Non-haematophagous ectoparasite populations of Procellariiform birds in Shetland, Scotland.

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Ectoparasites are known to occur widely on seabirds (Rothschild and Clay, 1952) but very few investigations have extended beyond a simple collection of samples for identification. A notable exception is the study of feather lice (Insecta: Mallophaga) found on auks (Alcidae) in Newfoundland (Eveleigh and Threlfall 1976) — a study which depended on sacrificing a large number of wild birds. The killing of birds to obtain their parasites would not now be considered acceptable in the United Kingdom and this may, indeed, be one reason why studies on the biology of bird ectoparasites have been so few.

A method described recently permits the rapid removal of ectoparasites from batches of up to 20 live birds without harming them (Fowler and Cohen 1983). This method was adopted to determine the incidence of ectoparasites infesting Fulmars *Fulmarus glacialis*, Manx Shearwaters *Puffinus puffinus*, Storm Petrels *Hydrobates pelagicus*, and Leach's Petrels *Oceanodroma leucorhoa* captured in Shetland during July 1981. The results provide a basis for investigations into host-parasite relationships and enable a comparison to be made with the studies on auks by Eveleigh and Threlfall (1976).

METHODS

Fulmars were captured by hand or by fowling hook around the coastline of Yell; Manx Shearwaters were taken from burrows in the small colony reported on Yell by Fowler (1980); Storm Petrels were lured to mist nets by means of tape recordings as described by Fowler et al. (1982); Leach's Petrels were caught in mist nets near the colony discovered on Gruney (Fowler and Butler 1982). Delousing was conducted for 20 minutes in chloroform chambers by the method described by Fowler and Cohen (1983). The delousing time was restricted to 20 minutes as it has been shown (Fowler, *et al.* in press) that in this period statistically identical samples of ectoparasites are removed from equivalent batches of birds, and extension of the time removes very few more. There are recognised limitations to the method: it is known that certain feather louse species are commonly associated with the feather tracts of the head and neck and, as these tracts are excluded from the delousing chamber, those species will be under-represented in the sample. For this reason the interpretation of frequency distributions with high zero-class frequencies has to be undertaken with caution.

It has been shown (Fowler and Cohen 1983) that the delousing of Storm Petrels by means of chloroform vapour does not affect their recapture rates when compared with non-deloused birds.

The ectoparasites thus removed were carefully collected and preserved in 80% ethanol and classified into adult males, adult females and nymphs (unsexed). Representative samples of feather lice were cleared in potassium hydroxide (10%) and terpineol, mounted on glass slides in Canada balsam and identified at the British Museum (Natural History). Feather mites, whose taxonomy is difficult, were not identified beyond genus and, in this investigation, are considered collectively as a single taxonomic unit.

RESULTS

A total of 240 Storm Petrels, 35 adult and 9 unfledged Fulmars, 7 Leach's Petrels and 4 Manx Shearwaters were deloused, resulting in the collection of 1564 feather lice of 8 species (Table 1). The feather lice species were readily sorted on the basis of head shape

TABLE 1. SPECIES AND NUMBERS OF FEATHER LICE (MALLOPHAGA) COLLECTED FROM FULMARS, MANX SHEARWATERS, STORM PETRELS AND LEACH'S PETRELS IN SHETLAND DURING JULY 1981. MALLOPHAGA WERE IDENTIFIED BY C. LYAL, BRITISH MUSEUM, (NAT. HIST.).

Host	*Number of birds deloused*	*Species of feather louse*	*Number collected*
Storm Petrel	240	Amblycera: *Austromenopon* sp.	4
		Ischnocera: *Halipeurus pelagicus* (Denny, 1842)	1353
		Ischnocera: *Philoceanus robertsi* (Clay, 1940)	35
		Ischnocera: *Saemundssonia thalassidromae* (Denny, 1842)	3
Fulmar	34	Ischnocera: *Perineus nigrolimbatus* (Giebel, 1874)	91
		Ischnocera: *Saemundssonia occidentalis* (Kellogg, 1896)	1
Leach's Petrel	7	Ischnocera: *Halipeurus pelagicus* (Denny, 1842)	11
Manx Shearwater	4	Ischnocera: *Halipeurus diversus* (Kellogg, 1896)	38
		Ischnocera: *Trabeculus aviator* (Evans, 1912)	28

(Fig 1). In addition, 381 feather mites were collected from Storm Petrels, and a single one from a Leach's Petrel. All belonged to the order Astigmata, Superfamily Analgoidea (genus *Zachratkinia*). No haematophagous ectoparasites, e.g. fleas (Insecta: Siphonaptera) or ticks (Acarina: Ixodoidea) were present in the collections.

