Community structure of arthropod ectoparasites on Alaskan seabirds[1]

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A total of 28 species of arthropods was recovered from 29 common murres (*Uria aalge*), 8 thick-billed murres (*Uria lomvia*), 22 black-legged kittiwakes (*Rissa tridactyla*), and 10 red-legged kittiwakes (*Rissa brevirostris*) collected from the Pribilof Islands, Alaska, U.S.A. The ectoparasite community on each bird species almost invariably consisted of three species of chewing lice, two species of ticks, and five to nine species of mites. Astigmatid feather mites (*Alloptes* spp., *Laronyssus martini* (Trouessart)) were the most numerous group of ectoparasites except on black-legged kittiwakes on which *Ixodes* ticks were the most abundant. The second most abundant taxa were ticks on common murres and thick-billed murres, and quill mites (Syringophilidae) on red-legged kittiwakes. Kittiwakes usually supported more diverse communities of ectoparasites than did murres, probably because of differences in nesting and foraging behavior. Ectoparasite communities between the congeneric species of birds were particularly similar in terms of species composition and general structure, and supported our hypothesis that phylogenetic relatedness of hosts is reflected in similarity of their ectoparasite communities. Community structure of ectoparasites was much more similar between the two murre species than between the two kittiwake species, probably because of gregarious flocking and mixed-species nesting of murres.

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Vingt-huit espèces d'arthropodes ont été recensées chez 29 Marmettes de Troïl (*Uria aalge*), 8 Marmettes de Brünnich (*Uria lomvia*), 22 Mouettes tridactyles (*Rissa tridactyla*) et 10 Mouettes à pattes rouges (*Rissa brevirostris*) des Îles Pribilof en Alaska (É.-U.). La communauté d'ectoparasites sur chacune des espèces consiste presque toujours en trois espèces de ricins, deux espèces de tiques et cinq à neuf espèces d'autres acariens. Les Aestigmatidae, acariens des plumes, (*Alloptes* spp., *Laronyssus martini* (Trouessart)) constituent le groupe d'ectoparasites le plus nombreux, sauf chez les Mouettes tridactyles où ce sont les tiques *Ixodes* qui prédominent. En seconde position, viennent les tiques qui parasitent les Marmettes de Troïl et les Marmettes de Brünnich, puis les acariens des pennes (Syringophilidae) chez les Mouettes à pattes rouges. Les Mouettes portent des communautés d'ectoparasites plus diversifiées que les Marmettes, probablement à cause de différences dans leurs comportements de nidification et de recherche de nourriture. Les communautés d'ectoparasites des espèces congénères sont très semblables dans leur composition spécifique et leur structure générale; la parenté phylogénétique des hôtes se reflète donc dans la similarité de leur communautés d'ectoparasites. La resemblance est plus forte entre les communautés parasites des Marmettes qu'entre les communautés parasites des Mouettes, sans doute parce que les marmettes se rassemblent en bandes et que les espèces nichent les unes avec les autres.

[Traduit par la revue]

Host–ectoparasite associations provide a natural ecological system which is unique for the study of community structure. Ectoparasites on host animals form well-defined, physically separated communities which are mobile. Ectoparasite communities are sufficiently diverse for such studies to be valid (Marshall 1981; Kim 1985*a*) and experimentally manageable (Kim 1972). The structure of ectoparasite communities may be strongly influenced by host animals. Hosts not only provide habitats for ectoparasites, but also interact actively with them. Host animals can defend themselves against ectoparasites by physiological and behavioral reactions (Nelson et al. 1975, 1977; Marshall 1981; Allen and Nelson 1982). Through the process of interactions, i.e., action, reaction, and counterreaction, ectoparasites have closely coevolved with their hosts (Kim 1985*b*). A number of paradigms have been formulated to explain host–parasite coevolution (Brooks 1979; Waage 1979; Price 1980; Kim 1985*c*). However, very little has been studied concerning relationships at the community level.

