct contact with host or active parasite dispersal (Gregoire *et al.* 2002). Newly fledged infested chicks are presumably the main dispersal agent between colonies (Danchin 1992). Ticks from the genus *Ixodes* are highly mobile and are found to exploit any hosts available in a communal roost (Eveleigh and Threlfall 1975; Mehl and Traavik 1983)

Heavy infestation of ticks can have a detrimental effect on the host through blood loss (Janovy 1997; Bosch and Figuerola 1999). Besides their direct effects ticks are potential vectors of different microparasites like arbovirus (Boulinier *et al.* 1997) and *Borrelia burdorferi* (Gregoire *et al.* 2002) and ticks have been observed to cause nest desertion and nestling mortality in many bird species (Duffy 1983).

Figure 2.4 Seabird tick *Ixodes uriae.* Male (left) and female (right). Reprinted from www.invasive.org.

3. The Great Cormorant in Denmark

Six subspecies of Great Cormorant (*Phalacrocorax carbo*) are normally recognized (del Hoyo *et al.* 1992). Two subspecies occur in Denmark: *P. c. sinensis* and *P. c. carbo*. Only *P. c. sinensis*, which is distributed from Europe in the West to India and China in the East, breeds in Denmark. *P. c. carbo* breeds among other places at the North Atlantic coasts of Norway and Great Britain and occurs in Denmark from August to May (Meltofte and Fjeldså 2002). In this chapter, I describe some aspects of the biology, development and management of the Danish population of *P. c. sinensis* (hereafter referred to as cormorants), the host species in my study of ectoparasites.

Biology

Cormorants are colonial birds and breed in colonies situated along inlets, shallow coasts, and larger lakes. They are very adaptable in their nest location and the nests can be placed on cliff ledges, human structures, in trees, bushes, reedbeds or on bare ground (del Hoyo *et al.* 1992). Nests are made of sticks, twigs, seaweed, and reeds, and laying of eggs can occur during a period of 6 months (Gregersen 1982). The eggs are laid at intervals of 2-3 days and the chicks are hatched asynchronously after an incubation period of 27-31 days. Most chicks hatch in April to May. The brood size is 1-5 chicks, most often 2 or 3 chicks. Chicks are naked and blind when they hatch. Eyes open after 3 days and growing of down starts from the 6^{th} day of age. Approximately 10-14 days old the chicks are covered by brown-blackish woolly down; feathers appear after 18-20 days and growth of flight - and tail feathers starts during the age of 14-20 days (Berry 1976; Olver and Kuyper 1978; del Hoyo *et al.* 1992). The chicks stay in the nest till they are about 50 days old and fledged, and they leave the colony at 10-13 weeks of age.

Cormorants are agile swimmers and divers and catch their prey that consists of fish under water. Their feathers are permeable and can become soaked with water thus

reducing buoyancy and facilitating diving. In return they have to spend some time drying the plumage (del Hoyo *et al.* 1992).

Most of the Danish cormorants migrate from August - October to wintering areas especially at central and western coasts of the Mediterranean. They return to Denmark during March - April. 5-10% stays in Denmark over winter (Bregnballe *et al.* 1997).

Population development and management

After having been breeding in Denmark almost continuously during the last 7000-8000 years at the minimum, the cormorant became extinct as a Danish breeding bird around 1876. The extinction was a result of intensive persecutions and shooting in the colonies during breeding time, as cormorants were considered harmful to fishing and forestry (Meltofte and Fjeldså 2002). The cormorant did not breed in Denmark again until 1938 and as it continuously was being intensively persecuted the following 30 years, the number of breeding pairs did not exceed 900 until after 1974 (Bregnballe and Gregersen 1995). The population then increased steeply from approximately 2,000 pairs in 1980 to more than 40,000 pairs in 1996 (Fig. 3.1). From 1973 to the end of the 1980s the cormorant population was distributed among three main colonies. During the 1980s and the 1990s especially juveniles spread from these three and other later founded colonies, and today breeding colonies are established in most regions in Denmark (Bregnballe and Gregersen 1995, 1997).

The steep increase in the number of breeding pairs in Denmark was mainly caused by measures of protection. In 1972 the annual shooting of cormorants in the largest colony was stopped, and in 1981 the cormorants were protected in many European countries as a result of a Birds Directive from the EU (Meltofte and Fjeldså 2002). Also the increased amount of nutrients in Danish waters and more efficient fishing of larger fish have resulted in larger numbers of the fish species cormorants mainly feed on (Meltofte and Fjeldså 2002).

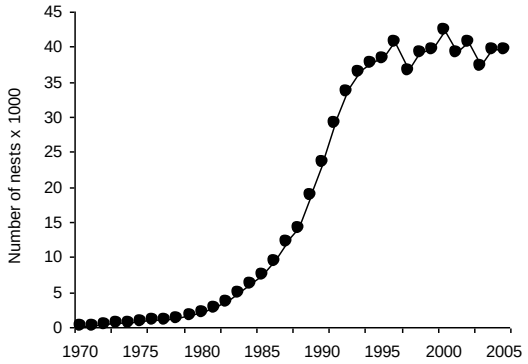

Figure 3.1 Development of the Danish breeding population of Great Cormorant 1970-2005 expressed as the number of assumed occupied nests (from DMU, unpubl. data).

The annual rate of increase declined from 1989 (Fig. 3.2) and breeding numbers have stabilised since 1996 until today with an average between 39,000 and 40,000 pairs (Bregnballe *et al.* 2003, Eskildsen 2005). The proportion breeding in Denmark thus accounts for almost 30% of the European breeding population of *P. c. sinensis* (Bregnballe *et al.* 2003).

The stabilization of the breeding population is believed to be due to limitations of the availability of food resources around existing colonies combined with legal and illegal human actions taken to limit the number of colonies and their distribution (Bregnballe *et al.* 2003). A management practice was introduced in 1994 in order to control the number of new colonies. Landowners and national forest districts were allowed to scare off cormorants trying to establish new colonies. Oiling of eggs to prevent them from hatching was also allowed for national forest districts in newly established ground nesting colonies. In 2002 a new management plan was introduced which among other things allows oiling of eggs not only in new but also in existing ground nesting colonies (Bregnballe *et al.* 2003).

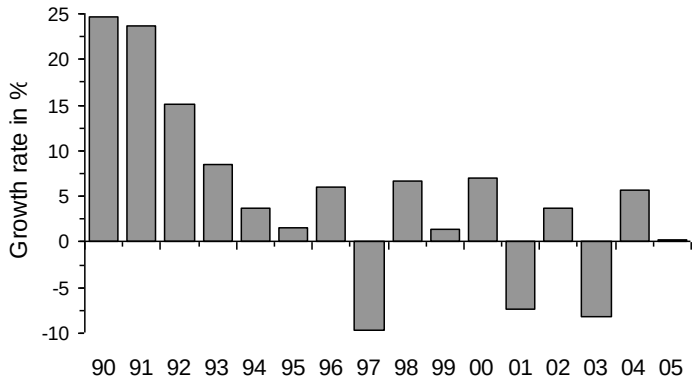

Figure 3.2 The annual rate of increase (%) in the number of cormorant nests in Denmark 1990-2005 (from DMU, unpubl. data).

The number of colonies increased during 1996-2000 and during 2002-2004 (Fig. 3.3) despite the actions to prevent establishment of new colonies (Bregnballe *et al.* 2003). Experience has shown that scaring of cormorants or regulation of breeding success in existing larger colonies can enhance the attempts of the cormorants to establish new colonies. However, oiling of eggs seems to have a limiting effect on the growth of both new and existing colonies (Bregnballe and Eskildsen 2002).

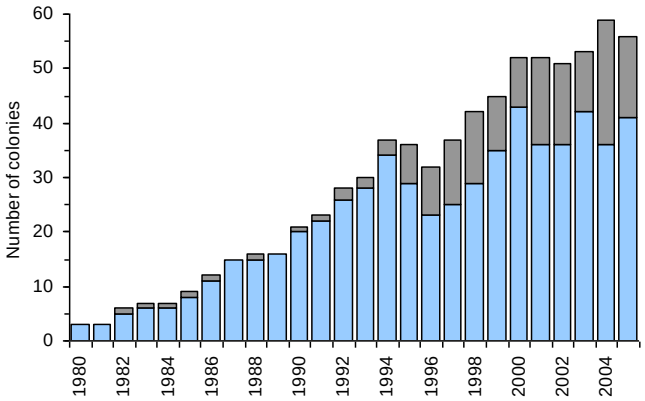

Figure 3.3 Development in number of breeding colonies of cormorants in Denmark 1990-2005. The marked parts of the columns indicate colonies that have been subjected to human interference like oiling of eggs (from DMU, unpubl. data).

4. Effects of parasites on Great Cormorants

In this final chapter of the synopsis I will try to estimate the potential effects of parasites on the Danish breeding population of Great Cormorants based upon my own and previous studies.

