AP

Morphological variation of chewing lice (Insecta: Phthiraptera) from different skua taxa

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The lice, *Haffneria grandis* and *Saemundssonia* were extracted from their hosts, skuas (Aves: Stercorariidae). Lice were extracted from dead birds by combing feathers, while lice from live birds were extracted using a delousing chamber containing chloroform vapour. Lice were measured and the data analysed by canonical discriminant analysis. Lice show variation in morphology that is useful in identifying some of these hosts. This variation is presumably due to micro-environmental pressure provided by each host. Our interpretation is that these chewing lice have evolved to be adapted to each skua taxon; different sizes and morphologies of skua taxa result in different sizes and morphologies of *Haffneria grandis* and *Saemundssonia.*

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ADDITIONAL KEY WORDS:—parasite host interactions – skuas – coevolution – morphological variation – taxonomic indicator – ecophenotypic variation – host specific – morphometric analysis.

CONTENTS

INTRODUCTION

Lice (Insecta: Phthiraptera) are ectoparasites of birds and mammals. The three suborders Rhynchophthirina, Amblycera and Ischnocera, are commonly known as

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chewing lice. These can be found on almost all birds and most mammals. Bird lice are morphologically more diverse than mammal lice, possibly due to a greater habitat range (feather types) provided by their hosts (Barker, 1994).

Lice are obligate ectoparasites, completing all of their life cycle on a single host by feeding on the host's tissues (such as blood, feathers, fur or skin debris). These insects do not possess wings, and therefore can only be transmitted to another host when hosts come into physical contact with each other, such as during breeding (Barker, 1994). Although there are reported cases that hippoboscid flies can carry lice to a new host through a process known as phoresy (Keirans, 1975), this mechanism is exceptional. Thus, louse distributions are limited to a small number of closely related host species, or often to a single species of host.

Being associated with a single host, lice have developed specific adaptations including modified morphology, behaviour and physiology (Barker, 1994; Hafner & Page, 1995). A louse's body is dorso-ventrally flattened to facilitate movement between feathers and escape from host grooming behaviour (Rozsa, 1993; Reiczigel & Rozsa, 1998). Body size also differs according to habitat selection (Waage, 1979). Larger, elongated lice usually exploit the wings of the host while smaller and rounded lice utilize head and neck areas. Due to the differences of feather size in these areas, each louse species has a specific claw size or oral groove width. Every species of louse, therefore, has different adaptations to correspond with its selected habitat on the host. These modifications make it unlikely that lice will survive on other species of bird or mammal.

There are several studies on the effects of host pressure on parasite morphology. Kellogg (1913) pointed out that the majority of variation resulting from host pressure occurs within every chewing louse species, caused by the separation of species members into little groups or family strains. Each group is subsequently isolated on its host island or succession of self-reproducing islands and develops variation. Data from simplified phylogenies of gophers and lice, show that evolution of louse body size is highly correlated with host size (Harvey & Keymer, 1991). Further studies also revealed that each species of chewing louse possesses a specific groove, the size of which correlates with the width of the hair of the host (Reed, 1994; Page, Clayton & Paterson, 1996; Reed & Hafner, 1997).

This paper explores the extent of morphological variation of chewing lice parasitizing skuas (Aves: Stercorariidae). Skuas are large seabirds, with nine taxa in two genera. The genus *Stercorarius* has three smaller species: long-tailed (*Stercorarius longicaudus*), Arctic (*S. parasiticus*) and pomarine (*S. pomarinus*) skuas. The genus *Catharacta* has four larger species: great (*Catharacta skua*), south polar (*C. maccormicki*), Chilean (*C. chilensis*) and brown (*C. antarctica*) skuas. This last is often separated into three well-defined subspecies: Falkland (*C. a. antarctica*), Tristan (*C. antarctica hamiltoni*), and brown skua (*C. a. lonnbergi*) (Furness, 1987). We sampled lice from each of these skua taxa, to test the hypothesis that the lice of a particular species would differ in morphometrics between skua taxa as a result of coevolution.