In this study, we compared the structures of ectoparasite communities between pairs of congeneric species of seabirds: the common murre (*Uria aalge* (Pontoppidan)) and thick-billed murre (*Uria lomvia* (Linnaeus)); black-legged kittiwake (*Rissa tridactyla* (Linnaeus)) and red-legged kittiwake (*Rissa brevirostris* (Bruch)). The common murre and thick-billed murre are very similar with regard to general morphology and behavior, except that the latter has a shorter and stouter bill (Tuck 1960). The only obvious difference between the kittiwakes is in the color of their legs (Bent 1963). This means that the congeneric birds furnish virtually identical microhabitats for their ectoparasites. We hypothesized that phylogenetically more closely related hosts would support more similar communities of parasites. Since all four species of birds share the same habitat on the Pribilof Islands, Alaska, there may be some general similarity in community structure of ectoparasites across the bird species. The objectives were (*i*) to describe the basic structure of ectoparasite communities on the four species of birds, (*ii*) to examine the ecological diversity of the ectoparasite community on each bird species in relation to its ecology and

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behavior, and (*iii*) to determine the evolutionary relationships at the community level between ectoparasites and hosts.

Materials and methods

The study birds were collected from the Pribilof Islands (56°35′–57°11′ N, 169°35′–170°24′ W), in the Bering Sea, Alaska. St. Paul Island, St. George Island, and three other very small islands are made up primarily of lava flows and basaltic sills that erupted during the past 400 000 years (Barth 1956). The mean monthly temperature varies from about −5°C in February to about 9°C in August (Foote et al. 1968). Summer temperature normally ranges from 3 to 10°C (Johnson 1978). Although precipitation, mostly in the form of fog and rain, is relatively low with an annual average of 550 mm, humidity is very high throughout the year (Foote et al. 1968).

A total of 69 adult birds (29 common murres, 8 thick-billed murres, 22 black-legged kittiwakes, and 10 red-legged kittiwakes) were collected during the summers of 1978 and 1980. All birds, except seven red-legged kittiwakes from St. George Island in 1978, were shot along the cliffs from Southwest Point to Zapadni Point of St. Paul Island. They were immediately frozen and transported in insulated containers to the laboratory.

Ectoparasites were extracted from the bird skins by using a dissolution technique modified from Cook (1954). Each section of skin was cut into pieces of approximately 5 cm^2 and mixed in a separate 2000-mL beaker with 500 mL of 0.5% trypsin buffered to pH 7.5 with disodium phosphate (Na_2PO_4). After the skins were soaked at 37–38°C for at least 24 h, 500 mL of 5% potassium hydroxide (KOH) were added to each beaker and the mixture was boiled until both skin and feathers were completely dissolved. Ectoparasites were not dissolved since their exoskeletons are made of chitinous carbohydrates. The boiled solution was filtered through an 80-mesh bronze screen and all ectoparasites were recovered from the filtrate under a dissecting microscope. Voucher specimens of all arthropod species were deposited in the Frost Entomological Museum, The Pennsylvania State University.

Ectoparasite populations on the host animal are conventionally described by two parameters (Marshall 1981; Kim 1985*b*): incidence rate (the percentage of hosts infested; infestation rate of Kim); and infestation rate (the mean number of ectoparasites per host examined; population rate of Kim). In addition to these two parameters, we added another one, infestation density (the mean number of ectoparasites per infested host). These three parameters, together with the total number of ectoparasites collected and the number of hosts examined, provide a more comprehensive description of ectoparasite populations on the host. H' (Shannon and Weaver 1963) and J' (Pielou 1966) were used to estimate the diversity and evenness of the ectoparasite communities, respectively:

$$H' = -\sum_{i=1}^{S} P_i \log P_i$$

and

$$J' = H'/\log S$$

where S is the total number of ectoparasite species and P_i is the relative frequency of the ith species. To determine the degree of structural similarity between the ectoparasite communities, we calculated Sorensen's similarity index (Sorensen 1948):

$$C_S = \frac{2S_{AB}}{S_A + S_B}$$

where S_A is the number of ectoparasite species on bird species A, S_B is the number of ectoparasite species on bird species B, and S_{AB} is the number of ectoparasite species in common between the two bird species. C_S ranges from 0 (no species in common) to 1 (identical).

Results

Species diversity and evenness

A total of 27 307 individuals of 28 arthropod species was recovered from 69 birds of 4 species (Table 1). Insects (9 spp.) constituted only 7% and acarines (19 spp.) 93% of the total arthropod population. Twenty-three species of parasitic arthropods made up 99.1% of the individuals. The other five species were nonparasitic.

Astigmata was the most abundant taxon of ectoparasites (63.7%). Ticks (Metastigmata) formed the second most abundant group (24.1%) (Tables 2 and 3). In terms of biomass, however, ticks were the dominant group of ectoparasites. Six species of chewing lice and three species of prostigmatid mites represented 6.9% and 4.0%, respectively. All other arthropod groups made up only 1.3%.

