

## SUMMARY

Kittiwake chick production was measured at 8 study plots in 4 Shetland colonies. While the 1.11 young fledged per incubating pair at Troswick Ness was comparable to that reported from other British colonies, production at the other 3 colonies (0.35 at Noss, 0.64 at Sumburgh Head and 0.70 at Eshaness) was considerably lower. Single visits prior to fledging were made to four other colonies and counts of chicks emphasised the variability in production between colonies. A mean brood size of 1.40 was recorded on these single visits, compared to 1.10 at the same colonies in 1985. In the Noss study plot, predation of Kittiwake chicks by Great Skuas was thought to be largely responsible for the low production. The consequences for a monitoring strategy of the variation in chick production within and between colonies are discussed.

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## A comparative study of the Ischnoceran Mallophaga of Wilson's Petrel *Oceanites oceanicus* and British Storm Petrel *Hydrobates pelagicus*

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Our understanding of host/ectoparasite relationships in birds is limited by the paucity of published data describing infestation levels and the structure and dynamics of mallophagan populations. Moreover, because data for particular hosts have often been collected over prolonged periods only 'average' seasonal patterns are revealed (Marshall 1981). Average values of infestation rates may be misleading because ectoparasites are rarely distributed randomly among their hosts, but rather exhibit a degree of aggregation, or contagiousness, in which most hosts have few parasites and in which large numbers of parasites may be found on a few hosts. It is therefore necessary to obtain parasites from a sufficiently large sample of hosts to describe a complete frequency distribution.

Attempts to describe mammalian ectoparasite frequency distributions mathematically have often resulted in good agreements with the negative binomial (e.g. Randolph 1975). Published descriptions of ectoparasite frequency distributions are more scarce for birds than for mammals, but negative binomial distributions were obtained for feather lice (Mallophaga) and feather mites (Acari) on Storm Petrels *Hydrobates pelagicus* and Mallophaga on Fulmars *Fulmarus glacialis* (Fowler & Miller 1984); Mallophaga and Acari on Reed Buntings *Emberiza schoeniclus* (Fowler & Williams 1985); and Mallophaga on Puffins *Fratercula arctica* (Fowler & Williams 1985, after Eveleigh & Threlfall 1976).

A static picture of a population structure may be obtained by sampling Mallophaga from birds over a period which is short in relation to their life cycles; population dynamics may be investigated by analysing a sequential series of such structures. In this way Fowler & Williams (1985) examined the population dynamics of Mallophaga on Reed Buntings, whilst Fowler *et al.* (1984) compared the population structures of a mallophagan, *Halipeurus pelagicus* Denny 1842, obtained from two population classes of Storm Petrel.

Ectoparasite populations infesting Storm Petrels in Shetland were described by Fowler and Miller (1984) and Fowler & Palma (1986). They found that, in July, two rather similar "elongate" Ischnoceran mallophagan species, *Halipeurus pelagicus* and *Philoceanus robertsi* Clay 1940, inhabited the wings of the host. The former had a relatively high infestation rate ( $\bar{x}=5.7$ ) and a negative binomial distribution. The mean infestation of *Philoceanus robertsi* was much lower (about 1 louse on one bird in seven) and the frequency distribution was probably Poisson. *Halipeurus pelagicus* was represented by a high proportion (62%) of nymphs, indicating that the population was in a phase of high reproductive rate. Nymphs of *P. robertsi*, on the other hand, accounted for only 17% of its population, suggesting that, at that time of year, the population had a lower reproductive rate, since a low proportion of nymphs is indicative of a declining population (Marshall 1981).

It is possible that the two mallophagan species exist on the host in a state of competition; indeed, wherever two elongate lice are known to co-exist on a petrel species, one of the species is invariably "dominant" in terms of numbers (R.L. Palma, *pers. comm.*). The fact

that two species co-exist at all suggests a degree of niche differentiation, and Fowler & Miller (1984) speculate on the basis of samples collected in July that the apparently asynchronous life cycles of the two species infesting the Storm Petrel could contribute to such differentiation; they suggest that the dynamics of the community could be further investigated by sampling at another time of year. Samples obtained in August and September are described in this paper.

