Ecology of Endoparasites of the Atlantic Puffin (*Fratercula arctica grabae*) (Alcidae: Charadriiformes)

Vistfrøðin hjá innvortis Sníkum í Lunda (*Fratercula arctica grabae*) (Alcidae: Charadriiformes)

Ámundur Nolsø
Corresponding address: Department of Marine Ecology, Institute of Biological Sciences, University of Aarhus
Finlandsgade 14, DK-8200 Aarhus N. Email: amundur.nolso@biology.au.dk

Úrtak

Hetta er tann fyrsta víðfevnda kanningin av innvortis sníkum í lunda. Í alt 173 lundar, fleygaðir á Urðini í Nólsoy, eru kannaðir. Viðurskifti millum vert og sník, fevnandi lívssøgueyðkenni, likamsstand, aldur, títtleika, og tíðarfrábrigdi (sesongvariatión) eru viðgjørd. Eitt slag av trematodu (*Gymnophallus* sp.); tvey sløg av bendilormi (*Alcataenia* sp. og ein limur úr familjuni Hymenolepidae); trý sløg av nematodum (*Streptocara* sp., *Seuratia* sp. og *Contracaecum* sp.); og eitt slag av pentastomidu (*Reighardia* sp.) vóru funnin. Eingi skaðilig árin, elvd av sníkunum, kundu staðfestast. Títtleiki og nøgd av sníkum í lunda er lægri enn í øðrum sjófugli, eitt nú havhesti, skrápi og mása.

Abstract

The first extensive study on the endoparasitic fauna in the Atlantic puffin is reported. A total of 173 puffins were collected at breeding sites at a colony in Nólsoy (Faroe Islands). Host-parasite relationships including life-history characteristics, host fitness and age, prevalence of infestation and seasonal variation are discussed. One digenean species (*Gymnophallus* sp.), two cestode species (*Alcataenia* sp. and a member of the family Hymenolepidae), three nematode species (*Streptocara* sp., *Seuratia* sp. and *Contracaecum* sp.), and one pentastome species (*Reighardia* sp.) were found. There was no negative effect on bird fitness owing to the presence of parasites. The prevalence and intensity of parasite infestation in Faroese puffins are lower than in other seabird species, namely, fulmars, great shearwaters and gulls.

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Introduction

Much work has been reported on the endoparasitic fauna of Pacific auks (Hoberg, 1981; 1982; 1984a; 1984b; 1984c; 1984d) and some investigations, mainly based on old material, have been made of Atlantic auks (Madsen, 1939; Baer, 1956; Threlfall, 1971; Dyck, 1975; Hoberg, 1991; Ólafsdóttir *et al.*, 1996).

Hitherto, the only reports on endoparasites in Faroese auks are those of Krabbe in 1869 on cestodes in black guillemot (*Cepphus grylle*) and in common murre (*Uria aalge*) (Madsen, 1939), and on pentastomes in *U. aalge* (Dyck, 1975). No previous work has been reported on the Atlantic puffin (*Fratercula arctica grabae*) .

Ecological aspects of the parasite-host relationship in seabirds and waterfowls have been investigated by several authors (Cornwell and Cowan, 1963; Threlfall, 1967; Avery; 1969; Threlfall, 1971; Kennedy *et al.*, 1985; Wallace and Pence, 1986; Edwards and Bush, 1989; Hoberg and Ryan, 1989). These workers have studied such aspects as the dependence of the prevalence and intensity of infestation on host gender and age, as well as on season/migrations. No conclusive statements can be drawn from the findings regarding gender and age, but there is a consensus that prevalence is dependent upon season/migrations.

The aim of this paper was to study, for the first time, the entire metazoan parasite fauna of the most common auk of the Atlantic area, the Atlantic puffin.

Materials and methods

Study area

The birds were collected on the exposed east coast of the isle of Nólsoy (62°00'N, 6°40'W). The island is 8.8 km long and 2.2 km wide. The puffins breed along the entire exposed east coast, but are far most concentrated at the colony 'Urðin', a 1 km long area with great piles of loose boulders and stones mostly overgrown by turf. The birds were collected while they were wheeling using 'fleygastong', the traditional Faroese fowling equipment, which comprises a triangular net fastened to a pair of 1.5 m long fibre glass supports lashed to a 3.5 m long pole. With this equipment is it possible to catch one puffin at the time as the birds fly by. The pole is quickly levered up to make the net overtake the passing bird, holding the pole at the end with one hand, and approximately a meter higher up with the other. During the fowling season, the first ten puffins caught by the fowler each day were used in the analyses. This restricted the diurnal collecting time to c. 8 to 11 a.m. The collection took place from the 03 July to 02 August, 2000.