Being colonial birds that breed in dense colonies, often return to the same nesting sites and colonies for generations and having a relative long life span (del Hoyo 1992), cormorants may have a high risk of being exposed to parasites. However, studies of parasite effects on cormorants are quite sparse. In a study of Double-crested Cormorants (*P. auritus*) from Saskatchewan, Canada, Kuiken *et al*. (1999) found three species of helminths, three species of chewing lice and one flea species in the dead cormorants examined. The most important causes of mortality were Newcastle disease, starvation from sibling competition, and coyote predation. Thus, none of the macroparasitic infestations were considered to be the primary cause of death, although they may have caused some degree of debilitation. Similar, Berry (1976) found in his study of Cape Cormorant (*P. capensis*) one helminth species, one chewing louse species, three mite species, and one tick species. The ticks were suggested to exert some stress on the birds, especially nestlings, however, the most important cause of mortality was considered not to be parasites or disease but starvation stress during the post-fledging period.

Adverse effects of parasites on colony breeding seabirds have been reported, especially for ticks (Feare 1974; Ballard and Ring 1979). Heavy infestations of ticks may as previously mentioned lead to nest desertion by adult birds with subsequent mortality of eggs and chicks, which has been observed for cormorants as well as other species of seabirds (Duffy 1983). A direct negative effect of ticks on chick fitness has been reported for Yellow-legged Gull (Bosch and Figuerola 1999).

In my study of parasites on cormorant chicks I found the three types of parasites described in chapter 2. As young birds tend to be more heavily infested than adults (Marshall 1981; Lehmann 1993), the occurrence of parasites on chicks can be considered to represent the maximum impact on the population. The chewing lice found in the study may have a negative impact on chick fitness, especially when present in

high numbers on sick or otherwise debilitated chicks. The chick may damage itself by excessive scratching resulting in secondary infections, and the development of feathers may also be impaired by chewing lice (Rothschild and Clay 1952). However, the negative impact of chewing lice is generally considered to be low compared to other factors such as poor nutrition and disease (Calvete *et al.* 2003). As for carnids most studies have not been able to show any negative effects on chicks (cf. chapter 2), but as they do feed on blood they may have the potential to harm at least debilitated chicks. The third type of ectoparasites found in the study is ticks that are potentially harmful to chicks as mentioned above. Very few were found during my field studies and the actual occurrence remains unclear, but most likely they have not been present in very large numbers.

The parasites found in my study may have adverse effects on some individuals, especially chicks that are already weakened. The asynchronous hatching of cormorant chicks can result in large differences in age and size among the chicks, and this may become even more pronounced because of the older chicks receiving more food (cf. Kuiken *et al.* (1999) who found starvation from sibling competition to be a major cause of mortality as mentioned above). The youngest and smallest chick in a brood thus may be more vulnerable to parasites. Also adverse weather conditions such as low temperatures and heavy rainfall may aggravate the negative impact of the parasites on some chicks. Furthermore, the management practice of preventing the cormorants in establishing new colonies might lead to increasing density of nests in existing colonies. This may result in increased transmission of parasites and enhance the pressure on susceptible individuals. For adults it might also lead to increased stress because of greater competition for nesting sites, which could cause a greater susceptibility to parasites.

Although the parasites may have a negative effect on some individual chicks, the impact of the parasites found in my study on the Danish breeding population of cormorants can most likely be considered to be of minor importance compared to other factors that act to regulate the size of the population. In this context mainly two issues are of major importance: the availability of food resources around existing colonies and to what extent the cormorants are allowed to establish new colonies, the latter being a question about management.

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Danish summary – dansk resumé

Betydningen af parasitters indflydelse på værtens livshistorie og populationsdynamik har fået øget opmærksomhed inden for de seneste årtier. Dette speciale fokuserer på interaktioner mellem fugle og parasitter, især ektoparasitter, med udgangspunkt i den danske skarvpopulation.

Fordelingen af de fleste parasitter i værtspopulationen er karakteriseret ved, at få individer har en høj forekomst, mens mange har få eller ingen parasitter. Effekten på størrelsen af værtspopulation afhænger af parasitternes virulens og fordeling. Mange faktorer kan påvirke parasitforekomsten, såsom værtens alder, køn, fysiologi, generelle adfærd og habitatvalg, samt faktorer knyttet til rede og omgivende miljø. Koloniynglende fugle er generelt mere udsatte for parasitter som følge af øget transmission. Effekten på værten kan variere meget. Mange parasitter har ikke nogen påviselige effekter på vilde fugle. For en del parasitter har man imidlertid påvist negative effekter på værtens reproduktion, fitness og overlevelse. Omfanget af negative effekter er bestemmende for, i hvor høj grad værten udvikler forsvarsmekanismer. Disse kan være af adfærdsmæssig eller fysiologisk karakter og omfatter blandt andet immunforsvar samt fjerpudsning, som er et vigtigt forsvar mod ektoparasitter.

Fugle er værter for en lang række parasitgrupper, både mikroparasitter omfattende virus, bakterier, svampe og protozoer, og makroparasitter som omfatter indvoldsorm og leddyr. De fleste leddyr på fugle er ektoparasitter og består af mider og flåter, fluer, næbmunde, fjerlus og lopper. Nogle grupper som fjerlus er permanente parasitter, mens andre er mere knyttet til reden og kun opholder sig kortvarigt på værten. Blandt skarver er de dominerende ektoparasitter flåter og fjerlus. Det var således også disse to grupper jeg fandt i min undersøgelse af ektoparasitter hos skarvunger, foruden en tredje gruppe bestående af parasitiske fluer (carnider). Biologi og adfærd for disse tre grupper beskrives nærmere i synopsen.

Mellemskarv (*Phalacrocorax carbo sinensis*), som har været udgangspunkt for denne undersøgelse, yngler i kolonier i blandt andet Danmark. Efter at have været udryddet som dansk ynglefugl indtil 1938 voksede populationen stærkt i forbindelse med

fredningstiltag i 1980'erne til ca. 40.000 par i 1996 og har nu stabiliseret sig omkring dette niveau.

Selv om de tre grupper af ektoparasitter, jeg fandt i min undersøgelse, kan have en potentielt skadelig effekt på enkelte individer, især unger som i forvejen er svækkede, må betydningen af parasitterne for skarvpopulationen som helhed antages at være perifer i forhold til andre faktorer, der påvirker populationens størrelse. Her vurderes især fødemængden omkring eksisterende kolonier, samt tiltag som forhindrer dannelse af nye kolonier at have betydning.

MANUSCRIPT

Occurrence of ectoparasites on Great Cormorant chicks in Danish breeding colonies

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Abstract

Ectoparasite loads of seabirds are found to vary with a number of factors related to variations in life history and environment. In this study, cormorant (*Phalacrocorax carbo*) chicks in eight colonies in Denmark were examined for occurrence of ectoparasites in relation to age of chicks, brood size, time of hatching, chick body condition, parasite load of siblings, and colony characteristics. The parasites most frequently found on the chicks were two species of chewing lice (*Pectinopygus gyricornis* and *Eidmanniella pellucida*), followed by the carnid fly *Carnus hemapterus* and a few *Ixodes* ticks. Cormorants have not been described previously as hosts for *C. hemapterus* and this is also the first record of carnids in Denmark. The average chewing louse number was higher on older than on younger chicks, whereas younger chicks had more carnids than older chicks. Larger broods had fewer chewing lice per chick but the load of carnids per chick was unrelated to brood size. The number of both chewing lice and carnids was lower for early hatched chicks than for chicks hatched later in the period. Chick body condition was not related to chewing lice number, but for the number of carnids a small positive relation was found. Chewing lice prevalence was dependent on infestation on siblings, whereas carnid prevalence was independent of this variable. Differences in chewing louse load between colonies could not be related to age, size or development of the colonies or to the location of nests. For carnids, differences in colony load were related to location of nests as they were found only in colonies with nests in trees.

Introduction

The increased risk of parasite and disease transmission is considered a major cost of living in colonies (e.g., Brown and Brown 1986; Duffy 1991). This also applies to seabirds that often breed in dense colonies. The occurrence of ectoparasites in birds has been associated with nest desertion (Feare 1976; King *et al.* 1977), adverse effects on host condition/fitness and survival for adults and chicks (Chapman and George 1991; Loye and Carroll 1991, 1995; Møller 1997; Bosch and Figuerola 1999; Brown and Brown 2002) and reduced reproductive success (Møller 1993; Richner 1993; Fitze *et al.* 2004).