Unlike the Storm Petrel, Wilson's Petrel *Oceanites oceanicus* is host to only one species of elongate mallophaga, namely *Philoceanus robertsi*. The fact that this is the same species as the "subordinate" one on the Storm Petrel offers the opportunity to investigate the frequency distribution and population structure in the absence of the "dominant" *Halipeurus pelagicus*. Furthermore, because samples of the louse can be obtained from Wilson's Petrels during the southern summer, the population structure may be described from this host at a time of year that is impossible for Storm Petrels because they are at sea during the northern winter.

## METHODS

Samples of Storm Petrels were captured in mist nets by attraction to tape-lures (Fowler *et al.* 1982) in Shetland, Scotland, on three dates in August and September 1986 for comparison with samples previously obtained in July and described by Fowler *et al.* (1984). Wilson's Petrels were captured in mist nets at Bernsten Point, Signy Island, South Orkney (60° 42' S, 45° 35' W) on six dates between 10 January and 6 March 1985 and on three dates between 13 February and 19 March 1986. Birds were deloused in glass vessels saturated with chloroform vapour, exactly as described by Fowler & Cohen (1983). The ectoparasites thus removed were identified and preserved in 70% ethanol.

Specimens of *Philoceanus robertsi* and *Halipeurus pelagicus* were readily sorted, using a  $\times 10$  binocular microscope, into 5 distinct size categories. Head widths of a sample of each size class were measured using a calibrated microscope eye-piece graticule and Dyar's law (Teissier 1936) was applied to confirm that each size class corresponded, in increasing size, to first, second and third instar nymphs, adult male and adult female population classes.

## RESULTS

### Wilson's Petrel

Sixty-one Wilson's Petrels were deloused in 1985, yielding 404 Mallophaga. All but 10 of these were *Philoceanus robertsi*, of which the mean ( $\bar{x}$ ) was 6.5 per bird, the variance ( $s^2$ ) 29.5 and the median 4.8. The corresponding values for the smaller sample of 41 birds obtained in 1986 are 6.9, 43.6 and 4.6. The differences between the three pairs of statistics are not statistically significantly different ( $z=0.30$ ;  $F_{60, 40}=1.48$ ; Mann-Whitney  $U$ -test; respectively). The mean infestation over the six sampling dates in 1985 showed no trend ( $r_s=0.314$ ) and all samples are therefore pooled for the purpose of constructing a frequency distribution of this species.

The remaining Mallophaga comprised *Austromenopon* sp. and *Saemundssonina* sp. but it is not at present possible to identify them specifically because insufficient specimens of each sex were obtained.

The frequency distribution of *Philoceanus robertsi* on Wilson's Petrels is shown in Figure 1. The distribution is clearly an aggregated (contagious) type. An exponent,  $k$ , estimated from  $k=\bar{x}^2 / (s^2-\bar{x})$ , is 1.56, and may be used to calculate the expected frequencies for a negative binomial distribution based on the sample mean and variance. The expected frequencies are shown in Figure 1, and are in close agreement with the observed frequencies