Dissection

All internal organs, except the lungs, were dissected out and frozen at –18 °C. Subsequently, the organs were thawed, dissected and examined separately. The small intestine was divided into three parts of equal length. The heart, trachea plus syrinx, oesophagus plus crop, gizzard, duodenum, the three sections of the small intestine and rectum were cut up lengthwise, scraped and rinsed. The internal membrane of the gizzard was also dissected and investigated. The gallbladder was cut up, scraped and rinsed. The kidneys and the liver were cut up cross- and lengthwise, scraped and rinsed. All the material was subsequently examined stereomicroscopically. Parasite specimens were fixed in formalin (6 % by volume) or preserved directly in ethanol (70 % by volume).

During dissection, the abdominal fat reserves were weighed to the nearest 0.1 g using a digital balance as an indication of bird fitness. The bird's sex was also recorded. The puffins were assigned to one of two age categories based on the developmental stage of the *Bursa Fabricii*; this body part regresses during sexual maturation, one reason for which is the presence of the sex hormones testosterone or progesterone (Møller and Erritzøe, 2001). The size of the *Bursa Fabricii* was measured to the nearest mm using a digital Vernier calliper.

Mounting

Nematodes: Each worm was taken directly

from the fixative and placed in lactophenol in a petri dish, observed stereomicroscopically until transparent, and then mounted in glycerine jelly.

Trematodes, cestodes, and pentastomes: the specimens were transferred from preservative to demineralized water, rinsed thoroughly, and left in the water for 5 minutes. The specimens were then transferred to Semichon's acetocarmine for 3 to 24 hours for staining, rinsed in 70 % ethanol, and dehydrated. Dehydration was achieved by transferring the specimens from 70 % ethanol to 80 % and to 90 % and then twice in 96 % leaving the specimens 5 to 10 minutes in each solution. Whilst 3 minutes in absolute ethanol is recommended at the end, this was not available. The specimens were then transferred to xylol for a minimum of 7 minutes for clearing. Finally they were mounted in Canada balsam.

Identification

The parasites were identified to the lowest possible taxon using keys in Yamaguti (1958-61), Anderson *et al.* (1974-80), Hoberg (1986), and Khalil *et al.* (1994). Each identification was checked subsequently by Isam Sadula Saeed (Danish Agricultural Academy, Department for Experimental Parasitology).

Statistical methods

For independent two-sample tests, the parametric student's t-test (t-test) was used for comparing means. However, heterogeneity of variance was common and standard transformation was usually unsuccessful in stabilising the variance. Non-parametric tests were applied therefore. In such cases two-sample tests were done using the Mann-Whitney test (M-W). Frequency analysis was carried out by Fisher's exact test. All tests were performed using the SPSS 9.0 version (Hull and Nie, 1981).

Results

Parasite infestation rates

Over-all, the prevalence of infestation in the 173 puffins was 66.5 %; trematodes occurred in 35.8 %, cestodes in 31.8 %, nematodes in 21.4 %, and pentastomes in 2.3 % (see also Table 1). No puffin infested with cestodes also harboured pentastomes.

Parasite identification

Only one trematode genus, *Gymnophallus* (Microphallidae) was found; the site of infestation was mostly the gallbladder, but occasionally also the kidneys. Two species of cestodes were found of which the most common by far was *Alcataenia* sp. (Dilepididae); it occurred primarily in the duodenum, but several individuals also occurred in most parts of the gastro-intestinal tract. A single specimen of the family Hymenolepidae was found in the anterior part of the duodenum. The three nematode species were: *Streptocara* sp. (Physalopteridae), *Seuratia* sp. (Acuariidae), and *Contracaecum* sp. (Anisakidae). The nematodes occurred in the oesophagus plus crop and gizzard. Four birds harboured pentastomes: *Reighardia* sp. (Reighardiidae); one contained 37 specimens in the trachea plus primary bronchi, whilst the other three birds harboured pentastomes in

Table 1. *Endoparasites in puffins (Number of examined birds; Number of infested birds; percent of birds infested (prevalence); Mean number of parasites in the infested birds (relative mean); The numerical range of parasites in the infested birds.*

Talva 1. Innvortis snýkar í lunda (Tal av kannaðum fuglum; Tal av fongdum fuglum; Prosent av fongdum fuglum (Útbreiðsla); Miðal nøgd av snýkum í fongdum fuglum; Minsta- og mesta nøgd av snýkum í fongdum fuglum).