In terms of relative abundance, the feather mites were the dominant ectoparasites on the study birds except on black-legged kittiwakes, on which *Ixodes* ticks were most abundant (Fig. 1). Ticks formed the second most abundant member of the ectoparasite communities on both common and thick-billed murres. On red-legged kittiwakes, however, the quill mites were the second most abundant group, followed by ticks. In general, ectoparasite communities on all study birds were dominated by ticks and feather-inhabiting mites. They comprised over 90% of individuals in each community (Fig. 1).

The heaviest infestation was recorded from common murres (Table 2). Individual common murres harbored on average just over 600 ectoparasites, which is nearly twice as many as the next highest infestation density, found on thick-billed murres. However, most of the ectoparasites on common murres were feather mites of *Alloptes* (*Conuralloptes*) sp. (73% of thc total ectoparasites). Infestation densities of kittiwakes (Table 3) were generally lower than those of murres.

Black-legged kittiwakes supported the most diverse community of ectoparasites (Table 4). They supported the greatest number of species which were also most evenly distributed. The ectoparasite community on red-legged kittiwakes was the second most diverse (Table 4). The ectoparasite community on common murres yielded a lower diversity measure (H') than that on thick-billed murres, although the former supported a greater number of species (Table 4). The ectoparasite community was completely dominated by three species of ectoparasites, *Alloptes* (*Conuralloptes*) sp., *Ixodes uriae* White, and *Quadraceps obliquus* (Mjöberg), which together represented 96% of the total individuals (Fig. 1). Domination by major species appeared to a large extent on red-legged kittiwakes also (Fig. 1), but the domination was shared by more species (Table 3).

We found a strong similarity in the structure of ectoparasite communities between the two murre species, as indicated by an extremely high value of Sorensen's index of community similarity (Table 5). The two murre species harbored an almost identical set of arthropods, except that common murres also harbored *Liposcelis rufus* Broadhead and *Calamicoptes* sp. (Table 2). The second highest measure of Sorensen's index was found between the two kittiwake species (Table 5). They shared 11 species, 6 of which were permanent ectoparasites (Table 3). Between murres and kittiwakes, only the two species of ticks and a few nonparasitic arthropods were shared. None of the permanent ectoparasite species occurred on both murres and kittiwakes.

Species composition and abundance

Lice

Six mallophagan species, two from each of three genera, were recovered from the study birds. Three species, one from each genus, parasitized both murre species (Table 2). Both

TABLE 1. Arthropods associated with the four species of seabirds (CM, common murre (*Uria aalge*); TM, thick-billed murre (*U. lomvia*); BK, black-legged kittiwake (*Rissa tridactyla*); and RK, red-legged kittiwake (*R. brevirostris*))

	CM	TM	BK	RK
Insecta				
Mallophaga				
Suborder Ischnocera				
Family Philopteridae				
Saemundssonia calva (Kellogg)	*	*		
Saemundssonia lari (O. Fabricius)			*	*
Quadraceps obliquus (Mjöberg)	*	*		
Quadraceps ornatus (Grube)			*	*
Suborder Amblycera				
Family Menoponidae				
Austromenopon uriae Timmermann	*	*		
Austromenopon transversum (Denny)			*	*
Psocoptera				
Family Liposcelidae				
Liposcelis rufus Broadhead	*		*	*
Coleoptera				
Family Dermestidae				
Dermestes sp.			*	*
Siphonaptera				
Family Ceratophyllidae				
Mioctenopsylla artica hadweni (Ewing)			*	
Acari				
Metastigmata				
Family Ixodidae				
Ixodes uriae White	*	*	*	*
Ixodes signatus Birula	*	*	*	*
Mesostigmata				
Family Rhinonyssidae				
Rhinonyssus caledonicus Hirst	*	*		
Family Dermanyssidae				
Dermanyssid sp.				*
Prostigmata				
Family Trombiculidae				
Neotrombicula sp.	*	*	*	
Family Syringophilidae				
Syringophilid sp. nov. No. 1			*	
Syringophilid sp. nov. No. 2				*
Astigmata				
Family Alloptidae				
Alloptes (*Alloptes*) sp.			*	*
Alloptes (*Conuralloptes*) sp.	*	*		
Family Avenzoariidae				
Laronyssus martini (Trouessart)			*	*
Family Epidermoptidae				
Dermation sp. nov.				*
Family Laminosioptidae				
Laminosioptes sp. nov.				*
Calamicoptes sp. nov.	*			
Family Acaridae				
Tyrophagus sp.				*
Family Evansacaridae				
Evansacarus sp. nov.			*	
Unidentified sp.			*	
Cryptostigmata				
Family Ameronothridae				
Ameronothrus nidicola Sitnikova	*	*	*	*
Family Ceratozetidae				
Svalbardia sp. near *paludicola*	*	*	*	*
Family Camisiidae				
Camisia sp.			*	