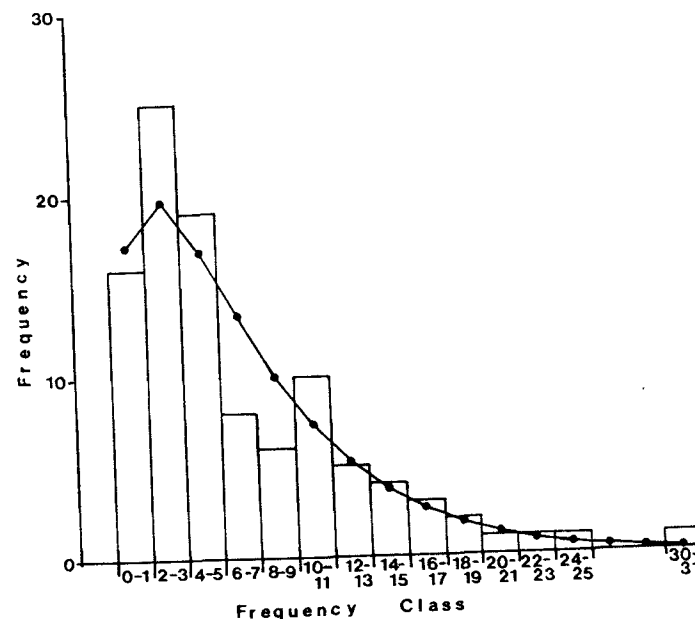


Figure 1. Frequency distribution of *Philoceanus robertsi* on Wilson's Petrels. Joined closed circles are the expected frequencies of a negative binomial distribution estimated from the sample statistics.

( $\chi^2=6.98$ ,  $p>0.50$ ). The value of  $k$  is significantly lower than that of 4.27 recorded by Fowler & Miller (1984) for *Halipeurus pelagicus* on the Storm Petrel ( $z=3.24$ ,  $p<0.01$ ).

Mean head widths of each size class of *Philoceanus robertsi* ( $\pm 95\%$  Confidence Interval,  $n=10$  in each case) were  $0.194 \pm 0.00759$ mm,  $0.232 \pm 0.00826$ mm,  $0.2712 \pm 0.008$ mm,  $0.298 \pm 0.0051$ mm and  $0.327 \pm 0.007$ mm respectively. The incremental ratio is about 1.2 and a "Dyar plot" of log head width against instar number is linear and confirms that all nymphal instars had indeed been found.

To examine the population structure of *P. robertsi* on the hosts, sufficient numbers of lice were obtained in 1985 to divide the sampling units into three sub-samples corresponding to January, February and March. The number of lice collected, and the proportions of the different population classes in each sub-sample, is shown in Figure 2A. In all three sub-samples, the number of adult female *P. robertsi* exceeds the number of males. Although the sex ratio does not differ significantly from unity in any individual sub-sample, it does when the adults of all three sub-samples are combined ( $\chi^2=5.95$ ,  $p<0.05$ ).

The population structures of the three sub-samples are highly significantly different ( $\chi^2=22.6$ ,  $p<0.01$ ), and reflect a progressive increase in the proportion of adults through the sampling period. In March, first-instar nymphs account for only 7.4% of the sample.

A smaller sample of lice was collected over a shorter time-span in 1986. This is not pooled with the 1985 sample to describe the population structure in case the life cycles of the two

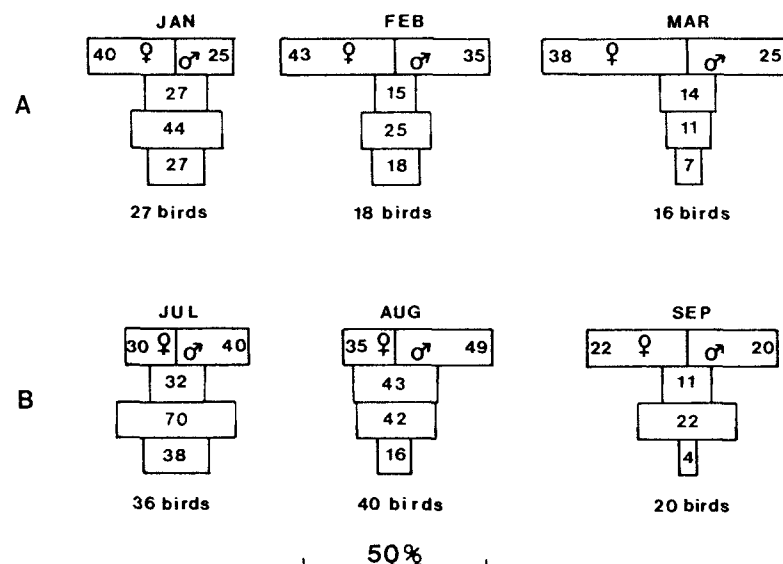


Figure 2. Population structures of elongate Mallophaga species on Wilson's Petrels and Storm Petrels. A: *Philoceanus robertsi* on Wilson's Petrels, January – March; B: *Halipeurus pelagicus* on Storm Petrels, July – September. Each "tier" in the structures represents, in ascending order, 1st, 2nd, 3rd instar nymphs, adults. Numbers within the structures are the numbers of lice obtained.