	No. of birds examined	No. of birds infested	Prevalence (%)	Relative mean number of parasites (±1std. error)	Numerical range of parasites in infested birds
Trematodes	173	62	35.8	5.0 (±1.0)	1-33
Cestodes	173	55	31.8	2.0 (±0.3)	1-14
Nematodes	173	37	21.4	1.4 (±0.1)	1- 4
Pentastomes	173	4	2.3	11.8 (±8.6)	1-37

the linings of various organs. (See Table 2, for position and number of parasites).

Host specific aspects

Host fitness

There was no difference in fitness between infested- and not infested birds (t-test, t_{173}= 0.123, p=0.90). The weight of the abdominal fat reserves was divided into two categories: <0.4 g, and ≥0.4 g. Comparing these two groups, there was no difference regarding the mean intensity of infestation with trematodes (M-W, U=3079; p=0.80) or cestodes (t-test, t_{173}= -0.115, p=0.91), but birds with the higher abdominal fat reserves had higher intensities of nematode infestation (M-W, U=2642; p=0.02). The mean weight of the abdominal fat reserves in the four birds, infested with pentastomes was 0.4 g, the same as in birds not infested by parasites (the weight was 0.3 g in the puffin that harboured 37 specimens).

Host sex

There was no sexual bias with respect to prevalence of infestation: trematodes (Fischer's exact test, p=0.08), cestodes (Fischer's exact test, p=0.87), and nematodes (Fischer's exact test, p=0.27). Furthermore, there was no difference in mean intensity of infestation: trematodes (M-W, U=3361; p=0.21), cestodes (M-W, U=3554; p=0.57), and nematodes (M-W, U=3423; p=0.22). Three of the four birds infested with pentastomes were female. Considering the relative intensity of helminth infestation in the birds, males were significantly more heavily infested with trematodes than females (M-W, U=337; p=0.04), and a non-significant difference was shown for cestodes (M-W, U=379; p=0.07), but not for nematodes (t-test, t_{35}= -0.91, p=0.37).

Host age

The mean intensity of infestation did not differ between the two age classes for trematodes (M-W, U=3341, p=0.52), cestodes (M-W, U=3129, p=0.15) or nematodes (t-test, t_{170}=0.12, p=0.91). Regarding the relative intensity of infestation, there was a significant age difference with respect to trematode infestation; the older birds being more heavily infested than the younger ones (M-W, U=293; p=0.02). There was no statistical difference for the relative intensity of infestation with cestodes (M-W, U=466; p=0.69) or nematodes (t-test, t_{35}= -0.04, p=0.97). Only the older category of puffins was infested with pentastomes.

Seasonal effects

To investigate a possible seasonal pattern, the period of collection was classified into two: period 1 (03 to 17 July) and period 2 (18 July to 02 August). There was no difference in mean intensities of infestation between the two periods: trematodes (t-test, t_{173}=0.744 p=0.46), cestodes (M-W, U=3440; p=0.34) and nematodes (M-W, U=3379, p=0.16). Three of the four birds infested with pentastomes were collected in the latter period.