Ectoparasite loads of seabirds vary with a number of extrinsic and intrinsic factors. For example, ectoparasite load has been shown to vary with colony dynamics (Boulinier and Danchin 1996), parental age (Daunt *et al.* 2001) and chick age (Duffy and Campos de Duffy 1986). Similarly, Boulinier and Danchin (1996) found that Kittiwake (*Rissa tridactyla*) chicks of intermediate age were much more parasitized than very young and old chicks. The age of parents also seems to influence parasite load of chicks. Daunt *et al.* (2001) found for European Shags (*Phalacrocorax aristotelis*) that broods raised by young pairs were more infested by lice than broods raised by older pairs. Another factor that might influence the parasite load of chicks is the time of hatching. Chicks hatched early can be expected to be less parasitized than later hatched chicks because some ectoparasites like lice are able to synchronize their peak reproduction to the nesting period of the host (Foster 1969) and parasite populations tend to accumulate during the breeding season (Duffy 1991). Brood size has been found to influence the total load of parasites in a nest with the prevalence of parasites being higher in larger broods than in smaller broods (Dawson and Bortolotti 1997). However, the parasite load on individual nestlings seems to be unrelated to brood size (Dawson and Bortolotti 1997; Liker *et al.* 2001; Wesołowski 2001). The relationship between body condition of chicks and their load of ectoparasites has been reported for ticks on Yellow-legged Gulls (*Larus michahellis*) (Bosch and Figuerola 1999) showing that the more infested chicks had a poorer body condition than their less infested siblings at a similar age. Differences in chick ectoparasite load between colonies have been found to be related to nesting density (Duffy and Campos de Duffy 1986), age of colonies (Danchin 1992) and to

whether the colonies had increasing or decreasing populations (Boulinier and Danchin 1996).

Chewing lice (Mallophaga) and ticks (Acari) appear to dominate among ectoparasites within the family of cormorants and shags (Phalacrocoracidae). Duffy (1983) gives a review of tick outbreaks from literature including records of Argasid ticks (*Ornithodoros* sp.) in two species of cormorants (*P. lucidus* and *P. nigrogularis)* and unknown tick species in two other cormorant species (*P. capensis* and *P. coronatus*). Furthermore Duffy (1991) found Argasid ticks (*Ornithodoros* sp.) in breeding populations of Cape Cormorant (*P. capensis*) and Guanay Cormorant (*P. bougainvillii*). Berry (1976) also found *Ornithodoros* sp. on Cape Cormorant besides three species of mites (*Scutomegninia* sp., *Alloptes* sp., *Metingrassia* sp.) and a louse-fly (Hippoboscidae). Two species of *Ixodes* ticks (*I. uriae, I. signatus*) and three species of mites (*Neottialges* sp., *Scutomegninia* sp., *Ameronothrus* sp.) were found on Pelagic Cormorant (*P. pelagicus*) by Choe and Kim (1987). *I. uriae* have also been found on European Shags (Mehl and Traavik 1983). Threlfall (1982) reported findings of Argasid ticks (*Argas* sp.) and two species of mites (*Ornithonyssus* sp., *Michaelichus* sp.) on Double-crested Cormorant (*P. auritus*). Three genera of chewing lice have been associated with cormorants: *Eidmanniella* (Menoponidae), *Pectinopygus* (Philopteridae) and *Piagetiella* (Menoponidae). *Eidmanniella* has among others been found on Great Cormorant (*P. carbo*) (Hackman 1994), European shag (Daunt *et al.* 2001), Pelagic Cormorant (Choe and Kim 1987), Cape Cormorant (Berry 1976) and Double-crested Cormorant (Ryan and Price 1969, Kuiken *et al.* 1999). The genus *Pectinopygus* has been reported on Great Cormorant and European shag (Hackman 1994) and on Double-crested Cormorant (Threlfall 1982; Kuiken *et al.* 1999). Price (1970), Threlfall (1982) and Kuiken *et al.* (1999) reported of *Piagetiella* on Double-crested Cormorant and Kuiken *et al.* (1999) also found a flea (*Ceratophyllus* sp.) on this cormorant species.

Great Cormorants (*Phalacrocorax carbo*) are colony breeding birds. Apparently there have been no studies of potential sources of variation in chick ectoparasite load in this species such as chick age, brood size, time of hatching, chick body condition, parasite load of siblings, and colony characteristics. The present study investigated the occurrence of ectoparasites among chicks of Great Cormorants belonging to the subspecies *P. c. sinensis*. This subspecies is distributed from Europe in the West to

India and China in the East in breeding colonies of up to 9,000 pairs (del Hoyo *et al.* 1992). The purpose of the study was to investigate ectoparasite load in relation to age of chicks, brood size, time of hatching, chick body condition, parasite load of siblings, and characteristics of the colonies, testing the following predictions:

1. Chick load increases until a certain age and then decreases as a result of more efficient preening and immune defence among older chicks.
2. The parasite load per chick is unrelated to brood size.
3. Chicks hatched early in the breeding season are less infested than chicks hatched later due to a build up of ectoparasites during the breeding season.
4. The load of parasites increases with decreasing body condition of chicks.
5. The probability of a chick being infested is related to whether its siblings are infested or not.

Furthermore, it was examined whether possible colony differences in parasite load on chicks were related to colony age, colony size and characteristics of the nesting site.

Materials and methods

Study species and study area

Great Cormorants (after this referred to as cormorants) are very adaptable in their nest location; the nests can be placed on cliff ledges, human structures, in trees, bushes, reedbeds or on bare ground (del Hoyo et al. 1992). Laying of eggs can occur during a period of 6 months (Gregersen 1982). The brood size is 1-5 chicks, most often 2 or 3 chicks, and the chicks are hatched asynchronously. Growing of down starts from the 6th day of age, approximately 10-14 days old the chicks are covered by brown-blackish woolly down, and growth of tail – and flight feathers starts during the age of 14-20 days (Berry 1976; Olver and Kuyper 1978; del Hoyo *et al.* 1992). The chicks stay in the nest till they are about 50 days old and fledged.

The parasites found in the present study were chewing lice, carnids and ticks. Chewing lice are permanent ectoparasites and spend their entire life cycle on the host. They are extremely host-specific and different species are restricted to specific areas on the host (Ash 1960). The dispersal is first and foremost by direct contact, mainly by

vertical transmission from parent to offspring, but dispersal can also occur among hosts that use the same nesting site or resting place, or by phoresis (Marshall 1981). Chewing lice feed on feathers and dermal debris and some species also on blood. Host anti-parasite behaviour like preening normally keeps the number of lice down (Hart 1997), so usually the negative impact on host is low (Ash 1960; Blanco *et al.* 2001), but when present in large numbers they have the potential to cause extensive plumage damage, resulting in reduced host fitness (Clayton 1991, 1999).

Carnus hemapterus (Carnidae, Diptera) is a c. 2 mm long fly that parasites nestlings (Walter and Hudde 1987). The larvae live in nests where they feed on dead organic matter and where they usually overwinter as pupae (Papp 1998). The adults feed on blood of nestlings and maybe also on skin debris and secretions (Grimaldi 1997; Papp 1998). They initially possess wings which break off when they have located a suitable host (Walter and Hudde 1987). Neither the adults nor the larvae have been found on adult birds, so flies are assumed to colonise new hosts actively during the winged phase of their life cycle (Grimaldi 1997). Most studies have failed to show any detrimental effects from *C. hemapterus* on nestlings (see Valera *et al.* 2003 for references).

Ticks (Ixodida) are haematophagous ectoparasites. Two of the three families of ticks occur as parasites among seabirds: soft ticks (Argasidae) and hard ticks (Ixodidae). They are associated with the substrate, such as nest material, more than to the birds themselves (Boulinier and Danchin 1996), and they, therefore, mainly occur on individuals which spend long time in the nest, i.e. adults during incubation and chicks (Danchin 1992). Soft ticks, which lack a hard dorsal scutum, spend little time on their host (minutes or few hours) compared to hard ticks that can stay on the host for days or weeks (Duffy 1991; Sonenshine 1991). Transmission of ticks between hosts is mainly horizontal and takes place through direct contact with host or active parasite dispersal (Gregoire *et al.* 2002). Newly fledged infested chicks are presumably the main dispersal agent between colonies (Danchin 1992). Heavy infestation of ticks can have a detrimental effect on the host through blood loss (Janovy 1997; Bosch and Figuerola 1999). Besides their direct effects, ticks are potential vectors of different microparasites like arbovirus (Boulinier *et al.* 1997) and *Borrelia burdorferi* (Gregoire *et al.* 2002).

The study took place in eight breeding colonies in Denmark (Fig. 1). The colonies were chosen so different age and different types of nests (in trees, on ground (soil/sand),

in bushes etc.) were included (Table 1). All colonies were located on small islands, except for one (TO) which was located at a lake. In three of the eight colonies (OP, RS and HI) eggs were oiled in 59-86% of the nests in order to limit the production of young. The colonies OP and VO had been decreasing in size in the years before the study was conducted, whereas the other six colonies had been stable. The inter-nest distance varied in ground colonies from c. 0.5 to 1.2 m and in tree colonies from c. 1.5 to 12 m. In ground colonies gulls were breeding near the cormorants and they often predated on the cormorant nests.

Collection of data

The eight study colonies were visited during the period from 8 May to 14 June 2003. The colonies MA and SF were visited 6 and 7 times respectively, the colonies VO and HI on 2 days in a row (VO: 5-6 June, HI: 13-14 June) and the remaining four colonies were visited only once (RS: 21 May, OP: 28 May, ME: 29 May, TO: 12 June). Information about ectoparasite load of chicks was collected when nest numbers in the colonies were counted and/or when chicks were ringed. The nests were randomly chosen except that nests in tall trees were not included in the study. All 459 chicks in 229 chosen nests were examined. Beside these 132 chicks which could not be localized to specific nests were examined – 591 chicks in total. All searches for ectoparasites on chicks were carried out by the same person.