years are not quite in phase. However, the structure is statistically indistinguishable from the February 1985 sub-sample ( $\chi^2=2.72$ ) and confirms the trend of a higher proportion of adults later in the season.

#### Storm Petrel

Sixty Storm Petrels were deloused and the sample of *Halipeurus pelagicus* obtained was divided into two sub-samples corresponding to August and September. The structures of these are shown in Figure 2B and are compared with the July samples described by Fowler *et al.* (1984). The difference between the three structures is statistically highly significant ( $\chi^2=27.9$ ) and is due to a progressive increase in the proportion of adults in the population over the sampling period; in September first instar nymphs account for only 4% of the sample.

The results (including data presented by Fowler & Miller 1984) are summarised in Table 1.

#### DISCUSSION

The most conspicuous difference between the ectoparasite complement of the two host species is that the Storm Petrel has two species of elongate Mallophaga whilst Wilson's Petrel has only one. The interesting feature is that the louse species *Philoceanus robertsi* found on the Wilson's Petrel is present also on the Storm Petrel, but is subordinate to its second louse species, *Halipeurus pelagicus* (in this discussion the terms "dominant" and "subordinate" are used to indicate relative numbers only).

TABLE 1. SUMMARY OF POPULATION CHARACTERISTICS OF THE ELONGATE MALLOPHAGA OF STORM PETRELS. DATA FOR *HALIPEURUS PELAGICUS* IN JULY DESCRIBED BY FOWLER & MILLER (1984) ARE INCLUDED

		Mallophaga species	
		<i>Halipeurus pelagicus</i>	<i>Philoceanus robertsi</i>
Storm Petrel	Source	Shetland, July-September	Shetland, July-September
	Mean lice per bird	5.75	0.15
	Variance, $s^2$	13.48	0.18
	Frequency distribution	Negative binomial, $k=4.27$	Probably Poisson
Wilson's Petrel	Population structure	High reproductive rate with 66% nymphs in July, declining to 45.7% nymphs in September	"Aged" with 14.3% nymphs in July
	Source	(NOT PRESENT)	Signy Isle, Antarctica January-March
	Mean lice per bird	(NOT PRESENT)	6.6
	Variance, $s^2$	(NOT PRESENT)	34.8
	Frequency distribution	(NOT PRESENT)	Negative binomial, $k=1.56$
	Population structure	(NOT PRESENT)	Actively reproducing with 60% nymphs in January, declining to 34.4% in March

The close agreement of the frequency distribution of *P. robertsi* on the Wilson's Petrel with that of a negative binomial is not unexpected. Reasons why ectoparasites should be contagiously distributed among their hosts have been discussed and reviewed by Crofton (1971), Randolph (1975) and Fowler & Williams (1985), and include such factors as seasonal variation in infestation rates; non-random spatial distribution of hosts in the habitat; resistance to re-infestation by previously infested hosts; and non-random differences in behaviour or physiology (e.g. moult) related to different age classes within the host population. Why the frequency distributions should conform mathematically so well with a negative binomial model, rather than some other model of contagiousness, is not clear, but Anderson & May (1978) postulate that the value of the binomial exponent,  $k$ , is a measure of the destabilising effect of the parasite on the host population, and is related to the relative reproductive rates of the parasite and host.

The frequency distribution is similar to that of *Halipeurus pelagicus* on the Storm Petrel, but the latter has a more symmetrical distribution with a mode of 3-4 lice which is reflected in the higher value of  $k$  (as  $k$  increases, so too does the degree of symmetry of the distribution until eventually the distribution conforms to Poisson). It is not possible to further discuss the biological significance of these sample statistics until more is known about the life histories of the lice, possibly from *in vitro* studies.