Discussion

Intermediate hosts

The various endoparasites, but for the pentastomes, enter the host in food organisms serving as intermediate hosts. Puffins are predominately piscivorous foragers. Their typical food species in the summer period are sandeel (*Ammodytes* spp.), sprat (*Sprattus sprattus*), capelin (*Mallotus villosus*), whiting (*Merlangius merlangus*), saithe (*Pollachius virens*), red fish (*Sebastes marinus*), haddock (*Melanogrammus aeglefinus*), herring (*Clupea harengus*), five-bearded rockling (*Ciliata mustela*), northern rockling (*Ciliata septentrionalis*) and three-bearded rockling (*Gaidropsarus vulgaris*), but there are variations within sea-

Table 2. *The position and number of parasites, and organ encountered (Oesoph. = Oesophagus; Intestine1 = Anterior part of the small intestine; Intestine2 = Middle part of the small intestine; Intestine3 = Posterior part of the small intestine (all of equal length); Trachea + Pr. br. = Trachea + Primary bronchi).*

Talva 2. Skipanarlig staðseting, mongd, og í hvørjum lívgagni sníkarnir eru skrásettir (Oesophagus + Crop = Vælindi + Kjós; Duodenum = Buggørn; Intestine1 = Fremsti partur av gørn; Intestine2 = Mittasti partur av gørn; Intestine3 = Aftasti partur av gørn (allir eins til longdar); Gall bladder = Gallbløðra; Trachea + Pr. br. = Barki + Høvuðslungnapípur).

	Oesoph. + Crop.	Gizzard	Duodenum.	Intestine 1	Intestine 2	Intestine 3	Rectum	Gall bladder	Kidneys	Liver	Trachea + Pr. br.
Trematodes											
Gymnophallus sp.								314	7		
Cestodes											
Alcataenia sp.	10	3	71	39	1		1				
Hymenolepidae sp. indet.				1							
Nematodes	34	16									
Pentastomes											
Reighardia sp.					1				3	3	37

sons and between years (Harris, 1984). Minor prey species include crustaceans (especially calanids and the euphausiids *Thysanoessa* and *Meganyctiphanes*), polychaetes (nereids) and squid (Harris, 1984; Nettleship and Birkhead 1985).

The winter diet of puffins varies between shelf waters, where there is numerical dominance by invertebrates (mainly the euphausiid *Thysanoessa inermis*) but in terms of biomass fish are dominant (*Ammodytes* spp., *Mallotus villosus*, and others), and oceanic waters in which the puffins fed almost exclusively on the glacier lantern fish (*Benthosema glaciale*) and on squid (*Gonatus fabricii*). In both areas polychaetes (*Nereis pelagica*) are present (Falk *et al.* 1992).

Trematodes

The only gymnophallid previously reported from puffins is *Gymnophallus deliciosus*, (Belopol'skaia, 1952 in Hoberg, 1981). Of the known gymnophallid life-cycle Hoberg (1981) postulates: "...the majority includes two intermediate hosts, both of which are usually intertidal lamellibranchs (Loos-Frank, 1971). Benthic polychaetes have been reported as second intermediate hosts for several species (Loos-Frank, 1969; Margolis, 1971; 1973; Popova and Nikitina, 1978). Most final hosts of these trematodes are species of Charadriiformes, including larids, and Anseriformes (primarily sea ducks) whose foraging occurs in relatively shallow marine littoral areas. A major component of their diets consist of intertidal lamellibranchs, gastropods, and benthic polychaetes." Ching (1995), however, claims that bivalves are the most common intermediate host of gymnophallids. Therefore the prey types that most likely serve as intermediate hosts for puffins are probably lamellibranchs and/or polychaetes associated with the littoral zone, so a seasonal/geographic fluctuation is probable therefore.

Cestodes

Crustaceans (gammarids, copepods, and ostracods) are common intermediate hosts of cestodes of wild birds (Avery, 1969; Burt and Jarecka, 1980; Graeves *et al.*, 1989). Thus, the specimen belonging to the family Hymenolepidae that was recovered from the anterior part of the small intestine together with *Alcataenia* sp. (Dilepididae) - found mostly in the duodenum - probably do not show intermediate host specificity.

Nematodes

Nematode species in general are oviparous. For *Contracaecum* spp. intermediate hosts include fish: flounder (*Platichtys flesus*) (Køie, 1999), open sea herring (*Clupea harengus*) (Podalska *et al.*, 1997), and invertebrates (copepods and the nauplii of *Balanus*) (Køie and Fagerholm, 1995). For *Seuratia* spp. a range of crustaceans serves as potential intermediate hosts (Anderson *et al.*, 1996). For *Streptocara* spp. two intermediate hosts are suspected (Cheng, 1964).