Skuas are very aggressive in chasing conspecifics and other skuas from their territory (Furness, 1987). Such behaviour ensures that their ectoparasite populations are unlikely to be transferred except to offspring or mate. Although most species of skua feed partly by killing other seabirds and so might be expected to acquire chewing lice from their prey, no species of louse has been found to live both on skuas and on their prey seabirds (Furness & Palma, 1992). However, skuas might acquire lice when they (rarely) feed on other skuas. Great skuas will eat Arctic skuas,

pomarine skuas will eat Arctic and long-tailed skuas, brown skuas will eat south polar skua chicks, so that closer affinities than predicted from their phylogenetic affinities might exist between lice on these species combinations. Morphological variation within skua taxa is small, but the taxa differ considerably in size, shape and ecology. Molecular and cladistic data are available from skuas for phylogenetical comparison (Cohen *et al.*, 1997; Andersson, 1999).

MATERIAL AND METHODS

Collection and measurement of ectoparasites

Chewing lice were extracted from skuas by standard procedures (Dunn, 1932; Spellerberg, 1971; Fowler & Cohen, 1983; Furness & Palma, 1992). Skuas were sampled from North and South Atlantic breeding colonies and from museum collections. In the latter, skuas were sampled to provide representatives from all major breeding areas of the world. In total, 956 lice were removed from 23 long-tailed skuas, 83 Arctic skuas, 25 pomarine skuas, 53 great skuas, 42 south polar skuas, 19 Chilean skuas, 22 brown skuas, 67 Falkland skuas and 30 Tristan skuas. Lice from live birds were extracted using a delousing chamber containing chloroform vapour. For dried and frozen birds, lice were extracted by thoroughly combing each feather with fine forceps. Species identifications of lice were confirmed by Ricardo L. Palma.

Two taxa of louse (*Haffneria grandis* (Piaget) and *Saemundssonia*) were chosen for this study due to their breadth of distribution across skua taxa. *Haffneria grandis* (HG) parasitizes the larger (*Catharacta*) skuas while *Saemundssonia* (SS) parasitizes all skuas (Palma, 2000). Only well preserved lice (with all of the characters required for measurement) were used in morphometric analysis. Measurements were made using a binocular microscope fitted with an eye-piece micrometer scale. Data were calibrated later with a standard eye-piece calibration scale. We examine size differences and shape variations. Eleven characters were measured for the study of size differences, while an additional four derived characters (ratios) were selected to investigate shape differences. These characters were based on those used by Eveleigh & Amano (1977) and were chosen for ease and reproducibility of measurement and overall morphological representation.

Analysis of morphological differences

Both species of lice were separated into groups based on sex and the host taxon. The hypothesis being tested was that species of lice show variation in morphology that is attributable to coevolution with their skua host taxon. A canonical discriminant analysis was used on standardized data categorized by skua host taxon. This is a frequently used and powerful method for investigation of morphometric differences between taxa (McLellan & Endler, 1998; Miyazaki & Shikano, 1998). In this analysis, the data are treated with one classification variable (with each value donating a different group) to several quantitative variables. This calculates the distance index within and between groups in a data set. The likelihood ratios produced by this

analysis can be used to determine how many axes can be used in differentiating observations in a data set.

<div align="center">RESULTS</div>

A total of 237 adult *Saemundssonia* (SS) and *Haffneria grandis* (HG) were extracted. However, only 161 adult lice were suitable for morphometric analysis (33 female HG, 25 male HG, 60 female SS and 43 male SS). Descriptive statistics show that the two species of lice are very distinct in terms of size and shape (Tables 1 and 2). HG is larger than SS.

