

# Worldwide Distribution and Diversity of Seabird Ticks: Implications for the Ecology and Epidemiology of Tick-Borne Pathogens

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## Abstract

The ubiquity of ticks and their importance in the transmission of pathogens involved in human and livestock diseases are reflected by the growing number of studies focusing on tick ecology and the epidemiology of tick-borne pathogens. Likewise, the involvement of wild birds in dispersing pathogens and their role as reservoir hosts are now well established. However, studies on tick–bird systems have mainly focused on land birds, and the role of seabirds in the ecology and epidemiology of tick-borne pathogens is rarely considered. Seabirds typically have large population sizes, wide geographic distributions, and high mobility, which make them significant potential players in the maintenance and dispersal of disease agents at large spatial scales. They are parasitized by at least 29 tick species found across all biogeographical regions of the world. We know that these seabird–tick systems can harbor a large diversity of pathogens, although detailed studies of this diversity remain scarce. In this article, we review current knowledge on the diversity and global distribution of ticks and tick-borne pathogens associated with seabirds. We discuss the relationship between seabirds, ticks, and their pathogens and examine the interesting characteristics of these relationships from ecological and epidemiological points of view. We also highlight some future research directions required to better understand the evolution of these systems and to assess the potential role of seabirds in the epidemiology of tick-borne pathogens.

**Key Words:** bird—*Borrelia*—*Carios capensis*—hard ticks—host–parasite interactions—*Ixodes uriae*—soft ticks—Soldado virus—vector-borne disease.

## Introduction

TICKS ARE WIDELY DISTRIBUTED in the world and transmit a greater variety of infectious agents than any other arthropod group (Jongejan and Uilenberg 2004). In recent years, there has been growing interest in understanding the evolutionary ecology of these vectors in relation to global change and the emergence of infectious diseases (e.g., Estrada-Pena et al. 2006, Ogden et al. 2006, Keesing et al. 2009). Numerous land bird species are parasitized by ticks and are thus involved in the epidemiology of a large diversity of pathogens (e.g., Morshed et al. 2005, Ogden et al. 2008). In contrast to these terrestrial systems, our knowledge about seabird–tick interactions and the role of seabirds as reservoirs and/or dispersal agents of ticks and tick-borne pathogens remains scarce. Ticks are present in seabird colonies of all biogeographic regions and climates. Due to their large population sizes, wide geographic distribution, and high dispersal

potential, seabirds may play an important role in the ecology and epidemiology of many tick-borne pathogens, both by maintaining enzootic cycles of infection and by dispersing ticks and their pathogens at large spatial scales.

A few pioneering studies have examined seabird tick systems, but most publications focus on morphological descriptions and concern only restricted geographical areas (e.g., Zumpt 1952, Arthur 1958, 1960a, 1960b, Yunker 1975, Dumbleton 1961, Amerson 1968, Chastel 1980, Nuttall 1984, Guiguen 1988). As seabirds often breed on isolated and seldom-visited islands, it can be difficult to obtain reliable information about these marine systems. As such, the ecology and distribution of seabird ticks are poorly understood or completely unknown, and there exists much confusion on species identification.

The aim of this article is to review the state of our knowledge about ticks associated with seabirds and to present some elements on the ecological relationships between seabirds, ticks, and their pathogens that may be important to consider