In colonies where chicks were collected from nests, all chicks from a brood were kept separate from other broods. Broods were transported in bags up to 20 metres away from the colony in order to exert least possible disturbance of the colony. Some of the chicks were kept in the bags for up to 15 minutes before they were examined and returned. At the last visit at colony MA chicks were approximately 30 days old and could not be divided into broods. Therefore, the chicks were gathered in enclosures to avoid their escape into the sea. There was physical contact between chicks because each enclosure held up to 25 chicks each.

The chicks were examined for ectoparasites by visual examination and palpation. Young chicks with no or sparse growth of down were examined 1 min. on the entire body. Older chicks were examined for 2 min. with special emphasis on the areas where the parasites were most frequently found, i.e. head, neck, wings, axillae and inguinal

area. Representative specimens of the parasites were collected and kept in 70% alcohol for later species identification. For each chick the number of parasites of each type (distinguishing between chewing lice, carnids and ticks) as well as their location on the chick was recorded. Wing length (to nearest mm) and body weight (to nearest 10 g) were determined for each chick. The wing length was applied to estimate age of the chick and the ratio between body weight and wing length to estimate body condition of the chick. The number of siblings in the nest was registered, except in ground colonies with chicks older than 25-30 days. Chicks of c. 11-40 days of age were examined in order to study the relationship between parasite load and age.

Data analysis

The main emphasis was laid on the analysis of data concerning chewing lice as these were the ectoparasites most frequently found. The load of chewing lice was quantified as louse prevalence (proportion of infested chicks), louse intensity (mean number of lice per chick) and louse density (mean number of lice per infested chick).

GLM analyses

In order to analyse potential sources of variation in chewing louse load, Generalized Linear Models (GLM) (Venables and Ripley 1994) were used. A number of explanatory variables and their interactions could hereby be assessed and the variables that best explained the variation in louse load could be determined. Before GLM analyses were performed all variables were tested for multicollinarity by a Pearson correlation matrix (r's less or equal to 0.428). A forward stepwise procedure (SAS 1999) was used to fit the final model. The number of chewing lice were entered as response variable after transformation by $\log_{10}(x+1)$, which made the variance more equal to the mean and thus the data set more even. The following variables were entered in the GLM as explanatory variables.

- *Colony number*: arbitrary number assigned to each colony in order to distinguish between colonies.
- *Brood number*: arbitrary and unique number assigned to all chicks within a brood.
- *Brood size*: number of chicks in the brood, ranging from 1 to 4.

- *Age*: estimated from wing length by means of the formula: age (days) = 0.1064 x wing length (mm) + 7.7185 (M.R. van Erden and S. van Rijn, unpubl. data).
- *Body condition*: the ratio between body weight (g) and wing length (mm).
- *Date of hatching*: estimated from wing length on the date of examination and transformed to Julian date (1 January = day 1).

The GLM analyses were first performed on data from all eight colonies combined and with all variables present. Subsequently, the colonies were analysed separately with all variables included except 'colony number'. The analysis of colony OP did not include information on broods because chicks in this colony could not be assigned to known broods. For colony MA the analysis was performed both with and without brood information since such information could not be obtained for nearly half of the chicks in the colony. Colony RS was not analysed separately because of an insufficient sample size (n = 11). The number of carnids on chicks was analysed using GLM by the same procedure as for chewing louse load and using the same explanatory variables. The number of carnids transformed by $\log_{10}(x+1)$ was entered as the response variable. Only data from the two colonies (SF and VO) in which carnids were found were analysed.

Age-specific analyses

For further analyses of age-specific load of lice all chicks were divided into 12 age groups based on the wing length. The length of interval for each age group was 30 mm and when converted into age in days the age interval was 3.2 days. The colonies MA and SF had the best representation of chicks from different age groups so data from these colonies were used to examine chewing louse prevalence and density in relation to age. Since there was no significant difference in prevalence for chicks between the two colonies (Table 2; age group 2-4, $\chi^2_1 = 1.49$, $P = 0.2219$; age group 5-12, $\chi^2_1 = 1.41$, $P = 0.2351$) data from the two colonies were combined to obtain larger sample sizes within the age groups. To be able to compare colonies more closely chicks were pooled in two groups according to age, distinguishing between age groups 2-4 (c. 11-20 days) and age groups 5-12 (c. 21-46 days). This grouping was chosen because the effect of age within the two groups was low.

The mean number of chewing lice per chick per infested nest for each of the age groups 2-4 and 5-12 was determined by 1) selecting all infested nests, 2) selecting the

chicks in the relevant age group and 3) calculating the mean number of lice per nest for chicks from the relevant age group only.

It was not possible for the GLM from the existing data to obtain a variable that would express whether chicks being siblings had any influence on the variation of chewing louse load. However, brood number could indicate if there was any difference between broods in the number of chewing lice. To further examine chewing louse number in relation to siblings a t-test was used to compare the number of chewing lice on a chick to the mean number on its siblings. The number of chewing lice on the oldest chick (the longest wing length) in a brood was compared with the number on the youngest chick (the shortest wing length) by a paired t-test. Finally, the distribution of chewing lice among siblings was tested by a χ^2 test. A χ^2 test was also used to test the distribution of carnids among siblings and to test differences in prevalence of chewing lice in relation to age. Logistic regression was applied 1) to test differences in chewing louse prevalence in relation to age (age group 2 to 9) for MA and SF combined and 2) to test for differences in carnid prevalence between the age groups 2-9 at SF. One-way analysis of variance (ANOVA) was applied to test the mean number of lice per infested chick in relation to age and colony, and to test the mean number of carnids per infested chick in relation to chick age. Data that were not normally distributed were $\log_{10}$-transformed before parametric tests. All GLM analyses were performed in SYSTAT ver. 8.0 (SPSS 1998) and other statistical analyses were performed using SAS Windows V8 (SAS 1999).

Results

Chewing lice: Species and distribution on host

Two species of chewing lice were found: *Pectinopygus gyricornis* (Philopteridae, Ischnocera) and *Eidmanniella pellucida* (Menoponidae, Amblycera). No differentiation was made between the two species in the analysis.

The lice occurred primarily on neck, nape of the neck, head (particularly around ear openings), upper and lower side of wings, and on the body underneath the wings. *E. pellucida* appeared to be especially attached to the areas of the neck, the nape of the

neck and the head. In contrast, the number of *P. gyricornis* was highest on the wings, in the case of the older chicks mainly between the flight feathers. The white feathers on the neck which are present in a period during the chicks' development were more prone to be infested with chewing lice than other feathers on the neck.

Chewing louse load

On the 591 chicks examined, a total of 7896 chewing lice were found. The overall prevalence was 76.3% for chicks and the prevalence for nests (proportion of nests with minimum one infested chick) was 86.5% (n = 229). The mean number of lice per chick (the intensity) was 13.36 ± 0.85 and the mean number of lice per infested chick (the density) was 17.51 ± 1.04 (range 1-140). The mean number of lice per chick per nest for all colonies was 15.96 ± 1.39 and the mean number of lice per chick per infested nest was 18.46 ± 1.53 (values are given ± S.E.).

Sources of variation in chewing louse load

For the colonies combined, the most significant GLM explained up to 37% of the variance in chewing louse load (Table 3). This model included age of chicks, brood size and date of hatching. In the analyses of individual colonies no significant effect of any of the variables was found for TO and OP. For the remaining five colonies the analyses explained 23-45% of the variation.

Age of chicks

For the colonies combined age of chicks was the variable with the highest proportion of total deviance in the most significant GLM obtained for chewing louse load (Table 3). This also applied for the individual colonies SF (36%) and VO (14%) and age explained up to 13% at HI. In the analysis of all chicks from colony MA, age explained up to 17% of the variance. The regression coefficient *b* for age was positive for all analyses indicating a higher number of lice on older chicks. The proportion of infested chicks increased over the ages 21-30 days (i.e. age groups 5, 6 and 7) both in the two main study colonies MA and SF and in the remaining colonies (Fig. 2). For MA and SF the difference in prevalence between age groups was significant (log. regres., $\chi^2_1 = 39.74$, $P < 0.0001$).

The mean number of lice per infested chick for MA and SF increased by increasing age for age groups 5 to 8 (c. 21-33 days) and then decreased at SF (Fig. 3). For both MA and SF the change in relation to age was significant (one-way ANOVA; MA, $F_{8,97} = 2.37$, $P = 0.0233$; SF, $F_{8,103} = 4.84$, $P < 0.0001$). Among the remaining colonies the mean number of lice per infested chick could be compared for younger (age groups 2-4) and older chicks (age groups 5-12) at VO and ME (Table 2). Older infested chicks at VO had on average 2.8 times more chewing lice than younger infested chicks and at ME older infested chicks had 7.5 times more chewing lice than younger infested chicks.