Plots of canonical variables (variation in size of 15 morphological features) of female HG produced three major clusters representing different groups of HG (Fig. 1). Variations in HG morphology can be understood by studying the first two canonical variates which represent 93% of total variation. The first canonical variable shows that female HG from Tristan, great, and Falkland skuas were morphologically similar but slightly different from female HG living on south polar or Chilean skuas (ANOVA: $F=3.22$; df$=70.81,44$; $P<0.0001$). HG from the former hosts differ from those on the latter in head length, body length and the distance between head tip to mouthpart base. HG from south polar skuas are significantly distinct from HG on other skuas by having a shorter femur and a narrow head (ANOVA: $F>3.24$; df$=18,11$; $P<0.01$). The second canonical variable suggests that HG from Chilean skuas possess a longer femur and prothorax and, therefore, are distinct from other HG on other large skuas (ANOVA: $F=1.82$; df$=56.44,30$; $P<0.025$).

Analysis of female HG reveals a similar pattern (Fig. 2). This analysis reveals that female HG from south polar skuas possess slightly different morphologies than female HG from other large skuas (ANOVA: $F>5.17$, df$=25,4$; $P<0.003$). Female HG from south polar skuas have a smaller body length relative to their body-width and head-length. Female lice of Chilean skua tend to have a smaller head, whereas female HG living on Falkland and Tristan skuas generally have a large prothorax.

Analysis of size differences among male HG also produced three groups (Fig. 3), as revealed by their female counterparts. However, the allocation of skua species by these data is slightly different from the analysis of female HG. The first two canonical variates represent a high cumulative value; 81% of total variation. The second canonical variable successfully separates male HG on great, south polar and Falkland skuas from male HG on brown and Tristan skuas. Male HG from the former hosts have a narrow prothorax and a shorter femur and tibia. Data from the first canonical variables show that male HG on great, brown and Tristan skuas are significantly different from male HG on south polar and Falkland skuas (ANOVA: $F=2.53$; df$=40.21,44$; $P<0.001$). Male HG from the former skuas differ from the latter in body length and body width characters. The male HG of the former skuas are also larger in body size compared to male HG from the latter hosts. This coincides with differences in size between the skua taxa, south polar and Falkland skuas being the smallest of the *Catharacta* genus (Furness, 1987).

Shape analysis of male HG shows a wide range of body morphologies (Fig. 4). Further investigation of the first canonical variate indicates those male HG from brown and Tristan skuas are slightly different from those from south polar and Falkland skuas. Male HG from the former hosts have a significantly higher value

TABLE 1. Variation in morphometric data for *Haffneria grandis* (in mm)

Characters	Female (n=33)			Male (n=25)		
	Mean	SD	Range	Mean	SD	Range
1. Total body length	4.26	0.17	3.85–4.50	4.19	0.27	3.56–4.66
2. Body width, taken at widest point	0.79	0.06	0.65–0.85	0.68	0.05	0.57–0.73
3. Ratio of body length to body width	5.37	0.31	4.93–6.19	6.15	0.30	5.65–6.76
4. Head length	0.89	0.08	0.69–0.97	0.92	0.04	0.85–0.97
5. Head width, taken at widest point	0.59	0.05	0.53–0.81	0.54	0.07	0.26–0.61
6. Ratio of head length to head width	1.51	0.17	1.05–1.71	1.69	0.12	1.49–2.09
7. Ratio of body length to head length	4.79	0.36	4.39–5.83	4.57	0.27	4.00–5.11
8. Prothorax length	0.33	0.04	0.28–0.41	0.32	0.03	0.27–0.41
9. Prothorax width	0.43	0.04	0.23–0.49	0.43	0.03	0.36–0.49
10. Ratio of prothorax width to prothorax length	1.29	0.17	0.81–1.58	1.34	0.15	1.10–1.71
11. Distance between head tip to mouthpart base	0.65	0.05	0.57–0.77	0.61	0.11	0.28–0.73
12. Distance between mouthpart bases	0.16	0.03	0.12–0.20	0.16	0.03	0.12–0.24
13. Length of femur of third leg	0.33	0.06	0.24–0.61	0.32	0.03	0.24–0.41
14. Length of tibia of second leg	0.47	0.04	0.36–0.53	0.49	0.04	0.45–0.57
15. Degree of sclerotization	0.32	0.08	0.16–0.47	0.35	0.10	0.17–0.56