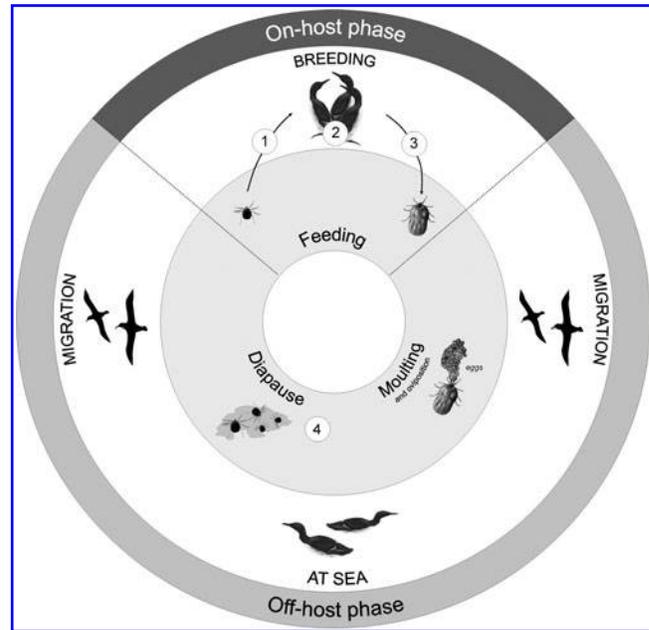
from an epidemiological and conservation points of view. The different tick species reviewed here are considered in relation to their geographical distribution, the diversity of seabird hosts exploited, and their known association with tick-borne pathogens. For each aspect, we discuss the gaps in our knowledge and highlight future research directions.

### Seabirds and Ticks

Seabirds may be divided into true seabirds, for which the sea represents the main source of food, and occasional seabirds, which typically frequent lakes, rivers, estuaries, bays, and only occasionally marine coastlines (Chastel 1988). As we focus on marine systems in this review, only true seabirds will be considered. These species include 14 avian families: Alcidae (auks), Diomedidae (albatrosses), Fregatidae (frigate birds), Hydrobatidae (storm-petrels), Laridae (gulls), Pelecanidae (pelicans), Pelecanoididae (diving-petrels), Phaethontidae (tropicbirds), Phalacrocoracidae (cormorants and shags), Procellariidae (petrels and shearwaters), Spheniscidae (penguins), Stercorariidae (skuas), Sternidae (terns and noddies), and Sulidae (gannets and boobies).

From the perspective of parasites, a key feature of seabird ecology is colonial breeding (Møller et al. 1990), which, in some species, can lead to the aggregation of hundreds of thousands, and sometimes millions, of individuals during the breeding season (Coulson 2001). Seabird colonies provide spatially discrete habitats that are often ideally suited to shelter-seeking (i.e., endophilic) ticks, and guarantee a nearby source of food at least during the breeding season. Moreover, most seabirds exhibit strong interannual fidelity to their breeding sites, and have relatively long chick-rearing periods, providing a reliable and predictable host resource for ticks. It is not surprising therefore that many seabird colonies support large tick populations and that these populations build up over time (Danchin 1992).

Due to the frequent seasonality of seabird reproduction, seabird–tick interactions can be restricted in time, such that the life cycle of the tick is coupled with that of its seabird host with interactions occurring almost exclusively during the breeding season (e.g., Feare and Gill 1997) (Fig. 1). In places with a high diversity of seabird species or where seabird breeding is continuous (i.e., birds breed all year round or breeding times for different species are asynchronous), tick activity can occur year round (e.g., Ramos et al. 2001). In all cases, after engorgement on the host is complete, ticks drop off the host and remain in or around the nest habitat until the next blood meal. During this free-living phase, which represents the greatest part of the life cycle, engorged ticks molt (for larva and nymphs) or oviposit (for females). These ticks can readily survive from 1 year to the next, waiting for the host to return the next breeding season. Both host availability and environmental conditions can therefore affect the number of complete generations within a year, and thus will have important consequences for the evolution of seabird–tick interactions. Predation may also be a significant factor affecting ticks during this part of the life cycle. Indeed, although little work has focused on this aspect, some studies suggest that predation may regulate tick population dynamics and may enable seabirds to continue to reproduce at permanent nests and colonies by preventing the build-up of massive infestation levels (Duffy 1991, Samish and Rehacek 1999).



**FIG. 1.** Ecological features of the seabird–tick interaction. Note that the timing and duration of the different periods in the life cycles vary among species. (1) Unengorged tick seeks a host. (2) Parasitism of the seabird host (the blood meal may last several days). (3) Engorged tick drops off the host. (4) Overwintering of ticks in the area around the nest habitat.