For colony SF sufficient chicks from nests had been examined to compare the prevalence of lice for nests for younger and older chicks (Table 4). The difference in prevalence between the two age groups was significant ($\chi^2_1 = 7.48$, $P = 0.0062$). The mean number of lice per chick per infested nest in SF was approximately nine times higher for older than for younger chicks (Table 4).

Brood size

Brood size which ranged from 1-4 chicks was included by the GLM analyses as a significant variable in three out of seven colonies (Table 3). The load of chewing lice per chick was negatively related to brood size. The mean number of lice per chick for age groups 2-4 decreased as brood size increased from 1 to 3 chicks for all colonies combined and from 2 to 3 chicks for colonies MA and SF (Fig. 4a). For age groups 5-11 the mean number of lice per chick decreased as brood size increased from 1 to 4 chicks for all colonies combined and from 1 to 2 chicks for VO (Fig. 4b).

Time of hatching

The date of hatching for the chicks from all colonies combined ranged from 10 April to 27 May. Date of hatching explained a small fraction (1.5-1.9%) of the variation of chewing louse load in the GLM analyses of all colonies combined and SF separately (Table 3). The relationship was positive indicating that chicks hatched early in the period had fewer lice than chicks hatching later. For colony ME date of hatching was included as the only significant variable in the final model but with a negative regression coefficient. However, the distribution of chewing lice in this colony was highly skewed, since three chicks with high numbers of lice (30, 50 and 73) were

hatched on the first two days of the period while the remaining 21 chicks had 0-5 lice and were evenly distributed during the period.

Body condition

No significant effect of chick body condition on variations in chewing louse load was found in the GLM analyses.

Siblings

The number of chewing lice on one chick was significantly related to the mean number of chewing lice on its siblings. This was the case both for all chicks (R^2 = 0.2829; t-test, $t_{389} = 12.39$, $P < 0.01$) and for infested chicks only ($R^2 = 0.2096$; t-test, $t_{266} = 8.40$, $P < 0.01$).

Chewing lice prevalence among siblings differed significantly from the distribution that would be expected if the probability of a chick being infested was independent of its siblings being infested or not ($\chi^2_6 = 145.27$, $P < 0.01$). If one chick in a brood was infested it thus increased the probability that other chicks in the brood also would be infested. For broods with two chicks the number of broods in which both chicks were infested was higher than expected if the probability of a chick becoming infested was independent of presence/absence of lice on its siblings. For broods with three chicks the number of broods in which none or only some of the chicks were infested was higher than expected.

A comparison of the number of chewing lice on the youngest chick in each brood with the number of lice on the oldest chick in the same brood showed no significant difference (paired t-test, $t_{105} = 0.3698$, $P = 0.7125$).

Comparison of colonies

According to the GLM analyses colony number did not explain a significant fraction of the variation of chewing louse load. In order to examine the variation more closely the colonies were compared with regard to prevalence and mean number of chewing lice. For age groups 2-4 the prevalence for chicks could be compared between the colonies MA, SF and ME, ranging from 43% to 53% (Table 2); the differences were not significant ($\chi^2_2 = 1.51$, $P = 0.4696$). For age groups 5-12 the colonies MA, OP, TO, SF,

HI and VO could be compared and here the prevalence for chicks ranged from 82% to 98% (Table 2). The difference between these colonies was marginally significant (χ^2_5 = 11.25, P = 0.05). The mean number of chewing lice per infested chick (Table 2) did not vary significantly among the colonies MA, SF and ME for age groups 2-4 (one-way ANOVA, $F_{2,81}$ = 1.78, P = 0.1751). For age groups 5-12 there was a significant difference between the colonies MA, OP, TO, SF, HI and VO (one-way ANOVA, $F_{5,332}$ = 2.72, P = 0.0200).

A comparison of the prevalence for nests showed for age groups 2-4 no significant difference between MA and SF (Table 4; χ^2_1 = 0.85, P = 0.3580). For age groups 5-12 the difference between the colonies TO, SF, HI and VO was significant (χ^2_3 = 37.12, P < 0.001). Especially HI had a higher proportion of infested nests than the other colonies. The mean number of lice per chick per infested nest did not differ essentially for age groups 2-4 from MA and SF and this also applied to age groups 5-12 from TO, SF, HI and VO (Table 4).

Carnids

Carnus hemapterus was found on 78 of the 591 chicks examined. The species occurred mainly on naked skin of the axillae of the wings and of the inguinal area on younger chicks up to 30 days old. A total of 789 *C. hemapterus* was found but only in two (SF and VO) of the eight colonies examined. For VO the prevalence for the 100 chicks examined was 8% whereas 70 of 163 (42.9%) chicks at SF were infested. Of the 66 broods examined from SF 38 were infested, of which two broods came from ground nests. The number of carnids of infested chicks ranged from 1 to 45 at SF and from 1 to 9 at VO. The intensity of carnid infestation for chicks was 4.61 ± 0.76 at SF and 0.37 ± 0.14 at VO, and the density was 10.74 ± 1.49 and 4.63 ± 0.92 for SF and VO, respectively. The mean number of carnids per chick per nest was 5.03 ± 1.19 for SF and 0.25 ± 0.15 for VO, and the mean number of carnids per chick per infested nest for SF and VO was 8.74 ± 1.87 and 3.13 ± 1.46, respectively.

The most significant GLM obtained for carnid load explained up to 41% of the variance for SF and VO combined and up to 49% for SF and 23% for VO separately (Table 5). Date of hatching was included as a significant variable in the final models for SF and VO separately and for the two colonies combined with a positive regression

coefficient, indicating that chicks hatched early in the period had fewer carnids than chicks hatched later. The hatching period ranged from 25 April to 24 May for SF and from 18 April to 21 May for VO. Age of chicks was included by the GLM analyses as a significant variable at VO and SF combined and separately (Table 5). The number of carnids was negatively related to age. The proportion of infested chicks at SF reached a maximum at age 21-24 days (age group 5) and then decreased (Fig. 5a). Only one infested chick was found from age group 8, and in age group 9 and 10 no carnids were found. The difference in prevalence for chicks between age groups was significant (log. regres., $\chi^2_1 = 10.62$, $P = 0.0011$). Among the chicks examined from VO infested chicks were found within the age groups 2 to 5, but non within the age groups 6 to 10. The mean number of carnids per infested chick for SF increased by increasing age for age groups 2 to 4 (11-20 days) and then decreased (Fig. 5b). The change in relation to age was significant (one-way ANOVA, $F_{6,69} = 3.43$, $P = 0.0054$). The mean number of carnids per chick for SF was not clearly related to brood size (two chicks, $\bar{x} = 6.0 \pm 1.3$, n = 78; three chicks, $\bar{x} = 2.3 \pm 0.6$, n = 54; 4-5 chicks, $\bar{x} = 5.4 \pm 2.5$, n = 25). For broods with 3-4 chicks the prevalence was significantly higher than for broods with 1-2 chicks ($\chi^2_1 = 10.62$, P = 0.0011). The number of carnids among siblings was not significantly different from the distribution that could be expected if the probability of a chick being infested was independent of whether its siblings were infested or not ($\chi^2_6 = 9.88$, $P <$ 0.13).

Ticks

On the 591 chicks only three ticks were found, two of which were identified as *Ixodes ricinus*. It was not possible to determine whether the third tick was a variant of *Ixodes ricinus* or a variant of *Ixodes ventalloi*. The ticks were found in SF and TO.

Discussion

Observed species

The ectoparasites most frequently found on cormorant chicks in this study were chewing lice followed by carnids and a few ticks. The number of chewing lice on chicks

was found to be related to the age of chicks, brood size, date of hatching, and brood, but not to body condition and colony. For carnids the number on chicks was found to be related to age of chicks, date of hatching, brood, and body condition, but not to brood size or colony.

The findings of the chewing lice species *Pectinopygus gyricornis* and *Eidmanniella pellucida* on cormorant chicks were consistent with the species previously described for Great Cormorant (Hackman 1994). The chewing lice seemed to prefer white feathers to black when they had the choice. This observation confirms a study made by Kose *et al.* (1999), who found that white tail spots in swallows were preferred as feeding site by feather-eating Mallophaga, as they prefer to eat feathers that lack melanin.

The parasitic fly *Carnus hemapterus*, which was found on chicks in two of the colonies, has not previously been documented in Denmark, although it appears to be a widely distributed species (Kirkpatrick and Colvin 1989). It has been recorded for a number of bird species, mainly raptors and cavity-nesting birds (Cannings 1986; Grimaldi 1997), but not for cormorants or other members of the order Pelecaniformes. According to Papp (1998) it can be found in nests in trees and bushes, but not in nests on soil, in marshes, or on water surfaces. However, in the present study it was found mainly in tree nests, but also in two ground nests. Of more than 65 records, Grimaldi (1997) reported of only one former observation on *C. hemapterus* that was not from a nest of a tree-nesting bird (the one exception was Grey Egret *Ardea cinerea* from Holland). Grimaldi suggested that the reason was that tree nesters have predominantly altricial young, which stay in the nest for a long time contrary to the precocial young of most ground nesters that leave the nest short time after hatching. Cormorants have altricial young, but are very adaptable in their nest location and have also adapted to breeding on the ground. This may be the reason why cormorants are one of the rare exceptions to the rule that carnids can not be found in ground nests.