Pentastomes

Reighardia sternae is a non-specific parasite of various seabirds (Böckeler, 1984), which has been previously reported in a

Newfoundland puffin (Threlfall, 1971). Dyck (1975) mentioned pentastomes in Faroese puffins, but they were not further identified.

Reighardia is the only known obligatory one-host pentastome (Thomas *et al.*, 1999). Regarding its life cycle, Parker (1982) state: "Mature nymphs copulate in the abdominal cavity of the host; males then die, and females migrate to interclavicular air sacs. The eggs all mature together, and are liberated in one deposition, after which females die. Transmission from gull to gull is primarily by feeding of young by adult regurgitation. No alternate host is known." An alternative way of transmission is that the female doesn't shed the eggs, but serves as a living container, climbing up the trachea so irritates the host as to cause it to vomit or cough up the eggs; a subsequent bird swallowing the egg bulk may get infested (Riley, 1983; Thomas *et al.*, 1999). The life-cycle is also supplemented by autoreinfestation (Riley, 1983). As puffins do not regurgitate when feeding their chick, that leaves only the latter two possibilities for transmission.

The specimens found in the intestine, kidney and liver are evidently nymphs from the abdominal cavities, while specimens that occur in the trachea plus primary bronchi are adult females.

Host-parasite interactions

Infestation

Compared to earlier analyses of the endoparasitic fauna of various seabird species, the fauna of puffins is sparse both with respect to the number of species and the number of individuals. The range for infested puffins in this study is one to three species per host (1-39 individuals). Hoberg and Ryan (1989) found for great shearwaters (*Puffinus gravis*) two to five species per host (114-4,016 individuals) and Riley and Owen (1975) found in the intestine of fulmars (*Fulmarus glacialis*) three species per host in the intestines only (7-656 individuals). Threlfall (1967) recorded a prevalence of 98.10 % in herring gulls (*Larus argentatus*) in Britain. Fulmars, great shearwaters, and gulls are omnivorous, foraging only in the surface waters (gulls also over land). Puffins on the other hand are more selective regarding their food and are agile divers. Diving depths in the order of 40 m are common among puffins according to Burger and Simpson, (1986). This difference in foraging behaviour is inevitably an important variable determinating the prevalence and intensity of endoparasites in seabirds.

It seems that the puffins of the Faroe Islands are more heavily infested than auks in Newfoundland (Threlfall, 1971), and in particular the Newfoundland puffin (prevalence 8 %), but the study by Threlfall spans over three years of fieldwork, while the fieldwork of present study was accomplished during one month, and within the breeding season, the period in which the parasitic fauna of birds is richest (Hoberg, 1981; Cox, 1993).

The time of year and duration of collection in a study of nematodes in Icelandic puffins (Ólafsdóttir *et al.*, 1996) are the same as in the present investigation, rendering them comparable. The puffins in these two studies are approximately the same with respect to both prevalence and intensity of infestation.

Host fitness

There is no indication that the fitness of the birds is negatively associated with parasite infestation. As the intensity is relatively low, it is possible that the parasite burden is below the threshold value necessary to have an influence (Hoberg and Ryan, 1989).

There have even been speculations that trematodes in final hosts may not be parasitic at all. Lafferty (1997) claimed that adult trematodes have no negative effect on the final host (piscivorous birds). He even argued that final hosts may take advantage of trematodes, as the metacercariae change the behavioural pattern of the intermediate host so rendering it more accessible to the birds. This type of symbiosis might be categorized as commensalism, rather than parasitism.

There is a higher mean intensity of nematode infestation in puffins with the highest fitness. As many nematode infested birds had damaged tissue in the anterior part of the oesophagus, evidently caused by the worms, it seems unlikely that the higher fitness is a direct effect of the parasites. The same pattern has been reported for herring infested with *Contracaecum osculatum* larvae (Podolska *et al.*, 1997). This trend is probably the result of a higher feeding rate. It seems that the nematodes, at low intensities of infestation, are harmless to their hosts.

The low fitness of a great black-backed gull (*Larus marinus*), with a high intensity of the pentastome *Reighardia sternae* (Böckeler and Vauk-Hentzelt, 1979), was not confirmed in the puffin with a high intensity in the present study, and the mean fitness was not reduced in pentastome- infested birds, in agreement with Böckeler (1984). The hypothesis that cestode infestation leads to natural immunity to pentastome infestation (Riley, 1976; Böckeler and Vauk-Hentzelt, 1979) is supported by the present study, as none of the cestode-infested puffins hosted pentastomes.