Ticks associated with seabirds belong to two different families: the Ixodidae or hard ticks, and the Argasidae or soft ticks. These two groups show marked differences in their feeding behavior and life cycle pattern, differences that can greatly affect the dynamics of tick populations and their role as disease vectors (Randolph 1998). Hard ticks have a single nymphal stage in contrast to several nymphal instars for soft ticks. As a consequence, hard ticks can exploit up to three different host individuals during their life cycle, whereas the number of hosts can potentially be much higher for soft ticks. The reptilement time lasts several days for hard ticks, whereas it can be less than 1 h for soft ticks. Thus, under the same external conditions, the number of complete generations within a year can therefore be significantly higher for soft ticks. Finally, hard tick females typically oviposit in one single bout, whereas soft tick females have several ovipositions in different places, one after each blood meal.

Most seabird tick species of both families were described during the first part of the 20th century based on the interests of the scientist and site accessibility. As a consequence, observations are largely fragmentary and opportunistic. Host ranges and geographic distributions must be therefore interpreted with caution. Moreover, synonymies are common and may therefore lead to confusion about true diversity. The species names used in this article are based on the publications of Barker and Murrell (2004) and Guglielmo et al. (2009).

#### Hard seabird ticks

To date, 17 hard tick species are associated with seabirds (Table 1). Almost all belong to the genus *Ixodes*, with the exception of *Amblyomma loculosum*, which is the only representative of this genus associated with seabirds. Among hard

TABLE 1. HARD TICKS ASSOCIATED WITH SEABIRDS

Species	Observations	Seabird host species	Pathogens <sup>a</sup>	References (see Appendix)
<i>Ixodes amersoni</i> Kohls 1966	Australian (Central Pacific Ocean)	<i>Diomedea nigripes</i> , <i>Fregata minor</i> , <i>Gygis alba</i> , <i>Anous stolidus</i> , <i>Sula sula</i>	Unknown	1, 2
<i>Ixodes auritulus</i> <sup>b</sup> Neumann 1904	Australian and Antarctic (Argentina, Antarctic Ocean, South Atlantic Ocean, New Zealand)	<i>Diomedea chlororhynchus</i> , <i>D. exulans</i> , <i>Pelecanoides magellani</i> , <i>P. urinatrix</i> , <i>Pachyptila desolata</i> , <i>P. turtur</i> , <i>P. crassirostris</i> , <i>Puffinus griseus</i> , <i>P. gravis</i> , <i>Aptenodytes patagonica</i> , <i>Catharacta lombergi</i>	Unknown on seabirds but <i>Borrelia burgdorferi</i> is known from Passeriformes	3, 4, 5, 6, 7, 8
<i>I. auritulus</i> <i>zealandicus</i> <sup>b</sup> Dumbleton 1961	Australian (New Zealand)	<i>Fregata tropica</i> , <i>Larus dominicanus</i> , <i>Pelecanoides urinatrix</i> , <i>Diomedea melanophrys</i> , <i>D. exulans</i> , <i>Pachyptila turtur</i> , <i>P. crassirostris</i> , <i>P. vittata</i> , <i>Puffinus griseus</i> , <i>P. huttoni</i> , <i>P. carneipes</i> , <i>P. bulleri</i> , <i>Procellaria cinerea</i> , <i>Eudyptes robustus</i> , <i>Eudyptula minor</i> , <i>Megadyptes antipodes</i> , <i>Sterna vittata bethunei</i>	Unknown	9, 104, 105
<i>Ixodes diomedae</i> Arthur 1958	Paleotropical (Tristan da Cunha)	<i>Diomedea chlororhynchus</i>	Unknown	10
<i>Ixodes eudyptidis</i> Maskeil 1885	Australian (Australia, New Zealand)	<i>Larus novaehollandiae</i> , <i>L. dominicanus</i> , <i>Phalacrocorax carbo</i> , <i>P. punctatus</i> , <i>Pterodroma cooki</i> , <i>Eudyptula minor</i> , <i>E. albosignata</i> , <i>Eudyptes pachyrhynchus</i> , <i>Chlidonias albobristatus</i> , <i>Sula bassana</i>	S-TBFV: Saumarez Reef virus	6, 9, 12, 13, 14, 15, 16
<i>Ixodes jacksoni</i> Hoogstradi 1967	Australian (New Zealand)	<i>Phalacrocorax punctatus</i>	Unknown	17, 18
<i>Ixodes kerguelensis</i> André & Colas-Belcour 1942	Australian and Antarctic (Antarctic Ocean, Australia, New Zealand)	<i>Diomedea exulans</i> , <i>D. chlororhynchus</i> , <i>Phoebastria fusca</i> , <i>Pterodroma brevirostris</i> , <i>P. mollis</i> , <i>Pachyptila desolata</i> , <i>Puffinus tenuirostris</i> , <i>P. carneipes</i> , <i>P. griseus</i> , <i>Procellaria aequinoctialis</i> , <i>Pelecanoides urinatrix</i> , <i>P. georgicus</i>	Unknown	4, 11, 18, 19, 20, 21
<i>Ixodes kohlsi</i> Arthur 1955	Australian (Australia)	<i>Phalacrocorax fuscescens</i> , <i>Puffinus tenuirostris</i> , <i>Eudyptula minor</i> , <i>Sterna neretis</i> , <i>Sula bassana</i>	Unknown	14, 22
<i>Ixodes laysanensis</i> Wilson 1964	Australian (Central Pacific Ocean)	<i>Diomedea immutabilis</i> , <i>D. nigripes</i> , <i>Fregata minor</i> , <i>Anous stolidus</i> , <i>Phaethon rubricauda</i> , <i>Puffinus pacificus</i> , <i>Sterna fuscata</i> , <i>Sula sula</i> , <i>S. dactylatra</i>	Unknown	2, 23, 24