The number of ticks found in the study was surprisingly low. Since ticks have been described for other species of cormorants (e.g. Duffy 1983, 1991) a higher occurrence was expected. The sparse findings are most likely due to the method of visual examination and palpation used to examine the chicks, as ticks not yet engorged and especially larvae can be difficult to detect among the dark down and feathers of the chicks. The study showed that ticks can be found on Great Cormorant, but the actual

occurrence and distribution of ticks on this species require further investigations preferably by use of alternative methods.

Age-specific variation in parasite load

Chick age was found to be the most important source of variation in chewing louse load among the analysed variables. An inverted U-shaped relationship between chick age and parasite prevalence as observed for ticks on Kittiwake chicks by Boulinier and Danchin (1996) was found in this study, thus confirming the prediction stated in the introduction. The lower density of chewing lice among younger chicks can be explained by shorter exposure time and sparse development of down and feathers. The subsequent increase in chewing louse load by increasing age can be explained by various causes like increasing exposure time, growth of down and feathers, and increasing size of the host. Vertical transmission of chewing lice from parents to offspring is also likely to be an important factor, since this is believed to be the main route of transmission for chewing lice (Marshall 1981; Clayton and Tompkins 1994). Furthermore, it is most likely that breeding occurs on the chicks. Eveleigh and Threlfall (1976) and Ballard and Ring (1979) found this to be the case for chewing lice on auks (Alcidae) and Common Murre (*Uria aalge*) respectively. Whether this also applies to cormorants could be confirmed by study of the ratio of nymphs to adult lice on chicks compared to adult cormorants. The density of chewing lice on chicks reached its maximum at about 30 to 33 days of age and then decreased at SF. Feather-feeding lice like *P. gyricornis* are not impacted by the immune system (Moyer *et al.* 2002). However, *E. pellucida* can feed on blood, thus acquired immunologic resistance may be of some importance to the decrease in chewing louse load, but preening is most likely to be the main cause. The proportion of time spent on preening by chicks was found in one study to increase gradually by increasing age, until the chicks were about 31 to 35 days old and thereafter maintained more or less the same level comprising about 20% of the observed activities (Hansen 2005). The age with maximum abundance of chewing lice coincides with the age, when the chicks reach the maximum amount of time spent on preening. At this age they do not only spend more time preening, but are also likely to have achieved a greater skill at removing parasites and thus increase their grooming efficiency.

The prediction of the relationship between chick age and parasite load was also confirmed for *C. hemapterus*. The relation was negative indicating more carnids on younger chicks contrary to the positive relation for chewing lice. This is in accordance with the feeding and behaviour of the two types of parasites. Chewing lice are with their dorso-ventrally flattened body adapted to movement on and between feathers (Rothschild and Clay 1952) and they are dependent on chicks that have developed feathers, whereas carnids prefer the bare skin on young chicks. Carnid prevalence and density reached a maximum at 21-24 days of age and 17-20 days of age respectively, and no carnids were found after approximately 33 days of age. Previous studies on different host species have shown similar patterns with increasing load on young chicks followed by a marked decrease with age (Kirkpatrick and Colvin 1989; Dawson and Bortolotti 1997; Liker *et al.* 2001) and chicks being free of parasites close to fledging (Roulin 2003). The pronounced decrease in carnid load on chicks has been suggested to be connected with the moult from downy to contour feathers (Kirkpatrick and Colvin 1989; Dawson and Bortolotti 1997). Carnids are not adapted to movement between feathers, thus the increasing density and layering of feathers could make the chicks a less attractive habitat to the flies (Kirkpatrick and Colvin 1989). This could be a possible explanation of the decline in carnid load found in the present study, as cormorant contour feathers start growing at approximately 18 to 20 days of age appearing first on wings, tail and scapulars and at the latest at five weeks on the body (Berry 1976; Olver and Kuyper 1978). Also the increased time spent on preening and stronger immune defence among older chicks could be a contributory cause of the decline in carnid infestation.

Causes of variation in parasite load

The parasite load per chick was predicted to be unrelated to brood size. For chewing lice this appeared not to be the case; in fact it was found that the more chicks in the brood, the fewer lice per chick. This was surprising given that other studies have found no relation between parasite load per chick and brood size, but larger broods contained more parasites (Roulin 1998; Wesołowski 2001). Thus, if a relation between individual chick load and brood size was to be found, it would be expected to show more parasites per chick in larger broods. The fewer lice per chick in larger broods found in the present

study might be due to age of parents. Daunt *et al.* (2001) observed fewer lice on broods raised by older parents than on broods raised by younger parents, probably due to higher louse load on young parents and more effective removal of ectoparasites from chicks by older parents. As young birds typically produce fewer eggs than older, more experienced birds (Gill 1994), the fewer lice per chick in larger broods could be a result of the parents of larger broods generally being older than the parents of smaller broods. For carnids the results were consistent with the results of Dawson and Bortolotti (1997) who found for American Kestrel (*Falco sparverius*) that the prevalence of carnids was higher in larger broods, but load of carnids on individual chicks was unrelated to brood size.

For both types of parasites it was found that the number on chicks hatched early in the period was lower than the number on chicks hatched later, thus confirming the prediction stated in the introduction. The time of hatching seemed to be of greater importance for the number of carnids than for the number of chewing lice. Previous studies have also found the occurrence of carnids to be highly seasonally related (Cannings 1986; Dawson and Bortolotti 1997), but with the number being highest early in the nestling period, when the number of unfeathered or downy chicks is highest. For Germany (Walter and Hudde 1987) the main activity period of carnids was estimated to extend from mid May till end of June. However, the hatching period in this study ranged from 18 April to 24 May for the two colonies in which carnids were found. Thus the higher occurrence later in the period seems to correspond to the actual beginning of the carnid activity period.

The prediction that body condition of chicks would be negatively correlated to their load of parasites was not confirmed for chewing lice or carnids. However, a small positive correlation between body condition and number of carnid was found for colony SF (Table 5). Dawson and Bortolotti (1997) found a similar relation for American Kestrel, as carnids were more likely to infest the largest chicks in a nest, and suggested that carnids may actively choose the largest nestling within a brood. By choosing the largest chick and thereby usually the chick with the highest body condition, the carnids have ensured a host that has a competitive advantage. As it usually receives more food than the smaller chicks in the brood it represents a more secure source of food to the parasites. This would have to be clarified by further studies.

Effects of siblings

The probability of a chick being infested with chewing lice was found to depend on presence/absence of lice on its siblings, thereby confirming the prediction previously stated. For carnids, the prediction could not be confirmed, although brood number explained some of the variation in carnid load for the colonies SF and VO combined (Table 5), indicating that there was a difference in carnid number between broods. Thus the number of carnids was influenced by which brood the chick came from. However, the probability of a chick being infested with carnids was independent of whether its siblings were infested or not. Previous studies have found that carnids show intra-brood preferences (Kirkpatrick and Colvin 1989; Dawson and Bortolotti 1997), and age and size of chicks seem to be more important for the number of carnids than infestations of siblings. However, limited data on siblings in this study confine the conclusions that can be drawn from the relationship between parasite load and siblings both for chewing lice and carnids. Further studies with more information on siblings are thus needed.

Between colony aspects

According to the GLM analyses, no significant fraction of the variation of chewing louse number could be explained by which colony the chicks came from. However, a significant difference in chewing louse prevalence and density between the colonies was found. The colonies TO and HI had the highest prevalence for older chicks for both chicks and nests, whereas the colonies SF and VO had the lowest. However, there was no relation between louse prevalence and age or size of the colonies. For colony age this was expected, as permanent ectoparasites like lice do not overwinter at the nesting site (Hoi *et al.* 1998). Louse prevalence also seemed to be unrelated to whether the colonies were stable or decreasing or to the location of nests (Table 1). The prevalence of lice was expected to be higher in colonies with nests on the ground than in colonies with nests in trees, at least among older chicks, as the chicks wander off to other nests, especially in case of disturbance of the colony. The parents breeding at the colonies TO and HI are generally younger than the birds breeding at the colonies VO and SF; a knowledge that is obtained from ringing and surveys of the colonies. Since chewing lice mainly are transferred from parents to chicks (Marshall 1981), and chicks of younger parents are shown to have more lice (Daunt *et al.* 2001), this might be an explanation of

the higher louse prevalence of TO and HI. Furthermore, the geographical location of the colonies may influence the prevalence of chewing lice. Danchin (1992) found that ticks were presumably transferred between Kittiwake colonies when newly fledged infested juveniles visited neighbouring colonies. This may also apply to chewing lice on juvenile cormorants. The colonies VO and SF were located close to each other, and the level of louse load in the two colonies was quite similar for both prevalence and density. The similarity could be due to the movement between the colonies VO and SF of juveniles which have been found to be generally more infested with chewing lice than adults (Ballard and Ring 1979). However, colony MA was situated close to the colonies VO and SF, but had a significant lower louse density than these two colonies. So, altogether, it remains unclear which factors influence differences in chewing louse load on chicks between colonies. The experience from ringing of cormorant chicks during 1977-2005 is that there can be large inter-annual variation in chewing louse number on chicks. Thus studies of year-to-year variation in parasite load would be relevant.