TABLE 2. Variation in morphometric data for *Saemundssonia* (in mm)

| Characters	Female (n=60)			Male (n=43)		
	Mean	SD	Range	Mean	SD	Range
1. Total body length	1.89	0.28	1.09–2.31	1.79	0.13	1.49–2.10
2. Body width, taken at widest point	0.80	0.13	0.42–1.11	0.62	0.09	0.42–0.78
3. Ratio of body length to body width	2.43	0.48	1.20–3.75	2.92	0.46	2.39–4.18
4. Head length	0.67	0.06	0.50–0.78	0.64	0.06	0.46–0.76
5. Head width, taken at widest point	0.73	0.06	0.59–0.85	0.67	0.04	0.55–0.74
6. Ratio of head length to head width	0.93	0.08	0.76–1.21	0.95	0.08	0.71–1.13
7. Ratio of body length to head length	2.83	0.42	1.54–3.57	2.80	0.25	2.42–3.50
8. Prothorax length	0.18	0.04	0.13–0.42	0.16	0.02	0.15–0.21
9. Prothorax width	0.38	0.05	0.17–0.45	0.37	0.04	0.32–0.59
10. Ratio of prothorax width to prothorax length	2.15	0.48	0.18–3.17	2.25	0.29	1.70–3.11
11. Distance between head tip to mouthpart base	0.51	0.06	0.28–0.65	0.48	0.05	0.36–0.57
12. Distance between mouthpart bases	0.13	0.03	0.08–0.23	0.12	0.03	0.08–0.19
13. Length of femur of third leg	0.14	0.03	0.08–0.23	0.12	0.03	0.08–0.23
14. Length of tibia of second leg	0.17	0.02	0.12–0.23	0.17	0.02	0.13–0.21
15. Degree of sclerotization	0.16	0.08	0.00–0.33	0.04	0.07	0.00–0.29
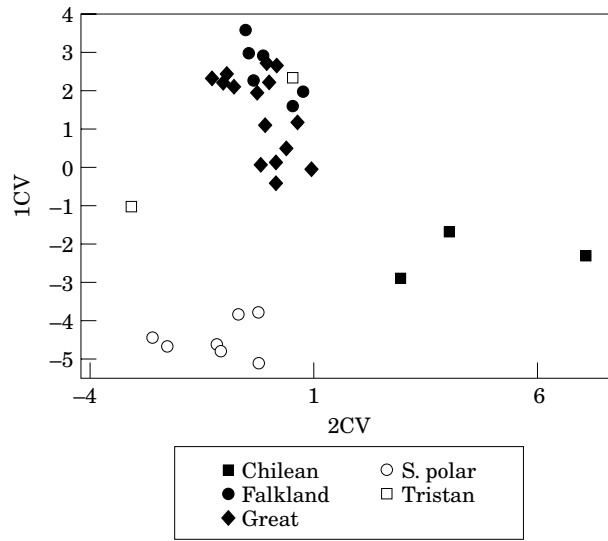
Figure 1. Plot of canonical variates of variation in the size of 15 features of female *Haffneria grandis*. Note that HG of South Polar and Chilean skuas differ from those infesting Falkland, Tristan and great skuas.
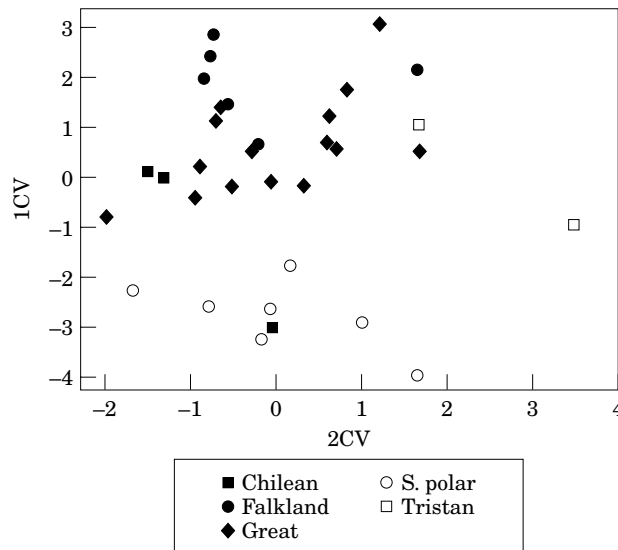