Host gender

The sexual bias in the relative intensity of infestation with trematodes (significant) and cestodes (non-significant), with males more heavily infested than females is a puzzle. There is no evidence that the higher relative intensity of infestation with these helminths is caused by a differentiation in behaviour in relation to reproduction, as the incubation and the feeding of the chick is split equally between the parents (Harris, 1984; Nettleship and Birkhead, 1985), and there does not appear to be evidence of a foraging differentiation in the literature. When birds of both sexes move and feed together they are probably exposed equally to larval parasites. Consequently, if other things are equal, differences in parasite burdens should be rare. However, there are studies showing that males and females do differ in susceptibility to parasites, males being the more susceptible (Alexander and Stimson, 1989; Zuk, 1990; Poulin, 1996). One possible explanation is that the efficiency of the immune system is determined by migration behaviour in the pre-reproductive stages of the birds' lives. In migrating birds, females typically have longer natal dispersal than males. (Møller and Erritzøe, 2001). The hypothesis is that the development of the immune system is positively correlated with the diversity of the parasitic fauna to which the host is exposed, which is again positively correlated to the dispersal distance of the host (Møller and Erritzøe, 2001). Further investigations are necessary to explore this hypothesis, especially as knowledge is sparse about the migration behaviour of pre-mature puffins.

Hoberg (1987); Bakke (1972); and Böckeler and Vauk-Hentzelt (1979) reported studies on a total of 265 birds; a total of 8 females and 7 males were infested with pentastomes. Whilst the present study appears to show a tendency for females being the more heavily infested with pentastomes, this is not supported by the literature.

Host age

The reason for adult birds tending to have a higher relative intensity of infestation with trematodes may reflect immunological suppression at a cost to reproductive effort, a phenomenon that may impose not only immediate effects but also possibly lifelong negative consequences for viability (Nordling *et al.*, 1998). An alternative or complementary cause might lie in the differences in the functional response of the immune system, in which information on immune responses is stored in memory cells in adult birds, rather than in the function of the Bursa Fabricii in juvenile birds (Møller and Erritzøe, 2001), the functional response of the adult being less efficient perhaps.

Regarding pentastomes, other investigators (Bakke, 1972; Böckeler and Vauk-Hentzelt, 1979; Böckeler, 1984) have shown a higher prevalence of infestation in juvenile than in adult birds; the converse was found in the present study, in which all pentastome-infested birds were adults.

Seasonal effects

The helminth fauna of migrating birds is generally seasonal, a natural consequence of seasonal and regional fluctuations in food supply (Bykhovskaya-Pavlovskaya, 1953; 1962; Bezubik, 1956; Jarecka, 1958; Polozhentsev and Negrobov, 1958; Kassimov *et al.*, 1962; Rysavy, 1962; 1964 *in* Wallace and Pence, 1986). A lack of replacement might also be an influence, when prey species change in connection with migration, and longevity of the parasites is limited (Avery, 1969). The helminth fauna of auks is also seasonal and related to the breeding areas (Hoberg, 1981), as there is a seasonal occurrence of pentastomes (Böckeler, 1984). Parasites usually adapt their reproductive period to the annual cycle of the host, with parasite population densities peaking late during the hosts' reproductive season (Cox, 1993). Such peaks may be in part at least to a consequence of the immunological cost of reproduction during the breeding season (Nordling, 1998). In addition, the risk of infestation is usually density-dependent (Begon *et al.*, 1986), and the puffin density is clearly highest in the breeding period. The great dispersion of the birds outside the breeding season spreads the risk of infestation. The density of the Atlantic puffin outside the breeding season is one for every 1 to 2 km^2 of ocean within the area of distribution (Harris, 1984). The reason for the lack of a clear fluctuation in the parasite burden in the present study probably reflects the limited time of collection, which was solely within the breeding season. Collection of Faroese puffins outside the summer period would present practical problems, as the puffins wintering in the Faroese area originate from Norway (Jensen, 1986), and the geographic areas occupied by Faroese puffin populations outside the breeding season are not yet known.

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