For carnids, the differences between colonies in prevalence were clearly related to the type of colony. The colonies SF and VO, in which carnids were found, both had nests located in trees, whereas the nests in the remaining colonies except colony TO were located on ground or in bushes (Table 1). A possible reason for absence of carnids at colony TO, despite having nests in trees, could be that the colony was visited later in the season than the colonies SF and VO, and the examined chicks were generally older. The prevalence of carnids at colony SF was significantly higher than at colony VO. Carnids overwinter as pupae in the nest (Papp 1998), thus a higher occurrence would be expected in older colonies, but as SF was actually the youngest of the two colonies other factors seem to be of more importance than colony age. One cause of the higher load of carnids at colony SF could be the higher density of nests in this colony facilitating the dispersal of not only the winged newly emerged adult flies, but also the later wingless phase that can reach new hosts by walking (Marshall 1981).

In conclusion, occurrence of chewing lice and carnids on cormorant chicks was found to be related to various factors, especially age of chicks, brood size, and date of hatching. The load of each of the two types of parasites was influenced differently by the factors depending on the biology and behaviour of the parasite.

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Table 1. Characteristics of the eight cormorant breeding colonies studied in 2003. For each colony are given year of establishment of the colony, number of nests in the colony in 2003, the habitat on which nests were located, and the main type of nesting material used (National Environmental Research Institute, unpubl. data).

Colony	Year of establish-ment	Size of colony (no. of nests)	Nest location	Nest material
MA (Mågeøerne)	1985	1840	On ground (sand)	Seaweed
OP (Olsens Pold)	1991	1880	On ground (soil/sand)	Seaweed
RS (Rønland Sandø)	1990	1075	On ground (sand)	Lyme grass, seaweed
TO (Toft Sø)	1982	3321	In trees (3-5 m above ground)	Sticks, twigs
SF (Stavns Fjord)	1991/89	3118	On ground (soil), in bushes (1-2 m above ground), and < 15% in trees (2-4 m above ground)	Sticks, twigs
HI (Hirsholmene)	1997	1400	On ground (soil) or in bushes (1-2 m above ground)	Sticks, twigs, seaweed
VO (Vorsø)	1944	1895	In trees (2-8 m above ground)	Sticks, twigs
ME (Melsig)	1991	1531	On ground (soil)	Reeds, seaweed

Table 2. Relationship between chewing louse load of cormorant chicks and age in seven Danish breeding colonies. Chewing louse load is expressed as prevalence (proportion of chicks infested), intensity (mean number of lice per chick) and density (mean number of lice per infested chick). Chicks were grouped according to age: group 2-4 included 11-20 day-old chicks and group 5-12 included 21-46 day-old chicks. Only data from colonies and age groups with n > 10 are included.

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Colony	Age group	Chewing louse load					
		Prevalence		Intensity		Density	
		%	n	$\bar{x}$	S.E.	$\bar{x}$	S.E.
MA	2-4	53.4	73	4.14	1.28	7.74	2.25
	5-12	89.4	66	11.95	2.08	13.37	2.26
OP	5-12	86.4	22	13.09	3.50	15.16	3.85
TO	5-12	97.7	43	21.49	3.93	22.00	4.02
SF	2-4	43.4	76	1.38	0.33	3.18	0.63
	5-12	82.6	86	19.72	2.77	23.89	3.14
HI	5-12	95.8	71	19.39	2.76	20.25	2.83
VO	2-4	42.9	14	3.93	3.03	9.17	6.78
	5-12	86.1	86	21.99	2.50	25.55	2.69
ME	2-4	50.0	20	1.25	0.38	2.50	0.50
	5-12	81.8	11	15.36	7.49	18.78	8.82

Table 3. The most significant generalized linear models of number of chewing lice on cormorant chicks for all colonies combined and individually. For each independent variable is given: sample size *n*, regression coefficient *b*(SEM), percentage of deviance explained by each variable over the total explained deviance and significance level (*p*, two-tailed). For all models the response variable is chewing louse load (= $\log_{10}$(louse number + 1)).

Independent term	n	*b*(SEM)	% of total deviance	*P*
All colonies[a,b]				
Age	459	0.035 (0.003)	28.4	< 0.0001
Brood size	459	-0.176 (0.030)	7.0	< 0.0001
Hatch date	459	0.008 (0.003)	1.5	0.001
SF[b]				
Age	160	0.048 (0.006)	36.4	< 0.0001
Brood size	160	-0.157 (0.050)	6.7	0.002
Hatch date	160	0.012 (0.005)	1.9	0.020
MA[b]				
Brood size	73	-0.280 (0.058)	25.0	< 0.0001
VO[b]				
Age	100	0.024 (0.009)	14.6	0.015
Brood size	100	-0.282 (0.104)	5.7	0.008
Brood number	100	0.006 (0.003)	3.1	0.050
HI[b]				
Brood number	54	0.010 (0.003)	17.5	0.001
Age	54	0.061 (0.015)	13.8	< 0.0001
ME[b]				
Hatch date	24	-0.065 (0.014)	35.5	< 0.0001

[a]Includes all eight colonies listed in Table 1.

[b]The full model included the following independent variables: [colony number, brood number, brood size, chick age, body condition, hatch date] for all colonies, [brood number, brood size, chick age, body condition, hatch date] for SF, MA, VO, HI, TO, and ME, and [chick age, body condition, hatch date] for OP. TO and OP are not included in the table, since no significant effect of any of the variables was found for these colonies.

Table 4. Relationship between chewing louse load of cormorant nests (broods) and age of chicks in five Danish breeding colonies. Chewing louse load for nests is expressed as prevalence (proportion of nests where at least one chick was infested), mean number of lice per nest (A), mean number of lice per chick per nest (B), and mean number of lice per chick per infested nest (C). Chicks were grouped according to age: group 2-4 included 11-20 day-old chicks and group 5-12 included 21-46 day-old chicks. Only data from colonies and age groups with n > 20 are included.

Colony	Age group	Chewing louse load							
		Prevalence		A		B		C	
		%	n	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.
MA	2-4	69.2	26	11.03	3.81	6.29	2.50	9.08	3.43
TO	5-12	96.7	30	30.57	6.63	22.30	5.04	23.07	5.16
SF	2-4	57.6	33	3.18	1.04	1.37	0.50	2.39	0.79
	5-12	85.7	42	39.12	6.75	19.47	3.47	22.11	3.74
HI	5-12	100.0	27	28.48	5.79	15.47	3.32	15.47	3.32
VO	5-12	89.7	58	32.60	4.44	23.54	2.84	26.25	2.94

Table 5. The most significant generalized linear models of number of *Carnus hemapterus* on cormorant chicks for the colonies SF and VO combined and individually. For abbreviations see Table 3. For all models the response variable is carnid load (= $\log_{10}$ (carnid number + 1)).

Independent term	n	*b*(SEM)	% of total deviance	*P*
SF and VO[a]				
Brood number	260	0.000 (0.000)	19.6	<0.0001
Age	260	-0.005 (0.003)	14.3	0.145
Hatch date	260	0.031 (0.003)	7.2	<0.0001
SF[a]				
Hatch date	160	0.046 (0.004)	41.6	<0.0001
Age	160	-0.014 (0.004)	5.7	0.001
Body condition	160	0.056 (0.020)	2.4	0.006
VO[a]				
Hatch date	100	0.096 (0.033)	18.2	0.005
Age	100	-0.084 (0.033)	5.0	0.013

[a]The full model included the following independent variables: [colony number, brood number, brood size, chick age, body condition, hatch date] for SF and VO combined and [brood number, brood size, chick age, body condition, hatch date] for SF and VO individually.

Figure captions

Figure 1. Location of the eight cormorant breeding colonies studied in Denmark in 2003. The location of other breeding colonies existing in Denmark in 2003 is also shown. Circle size is proportional to colony size.

Figure 2. Chewing louse prevalence (%) for the colonies MA and SF combined and for the other six colonies combined in relation to chick age. Sample size ranged from 24 to 54 chicks for MA and SF and from 17 to 63 chicks for other colonies. Chicks in age group 10 were pooled with chicks in age group 9.

Figure 3. Chewing louse density (± S.E.) for the colonies MA and SF in relation to chick age. Sample size ranged from 5 to 25 chicks. Chicks in age group 10 were pooled with chicks in age group 9.

Figure 4. Chewing louse intensity (± S.E.) in relation to brood size for A) age groups 2-4 (11-20 day-old chicks) and B) age groups 5-12 (21-46 day-old chicks). Sample size ranged from 10 to 93 chicks for age groups 2-4 and from 13 to 161 chicks for age groups 5-12.

Figure 5. Carnid load on chicks at colony SF in relation to chick age expressed by A) prevalence (%) of carnids and B) density of carnids (± S.E.). Sample size ranged from 10 to 34 chicks for prevalence and from 7 to 15 chicks for density.