kittiwake species shared the other three species (Table 3). *Quadraceps* spp. were most abundant on all four species of birds. *Quadraceps obliquus* on common murres was exceptionally abundant (38.7 per bird). All common murres examined were infested with this species, whereas only six of the eight thick-billed murres were infested. *Quadraceps ornatus* (Grube) occurred in higher densities on black-legged kittiwakes than on red-legged kittiwakes (Table 3). *Saemundssonia* spp. formed the second largest group of Mallophaga on all four species of birds. *Saemundssonia calva* (Kellogg) was more abundant on common murres than on thick-billed murres (Table 2). *Saemundssonia lari* (O. Fabricius) occurred less frequently but at a higher density on black-legged kittiwakes than on red-legged kittiwakes (Table 3). *Austromenopon* spp. were generally rare on the study birds.

Ticks

Two congeneric species of ticks, *Ixodes uriae* and *Ixodes signatus* Birula, were found on all four species of birds (Tables 2 and 3). Only five birds (7.2%) harbored no ticks. The highest infestation density of *I. uriae* was found on thick-billed murres, followed by black-legged kittiwakes and common murres. Red-legged kittiwakes had an unusually low density of *I. uriae*. *Ixodes signatus* was much rarer than *I. uriae*. Incidence rate of *I. signatus* was higher on thick-billed murres, but density was higher on common murres (Table 2). However, one black-legged kittiwake was found to harbor only *I. signatus*.

Mites

Sixty-seven nasal mites, *Rhinonyssus caledonicus* Hirst, were recovered from 10 common murres (Table 2). Infested birds harbored a mean of six to seven mites in their nasal passages. Two thick-billed murres also harbored the same species of nasal mites with a higher infestation density. Both murre species were new host records for this mite.

Chiggers (*Neotrombicula*) were collected from all species of study birds except red-legged kittiwakes (Tables 2 and 3). Incidence rates were very low, but infestation densities were relatively high on both murre species. The crops of most chiggers were red, indicating that they had been feeding on blood at the time of death. Specific identifications of chiggers were not possible, because the specimens were overcleared by the extraction method. Thus, whether the chiggers collected in this study represent a single species or more is not known.

A new species of quill mite (Syringophilidae) colonized black-legged kittiwakes in large numbers (Table 3). In fact, it was the second most numerous ectoparasite on the birds. Another new species of the Syringophilidae inhabited red-legged kittiwakes (Table 3). These two new species represent a new genus close to *Niglarobia* described from sandpipers (J.B. Kethley, personal communication).

The feather mite *Alloptes* (*Conuralloptes*) sp. on murres was by far the most numerous ectoparasite (Table 2). All murres examined harbored this species. Two species of feather mites, *Alloptes* (*Alloptes*) sp. and *Laronyssus martini* (Trouessart), actually coexisted on the wing feathers of both kittiwakes (Table 3). They were attached primarily between the adjacent barbs of the feathers. On black-legged kittiwakes, *Alloptes* (*Alloptes*) sp. occurred more frequently and more densely than *L. martini*. On red-legged kittiwakes, however, *L. martini* occurred in larger numbers on infested birds, although it occurred less frequently. Its mean infestation density was the highest among all ectoparasites on red-legged kittiwakes. *Alloptes* spp. were

TABLE 2. Infestation rate and density of arthropods on common murres and thick-billed murres