Storm Petrel

Two hundred and thirty four (97.5%) of the 240 Storm Petrels deloused were infested with feather lice (mean 6.0 per infested bird, range 1-22). Four species of lice were represented of which *Halipeurus pelagicus* was by far the most numerous and was present

TABLE 2. INFESTATION LEVELS OF FOUR SPECIES OF FEATHER LICE COLLECTED FROM STORM PETRELS IN SHETLAND, JULY 1981.

Feather louse	*% of total collected*	*% birds infested*	*Mean per infested bird (range in brackets)*
Austromenopon sp.	0.3	1.25	1 (1)
H. pelagicus	97.0	97.5	5.8 (1-22)
Ph. robertsi	2.5	11.7	1.25 (1-2)
S. thalassidromae	0.2	1.7	1 (1-2)

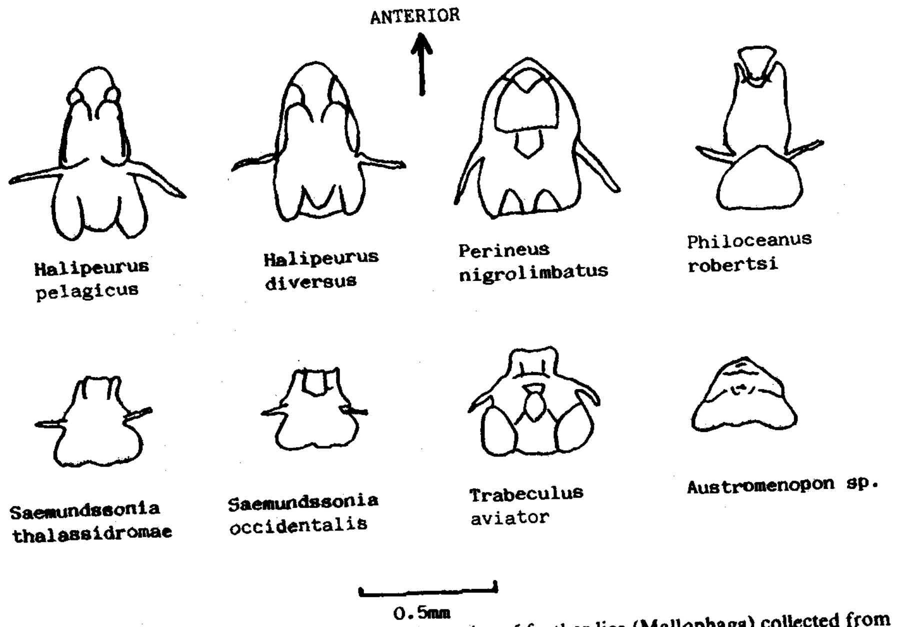

Figure 1. Head shapes (dorsal aspect) of eight species of feather lice (Mallophaga) collected from Procellariiformes in Shetland. This diagram is not a key, but may assist in the preliminary sorting of collections.

on all infested birds. A breakdown of the infestation is given in Table 2. *Austromenopon sp.* could not be identified beyond genus. 203 birds (84.6%) carried 1 species of louse, 30 (12.5%) carried 2 species and only 1(0.4%) carried 3 species, but there was no tendancy for the most heavily infested individuals to carry more than one species ($\chi^2 = 3.49$, $P<0.01$). It is not possible to analyse this relationship further because of the very high zero-class frequency of the rarer species, and the uncertainty of the distribution of *Austromenopon sp.* and *Saemundssonia thalassidromae* on the host's head. *Halipeurus pelagicus*, on the other hand, being one of the "elongate" lice, is known to be associated with the host's wings or back (Clay 1957). This species was often seen to lie along the primary or secondary shafts, especially after a bird had been at rest in a holding box; on handling, the lice would crawl up to hide under the coverts. Because of the greater likelihood of *Halipeurus pelagicus* being shaken free during the deparasitising treatment, and the very low zero-class frequency obtained, greater confidence may be placed in the analysis of the frequency distribution of this species.