Figure 2. Plot of canonical variates of differences in the shape of female *Haffneria grandis*. Note that HG of South Polar skua is separated from HG of other large skuas.

of body length to head length ratio compared to male HG from Falkland or south polar skuas (ANOVA: $F>4.27$; df$=17,4$; $P<0.01$). The first three canonical variates show that HG on Falkland skuas have a relatively larger body than male HG from south polar or Tristan skuas (ANOVA: $F>3.16$; df$=17,4$; $P<0.04$).
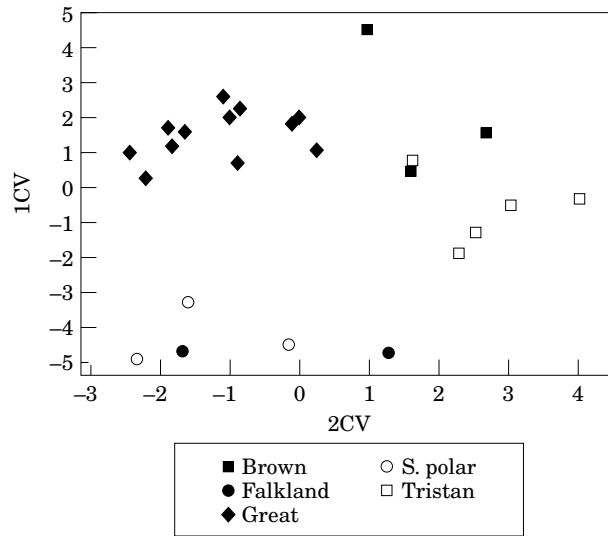
Figure 3. Plot of first two canonical variables of differences in size of male *Haffneria grandis* inhabiting large skuas. Note that HG from Falkland skuas are similar to those of South Polar skuas but different from HG infesting other skuas.
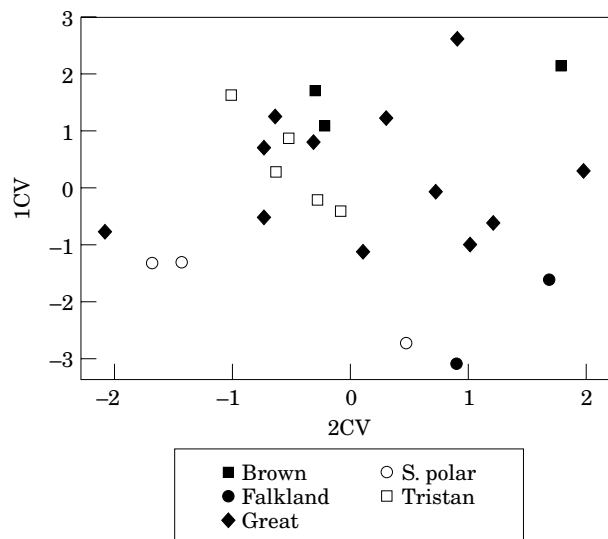

Figure 4. Plot of canonical variates of differences in shape among male *Haffneria grandis*. Note that HG on Falkland and South Polar skuas are different from HG from other skuas.

Morphometric analysis shows relatively little variation in morphology of *Sae-mundssonia*. Only female SS show significant size variation among hosts in one character: Female SS from Chilean skuas possess longer tibia than those from SS
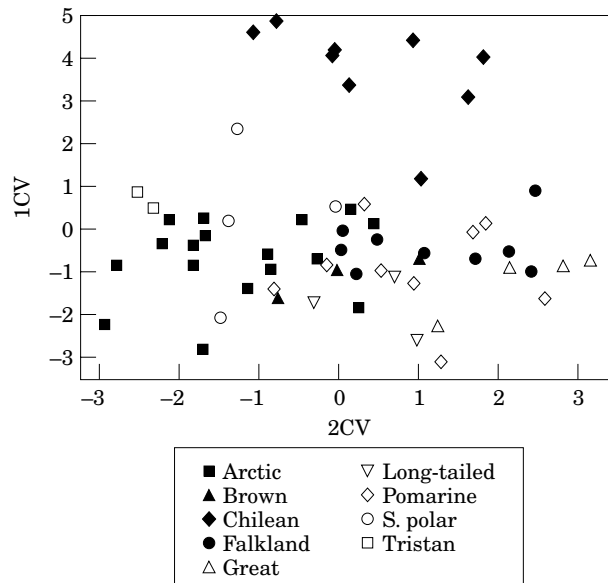
Figure 5. Plot of canonical variates of differences in size among female *Saemundssonia*. Note that SS from Chilean skuas are distinct from SS from other large skuas.