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Figure 1

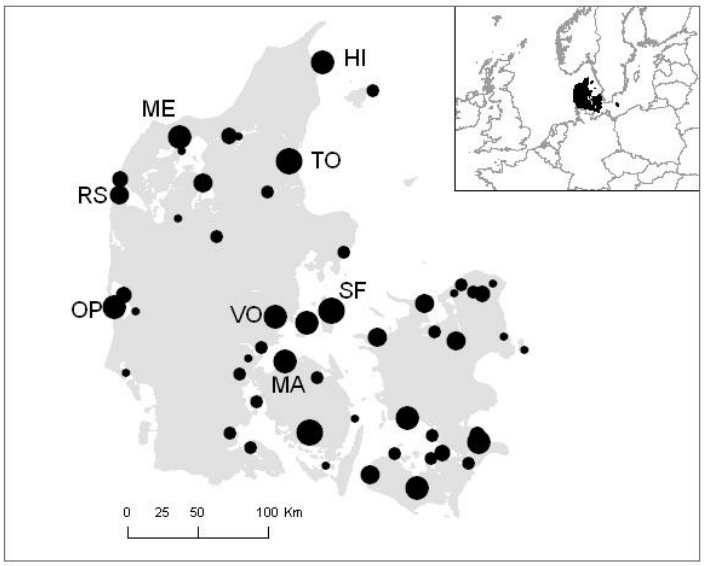

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Figure 2

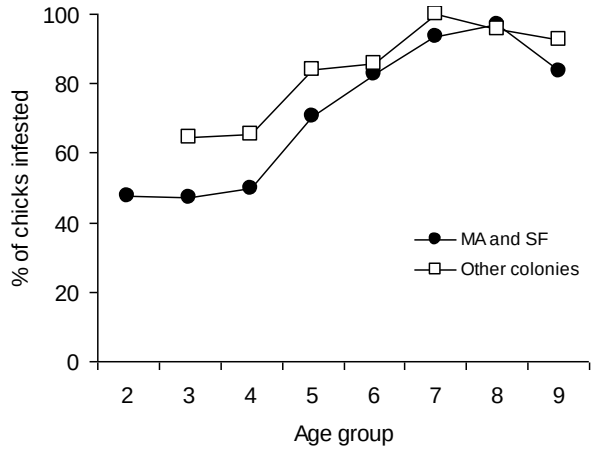

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Figure 3

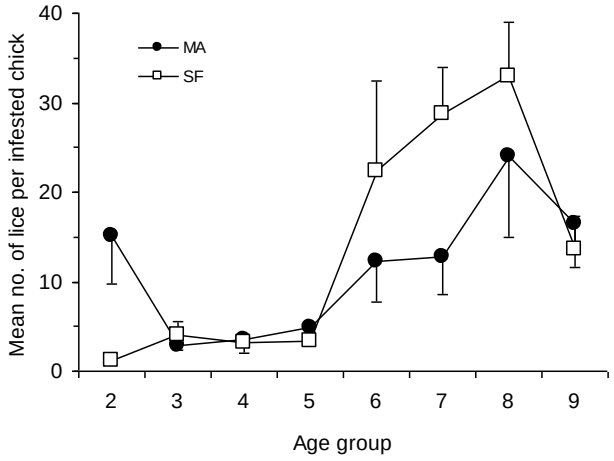

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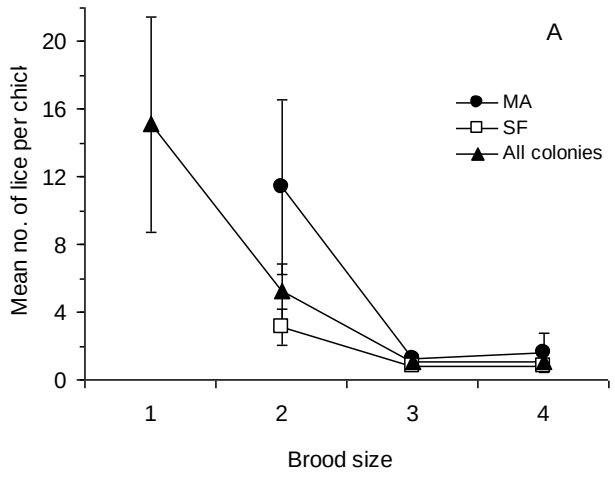
Figure 4



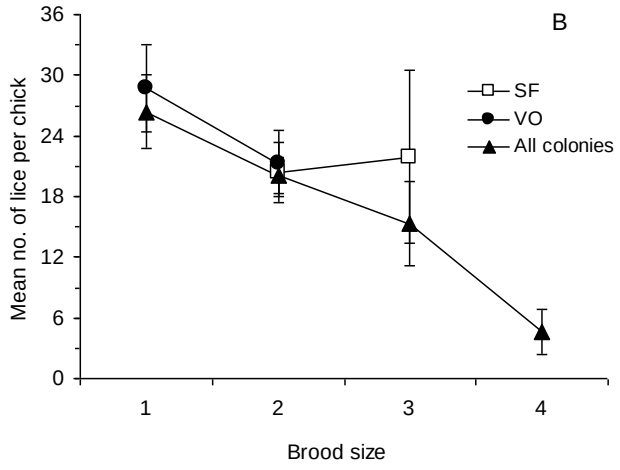


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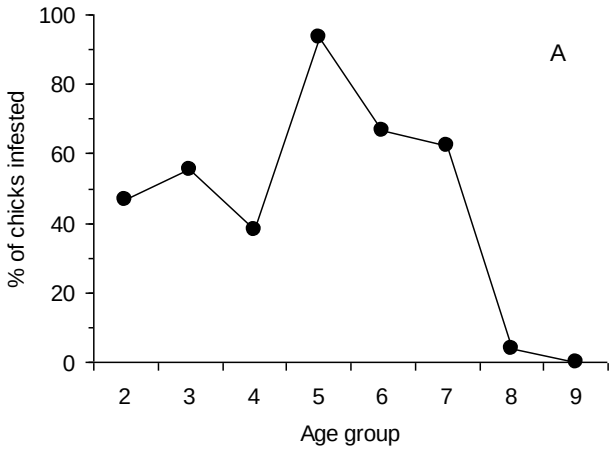
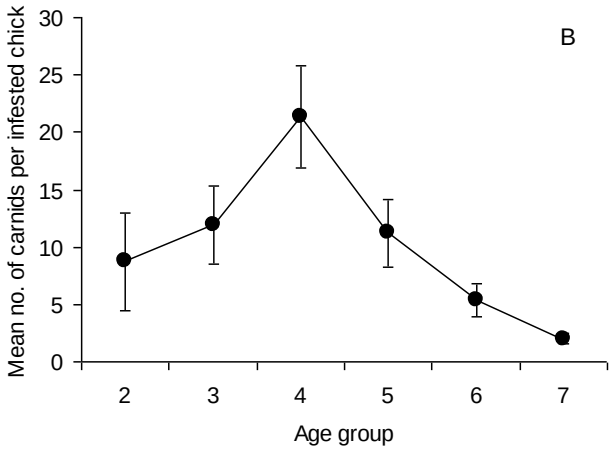
Figure 5


A
% of chicks infested
100
80
60
40
20
0
2
3
4
5
6
7
8
9
Age group


B
Mean no. of carnids per infested chick
30
25
20
15
10
5
0
2
3
4
5
6
7
Age group

APPENDIX

Preening behaviour of chicks in relation to chick age

The activity of Great Cormorant chicks was monitored in relation to other projects in two of the study colonies (Vorsø and Stavns Fjord) in 1994. Before recording activity, the chicks were aged based on wing length measurements. The activity of chicks was monitored by scan observations from towers and hides of 19-29 broods at 10-15 min intervals during 1-hour periods distributed between 0730 h and 1900 h. This resulted in 3,115 records of chick activity at Vorsø and in 1,525 records at Stavns Fjord. Preening of down or feathers was distinguished as separately from other activities. Chicks were grouped into age groups to ensure reasonable sample sizes. The result is presented in Figure 1.

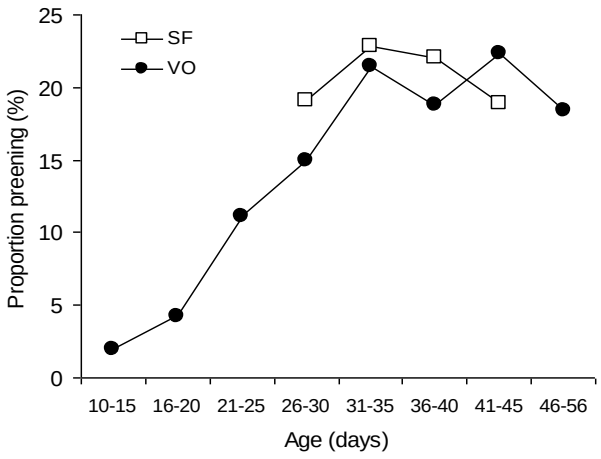


Figure 1. The proportion of chicks observed preening at the colonies SF and VO in relation to age of the chicks. Sample size ranged from 100 to 593 chicks.