Of the 1353 *Halipeurus* collected, 19% were males, 19% females and 62% were nymphs. The frequency distribution (Fig. 2a) is positively-skewed, with the mean $\bar{x} = 5.75$ and the variance $s^2 = 13.48$. The variance to mean ratio is significantly greater than unity ($\chi^2 = 39.9$, $P<0.05$) indicating an overdispersed ('clumped') distribution. Of the various statistical descriptions of overdispersion, that of the negative binomial has frequently proved a useful model on which to base host-parasite relationships (e.g. Anderson and May 1978). Calculation of the binomial exponent $k = 4.27$, and hence the expected

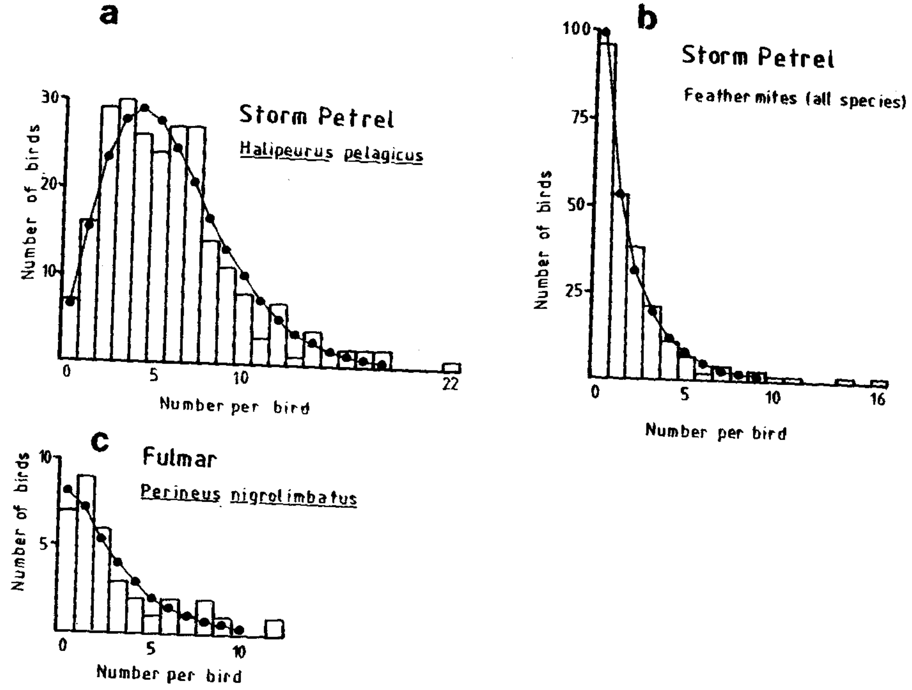

Figure 2. Frequency distributions of ectoparasites on Procellariiformes: (a) *Halipeurus pelagicus* on Storm Petrels; (b) aggregated feather mites on Storm Petrels; (c) *Perineus nigrolimbatus* on Fulmars. Histograms are observed frequencies and joined circles are calculated negative binomial frequencies.

frequency distribution for the negative binomial, enables the model to be tested. The observed and expected frequencies (Fig. 2a) show a close fit, and are not statistically significantly different ($\chi^2 = 9.58$, $P<0.01$).

The 35 *Philoceanus robertsi* were represented by 30 adults and only 5 nymphs. 7 birds carried 2 individuals, the remaining 21 were distributed singly.

144 (60%) of the Storm Petrels were infested with feather mites (mean 2.6 per infested bird, range 1-14). The frequency distribution (Fig. 2b) is of the 'hollow curve' type described by Williams (1964) in which most of the hosts have few parasites and most of the parasites are on few hosts. The variance to mean ratio (4.75: 1.60) is significantly greater than unity ($\chi^2 = 35.8$, $P<0.05$), indicating overdispersion, and the calculated value of the binomial exponent ($k = 0.807$) gives expected frequencies for a negative binomial distribution (Fig. 2b) which do not differ significantly from those observed ($\chi^2 = 3.86$, $P<0.01$).

It would be of interest to know if the individual birds carrying the heaviest *lice* burdens were the same as those with the greatest number of *mites*. Table 3 shows a cross-classification matrix of the lice and mite distributions; however, the relationship between their distributions appear to be random ($\chi^2 = 14.5$, $P<0.01$).