Although the mean infestation of Wilson's Petrels by *P. robertsi* did not change during the sampling period, the population structure of the louse altered markedly. The structures illustrated in Figure 1A show a progressive decrease in the proportion of nymphs in the population. The proportion of nymphs peaks when a population is in a vigorously reproducing phase (Marshall 1981). When reproductive rates decline, so does the proportion of nymphs as their more ephemeral stages moult into the longer-lived adults. Crude extrapolation of the observed trend suggests that by June the louse population structure would consist of about 80% adults – similar to the population structure of this species which is found on Storm Petrels in July (Fowler & Miller 1984). It seems likely that the reproductive rate reaches a minimum at about this time, before recovering through the latter part of the calendar year until the cycle is complete and the population structure observed in January is restored. The population structure of *P. robertsi* on Wilson's Petrels in January and February is statistically identical to that of *Halipeurus pelagicus* on Storm Petrels in July, and, as Figure 2B shows, the populations of both louse species undergo a parallel ageing process towards the end of their host's breeding season.

Until such time as large samples of both petrel species can be obtained from their respective wintering grounds for delousing, the complete annual cycles of the mallophagan populations cannot be elucidated with certainty. However, the evidence presented in this paper, when viewed with that of Fowler & Miller (1984), suggests that, on the Storm Petrel, the life cycles of the two louse species are out of phase with each other, possibly the outcome of an adaptive strategy which reduces competition. The observations can further be accounted for within the concepts of "fundamental niche" and "realised niche" described by a number of authors (e.g. Krebs 1985), in which the definition of "niche" includes a multiplicity of biological factors, including density and breeding strategy.

Either of two scenarios seem possible; in both the fundamental niches of *Philoceanus* and *Halipeurus* are taken to be similar to those now occupied on the Wilson's Petrel and Storm Petrel, respectively:

- (a) *Philoceanus* is an ancient taxon which infested an extinct precursor of both *Oceanites* and *Hydrobates*. As the petrel species diverged, *Philoceanus* remained on both and retained a synchronous life cycle on both hosts, even though the hosts' breeding season became asynchronous. *Halipeurus* emerged later and became successful on *Hydrobates*. Competing with *Halipeurus*, *Philoceanus* assumed a realised niche of greatly reduced density. Bearing in mind Hardin's (1960) axiom "complete competitors cannot coexist", *Philoceanus* maintains a stable, but sub-ordinate, population on *Hydrobates* by virtue of a life cycle which is asynchronous with *Halipeurus*.

Or,

- (b) *Philoceanus* and *Halipeurus* evolved separately on *Oceanites* and *Hydrobates*. *Philoceanus* then became established on *Hydrobates* through a secondary infestation brought about by chance encounter of the two petrel species (Fowler & Miller (1984), consider how this might arise). Unable to occupy its fundamental niche on the new host in the presence of *Halipeurus*, *Philoceanus* occupies a subordinate realised niche by retaining breeding synchrony with the population on its original host.

Detailed investigations of the phylogenetic relationships between the two hosts and those of their lice, supported by comparative studies of other petrels, may eventually suggest which of the alternative scenarios is the more likely.

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#### SUMMARY

The frequency distribution of an elongate feather louse *Philoceanus robertsi* found on the Wilson's Petrel *Oceanites oceanicus* conforms well with a negative binomial model. Its infestation density and frequency distribution are similar to those previously described for another elongate louse *Halipeurus pelagicus* found on the Storm Petrel *Hydrobates pelagicus*. An analysis of the population structures of the lice reveals that both species have highest reproductive rates during the breeding season of the host, but both structures became dominated by adults, suggesting an ageing and declining process, towards the end of the hosts' breeding season. *Philoceanus robertsi* is also found on the Storm Petrel, but at a much lower density. Its reproductive cycle on this host appears to be in synchrony with that of the population on Wilson's Petrels. Explanations in terms of niche differentiation are offered.

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