inhabiting other hosts (Fig. 5). Both sexes of SS showed no significant variation in their shape among the host taxa.

DISCUSSION

Although lice and hosts clearly coevolve, there is considerable debate as to whether bird lice cospeciate with their hosts (see Rozsa, 1993; Barker, 1994; Page *et al.*, 1996). However, it is known that lice have minimal opportunities to transfer from a given host species to another, mainly due to lack of transmission mechanisms, and therefore they have to modify and adapt to their current host species. This modification will involve alteration of behaviour, physiology and/or morphology (Tompkins & Clayton, 1999). Although alterations in behaviour and physiology are very difficult to study since lice cannot easily be reared, studies of morphological variation are possible.

The number of characters used in this study is considered adequate. Pankhurst (1991) suggested that more reliable results could be deduced when more characters are applied. However, this study shows that from fifteen characters used (including derived characters), only some of them were useful either in recognizing hosts or in distinguishing between them. Analysis of HG successfully separated their hosts (large skuas) by using data associated mainly with head length, femur length, prothorax length, and sometimes from the measurements of the distance between the head tip to the mouthpart base.

Increasing the number of characters may also produce negative effects on overall results. Results from analysis of variance indicate that male SS possess four informative

characters, but the total effect from the other 11 characters eliminates this information and produces no clear evidence for host identification.

Several previous studies also found that, although many characters are available for analysis, only some of them are informative for displaying differences between sets of morphological data. From 21 morphological and behavioural characters, Alexander (1991) successfully analysed the dance language of *Apis* (Insecta: Apidae) by using only data on genitalia. In analysis on cloacal anatomy of salamanders, from 25 characters used in the study, only 12 were useful for phylogenetical analysis (Sever, 1991). In another study, only ten out of 210 morphological characters were capable of presenting good information about phylogenetical relationships among *Drosophila* (DeSalle & Grimaldi, 1992).

Some morphological characters of chewing lice do vary between host taxa (e.g. tibia length) and are therefore very useful in identifying hosts (i.e. large skuas). Various degrees of morphological variation exhibited by HG parasitizing different species of hosts indicate that morphological coevolution has occurred in skua–louse systems. However, the degree of morphological variation is too small to permit easy allocation of these lice to subspecies. These small scale variations can only be detected by detailed morphometric analysis.

Several factors may be responsible for variations in chewing lice morphology. An interaction within and among species living in a similar environment can modify the overall size of an organism. In chewing lice, this interaction may be due to inter and intra-species competition for limited resources provided by their host. Inter and intra-species competition can act as a major factor in morphological modification of chewing lice anatomy. The differences among characters clearly show adaptation of this louse to different hosts. Modifications in femur or tibia length will presumably improve movement of lice on hosts. The ability to move faster is a key feature in enhancing louse efficiency in avoiding the beak and feet of the host during grooming. By increasing the efficiency of avoidance to host grooming, lice may increase their survival rate.

In this study, results from canonical analysis indicate that lice from different host taxa show variation in their morphologies. *Saemundssonia* showed rather little morphological variation among skua host taxa, while *Haffneria grandis* showed much host taxon-specific variation. Differences in size or shape of particular louse structures cannot easily be related to known evolutionary relationships between the skua taxa. However, there is a general trend in size of HG between hosts that mirrors the size differences between skua taxa, rather than their phylogeny.

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