TABLE 3. CROSS-CLASSIFICATION MATRIX OF THE FREQUENCIES OF FEATHER LICE AND FEATHER MITES ON STORM PETRELS. E.G. 4 BIRDS HAD 2 MITES AND 5 LICE.

Number of lice	Number of mites: 0	1	2	3	4	5	6	7+
0	3	2	1	0	0	0	0	0
1	5	4	2	0	0	1	0	1
2	9	6	4	1	2	1	1	0
3	9	9	3	4	3	0	0	1
4	12	5	2	3	0	2	0	2
5	9	3	4	4	1	1	0	0
6	11	4	8	1	1	0	0	3
7	9	8	4	3	0	0	0	0
8	6	6	4	2	1	0	0	1
9+	15	9	4	1	3	2	1	4

Fulmar

Twenty-eight (80%) of the 35 adult Fulmars examined were infested with feather lice (mean 3.29 per infested bird, range 1-22). No ectoparasites were collected from the unfledged birds. All lice, except a single individual, belonged to the species *Perineus nigrolimbatus*, of which 43% were males, 34% were females and 23% were nymphs; the sex ratio of the adults does not significantly differ from unity ($\chi^2 = 0.70$, $P<0.01$). This species is an 'elongate' louse, associated with the wings or back, and is therefore likely to be sampled representatively by the method. The frequency distribution (Fig. 2c) is positively-skewed, with a variance to mean ratio (8.67 : 2.74) that is significantly greater than unity ($\chi^2 = 34.8$, $P<0.05$), indicating over-dispersion. The calculated value of the binomial exponent ($k = 1.27$) gives expected frequencies for a negative binomial distribution which are not statistically significantly different from the observed frequencies ($\chi^2 = 0.906$, $P<0.01$; Fig. 2a).

Manx Shearwater

The four adult shearwaters examined were infested with 9, 13, 17 and 27 feather lice (mean 16.5). Two species of lice, *Halipeurus diversus* and *Trabeculus aviator*, were obtained, whose frequency distribution were, respectively, 7 and 2; 11 and 6; 10 and 3; 10 and 17. The percentages of males, females and nymphs of each species were, respectively, 18%, 37%, 45% and 11%, 64%, 25%. The sex ratio in the latter species is significantly different from unity ($\chi^2 = 9.2$, $P<0.01$).

Leach's Petrel

Five (71%) of the 7 Leach's Petrels examined were infested with feather lice (mean 2.2 per infested bird, range 1-5). All were of a single species, *Halipeurus pelagicus*, of which 9% were males, 18% were females and 73% were nymphs. The sex ratio does not differ significantly from unity. It is noteworthy that the species was the same as the most numerous one found on Storm Petrels.

DISCUSSION

Eight species of Mallophaga belonging to six genera (*Halipeurus*, *Perineus*, *Philoceanus*, *Saemundssonia, Trabeculus* and *Austromenopon*) were collected from the Procellariiformes examined. There are few published data with which to compare these results, but *Halipeurus, Perineus, Philoceanus* and *Trabeculus* have only been reported to occur on Procellariiformes. *Saemundssonia* and *Austromenopon* have additionally been found on Alcidae (Waterson 1914, Eveleigh and Threlfall 1976). Feather mites were found only on Storm Petrels and a Leach's Petrel; the absence of mites on Fulmars is in accordance with the observations of Fisher (1952).

All of the ectoparasite types which were collected are generally non-haematophagous, feeding principally on sloughed off skin and feather debris, and they exist in a fairly innocuous relationship with their hosts. Their populations are normally at low levels on healthy wild hosts, and high levels are seldom a cause of poor health but rather a symptom of it (Marshall 1981). Haematophagous ectoparasites, on the other hand, may cause great irritations which can be aggravated by scratching and become vulnerable to secondary infections; occasionally they may cause catastrophic damage to host populations as vectors of disease. Blood-sucking ticks are not removed by the deparasitising method adopted in this study as their mouthparts may be embedded in the host's skin, but the absence of fleas in the samples undoubtedly reflects a low incidence on the seabirds as they are known to be readily removed from birds by the method (Fowler et al. 1983).