	Common murre (N = 29)				Thick-billed murre (N = 8)			
	Total arthropods	No. of birds infested (%)	Infestation rate	Infestation density	Total arthropods	No. of birds infested (%)	Infestation rate	Infestation density
Mallophaga								
Saemundssonia calva	184	21 (72.4)	6.3	8.8	18	5 (62.5)	2.3	3.6
Quadraceps obliquus	1 122	29 (100.0)	38.7	38.7	29	6 (75.0)	3.6	4.8
Austromenopon uriae	159	21 (72.4)	5.5	7.6	1	1 (12.5)	0.1	1.0
Psocoptera								
Liposcelis rufus	1	1 (3.4)	0.0	1.0	—	—	—	—
Metastigmata								
Ixodes uriae	2 777	28 (96.6)	95.8	99.2	1006	7 (87.5)	125.8	143.7
Ixodes signatus	70	8 (27.6)	2.4	8.8	9	4 (50.0)	1.1	2.3
Mesostigmata								
Rhinonyssus caledonicus	67	10 (34.5)	2.3	6.7	16	2 (25.0)	2.0	8.0
Prostigmata								
Neotrombicula sp.	15	1 (3.4)	0.5	15.0	53	2 (25.0)	6.6	26.5
Astigmata								
Alloptes (*Conuralloptes*) sp.	12 326	29 (100.0)	425.0	425.0	1267	8 (100.0)	158.4	158.4
Calamicoptes sp. nov.	122	6 (20.7)	4.2	20.3	—	—	—	—
Cryptostigmata								
Ameronothrus nidicola	42	10 (34.5)	1.5	4.2	85	6 (75.0)	10.6	14.2
Svalbardia sp. nr. *paludicola*	8	3 (10.3)	0.3	2.7	7	3 (37.5)	0.9	2.3
Total	16 893	29 (100.0)	582.5	582.5	2491	8 (100.0)	311.4	311.4

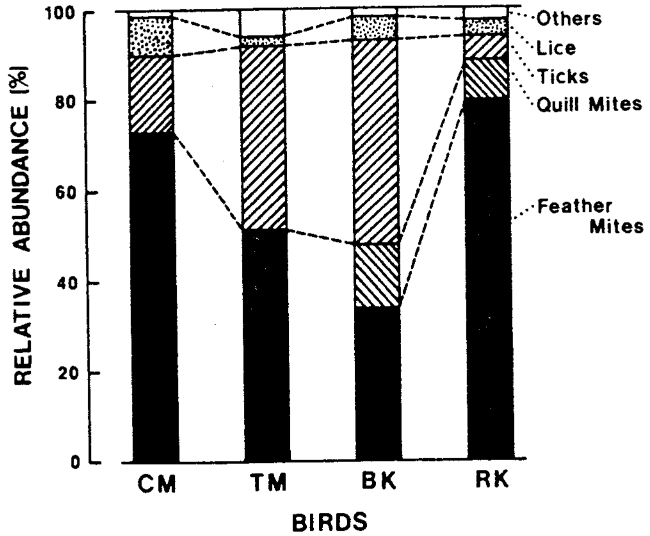

FIG. 1. A comparison of the community structure of ectoparasites on the study birds (CM, common murre; TM, thick-billed murre; BK, black-legged kittiwake; RK, red-legged kittiwake) showing relative abundances of different ectoparasite groups.

not identified at the specific level, because the genus has not been systematically revised.

Six common murres were found to harbor a new species of quill-wall mites, *Calamicoptes* (Table 2). Two species of astigmatid mites, *Evansacarus* sp. nov. and an unidentified one, were collected from black-legged kittiwakes (Table 3). Red-legged kittiwakes supported four more species of mites, *Dermation* sp. nov., *Laminosioptes* sp. nov., *Tyrophagus* sp., and a dermanyssid sp. (Table 3). These mites were highly host-specific.

Nonparasitic arthropods

Oribatid mites formed the major group of nonparasitic arthropods (Tables 2 and 3). Two species, *Ameronothrus nidicola* Sitnikova and *Svalbardia* sp. nr. *paludicola*, were occasionally encountered on all four species of birds. One additional oribatid mite, *Camisia* sp., was also found from a black-legged kittiwake (Table 3). Three specimens of a psocid, *Liposcelis rufus*, were collected from the common murre, black-legged kittiwake, and red-legged kittiwake (Tables 2 and 3). Both kittiwakes also harbored dermestid beetle larvae (Table 3).

Discussion

Community structure

Kittiwakes supported ectoparasite communities that were not only richer but also more even in distribution (Table 4). A number of factors may be responsible for this. First, the difference in the nesting habit may explain some of the differences in species richness. Kittiwakes build nests, whereas murres do not (Tuck 1960). Murres lay eggs on the bare rocks. Therefore, kittiwakes could harbor some additional ectoparasite species that are primarily nest dwellers. Second, murres and kittiwakes also differ in foraging behavior. Murres swim under water to obtain food (Tuck 1960). Common murres have been recorded to dive as deep as 60 m (Stettenheim 1959) and thick-billed murres are believed to dive even deeper (Spring 1968). Kittiwakes do not dive to forage. Instead, they usually swoop down gently with elevated wings to snatch prey from the water surface without wetting a feather (Bent 1963). Thus,

TABLE 3. Infestation rate and density of arthropods on black-legged kittiwakes and red-legged kittiwakes

	Black-legged kittiwakes (N = 22)				Red-legged kittiwakes (N = 10)			
	Total arthropods	No. of birds infested (%)	Infestation rate	Infestation density	Total arthropods	No. of birds infested (%)	Infestation rate	Infestation density
Mallophaga								
Saemundssonia lari	81	11 (50.0)	3.7	7.4	29	9 (90.0)	2.9	3.2
Quadraceps ornatus	205	15 (68.2)	9.3	13.7	53	7 (70.0)	5.3	7.6
Austromenopon transversum	5	3 (13.6)	0.2	1.7	1	1 (10.0)	0.1	1.0
Psocoptera								
Liposcelis rufus	1	1 (4.6)	0.1	1.0	1	1 (10.0)	0.1	1.0
Coleoptera								
Dermestes sp.	2	2 (9.1)	0.1	1.0	2	2 (20.0)	0.2	1.0
Siphonaptera								
Mioctenopsylla artica hadweni	6	2 (9.1)	0.3	3.0	—	—	—	—
Metastigmata								
Ixodes uriae	2582	20 (90.9)	117.4	129.1	113	8 (80.0)	11.3	14.1
Ixodes signatus	29	6 (27.3)	1.3	4.8	1	1 (10.0)	0.1	1.0
Mesostigmata								
Dermanyssid sp.	—	—	—	—	2	2 (20.0)	0.2	1.0
Prostigmata								
Syringophilid sp. nov. No. 1	823	8 (36.4)	37.4	102.9	—	—	—	—
Syringophilid sp. nov. No. 2	—	—	—	—	198	2 (20.0)	19.8	99.0
Neotrombicula sp.	8	2 (9.1)	0.4	4.0	—	—	—	—
Astigmata								
Alloptes (*Alloptes*) sp.	1250	19 (86.4)	56.8	65.8	1131	10 (100.0)	113.1	113.1
Laronyssus martini	675	11 (50.0)	30.7	61.4	588	4 (40.0)	58.8	147.0
Dermation sp. nov.	—	—	—	—	11	3 (30.0)	1.1	3.7
Laminosioptes sp. nov.	—	—	—	—	8	2 (20.0)	0.8	4.0
Tyrophagus sp.	—	—	—	—	1	1 (10.0)	0.1	1.0
Evansacarus sp. nov.	9	1 (4.6)	0.4	9.0	—	—	—	—
Unidentified sp.	7	2 (9.1)	0.3	3.5	—	—	—	—
Cryptostigmata								
Ameronothrus nidicola	69	16 (72.7)	3.1	4.3	27	8 (80.0)	2.7	3.4
Svalbardia sp. nr. *paludicola*	1	1 (4.6)	0.1	1.0	3	2 (20.0)	0.3	1.5
Camisia sp.	1	1 (4.6)	0.1	1.0	—	—	—	—
Total	5754	22 (100.0)	261.5	261.5	2169	10 (100.0)	216.9	216.9

TABLE 4. Diversity and evenness of the ectoparasite communities on the study birds

	Total no. of individuals	Total no. of species	No. of species Mean	No. of species SD	Diversity (H')	Evenness (J')
Murre						
Common	16 893	12	5.83	1.07	0.40	0.36
Thick-billed	2 491	10	5.63	0.52	0.46	0.46
Kittiwake						
Black-legged	5 754	17	6.73	1.61	0.66	0.53
Red-legged	2 169	16	6.30	1.06	0.59	0.49

ectoparasites not adapted to an underwater situation could not survive on murres. Third, the difference in body surface area between murres and kittiwakes may also be responsible. The theory of island biogeography (MacArthur and Wilson 1967) predicts that larger islands will support more species. Body surface area of kittiwakes was greater than that of murres largely due to differences in wing size. Wings of kittiwakes (1550–1780 cm^2) provided a much larger surface area than those of murres (1120–1270 cm^2).

Black-legged kittiwakes supported a more diverse and evenly distributed community of ectoparasites than did red-legged kittiwakes. Black-legged kittiwakes are observed to migrate out of the Bering Sea, whereas red-legged kittiwakes are endemic to the Bering Sea and are more or less sedentary (Bent 1963).

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