The close relationship of the frequency distributions examined (*Halipeurus pelagicus* and aggregated mites on Storm Petrels, and *P. nigrolimbatus* on Fulmars) to the negative binomial distribution is of great interest. Crofton (1971) has suggested that the negative binomial is a 'fundamental model' of parasitism in so far as it describes the distribution of parasites among hosts, and has postulated a series of situations in which such a distribution could arise in nature. According to Anderson and May (1978) the value of the binomial exponent k gives some indication of the destabilising effects of the parasite on the host population, and is related to the relative reproductive rates of the parasite and host.

Host-parasite specificity has often been implicated in the suggestion of taxonomic relationships between species of higher animals (e.g. Rothschild and Clay, 1952). Different species of feather lice were found on each bird species examined except for *Halipeurus pelagicus* which was found both on Storm Petrels and Leach's Petrels. Even though these birds belong to different genera, it is well-known that their breeding habitats may overlap (Sharrock 1976) where casual contracts could result in the transfer of ectoparasites. This is not unprecedented: Post and Enders (1970) describe the occurrence of the same mallophagan species on two species of sparrow which share the same habitat.

Eveleigh and Threlfall (1976) note that burrow or crevice nesting auks had lower infestation levels than those which nested on ledges; they speculate that opportunities for ectoparasite transfer would be greater on ledges where there may be social contact between birds. This situation was not reflected among the Procellariiformes: the ledge-nesting Fulmar had a lower infestation level and lower ectoparasite density then both the burrowing Manx Shearwater and Storm Petrel. However, Fulmars do not exhibit as much social contact on ledges as do auks.

Nymphs were the dominant age class of Mallophaga found on Storm Petrels and Leach's Petrels; this contrasts with auk mallophagan populations in which adults were invaribly the dominant age class (Eveleigh and Threlfall 1976). It is difficult to interpret these results until the various life histories are elucidated, but Marshall (1981) points out that a Mallophagan population with a high proportion of adults to nymphs indicates an old, declining population. The observed difference in population structures between the

Mallophaga on auks and petrels may reflect no more, therefore, than asynchronous sampling. Only in the case of *Trabeculus aviator* did the sex ratio differ significantly from unity; the most likely explanation for this is a differential mortality rate between the sexes (Marshall 1981).

No Mallophaga were recovered from the downy Fulmar chicks examined. Eveleigh and Threlfall (1976) note that auk chicks had received ectoparasites from their parents; it is possible that young Fulmars do not attract Mallophaga until the down pumage is replaced by feathers.

The random association of feather lice and feather mites on Storm Petrels suggests that the two occupy separate "niches" on the host and are not directly in competition for resources, in which case a negative association might be expected to occur.

The collection of *Philoceanus robertsi* from Storm Petrels is of exceptional interest as it has been previously reported only from Wilson's Storm Petrels *Oceanites oceanicus* (C. Lyal, *pers. comm.*). The breeding ranges of these two hosts do not overlap (indeed, the Antarctic breeding range of Wilson's Storm Petrel is about as far away from the Storm Petrel's as it is possible to get), but there is considerable overlap in non-breeding ranges (Nelson 1980) when birds of each species could at times be together at sea. It is not known how far south Storm Petrels wander in the northern winter, but Leach's Petrels have been found ashore as far as 44°S (Imber and Lovegrove 1982). When it is also taken into account that Storm Petrels can be attracted to the calls of Wilson's Storm Petrels (Zonfrillo 1982), it is not difficult to speculate a chance encounter between the two species. The very high proportion of adults to nymphs in the sample suggests that the species is not actively reproducing in July, and it is tempting to speculate that its life cycle is regulated to be out of phase with the rather similar *Halipeurus pelagicus* which is clearly actively reproducing at that time. It would be fascinating indeed to sample Storm Petrels during our winter months to seek an understanding of the dynamics of the ectoparasite community.

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SUMMARY

Feather lice and feather mites were collected from Procellariiform birds in Shetland during July, 1981. Lice were found on 80% of the 44 Fulmars examined, 100% of the 4 Manx Shearwaters, 97.5% of the 240 Storm Petrels and 43% of the 7 Leach's Petrels. *Halipeurus pelagicus* was collected from both Storm Petrels and Leach's Petrels, and *Philoceanus robertsi*, previously reported only from Wilson's Storm Petrels, was found on Storm Petrels. Frequency distributions of the numerous ectoparasite species conformed well with a negative binomial distribution. The population structures and ecology of the ectoparasites are discussed.

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