(continued)

TABLE 1. (CONTINUED)

Species	Observations	Seabird host species	Pathogens <sup>a</sup>	References (see Appendix)
<i>Ixodes murreleti</i> Cooley & Kohls 1945	Nearctic (Mexico)	1 <i>Synthliboramphus hypoleucus</i>	Unknown	25
<i>Ixodes percaratus</i> Neumann 1906	Paleotropical (South Africa, South Atlantic Ocean)	2 <i>Diomedea chlororhynchus</i> , <i>Eudyptula minor</i>	Unknown	26, 27
<i>Ixodes philipi</i> Keirans & Kohls 1970	East Palearctic (Japan)	2 <i>Oceanodroma castro</i> , <i>Calonectris leucomelas</i>	Unknown	28, 29, 30
<i>Ixodes rothschildi</i> Nuttall & Warburton 1911	West Palearctic (British and French coasts)	<10 <i>Alca torda</i> , <i>Fratercula arctica</i> , <i>Larus argentatus</i> , <i>Phalacrocorax aristotelis</i> , <i>Fulmarus glacialis</i> , <i>Puffinus puffinus</i>	UUK: Great Saltee Island virus	31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41
<i>Ixodes signatus</i> Birula 1895	East Palearctic and Nearctic (North Pacific Ocean)	3 <i>Larus crassirostris</i> , <i>Phalacrocorax pelagicus</i> , <i>P. penicillatus</i>	KEM: Kenai virus; SAK: Kachemak Bay, Okhotskiy, Avalon and Sakhalin viruses, UUK: Zaliv Terpeniya	42, 43, 44, 45, 46, 47, 48
<i>Ixodes umicavatus</i> Neumann 1908	West Palearctic (British and French coasts, Sweden, Crimea)	2 <i>Phalacrocorax aristotelis</i> , <i>P. carbo</i>	Unknown	32, 34, 49, 50, 51, 52, 53, 54, 55
<i>Ixodes uriae</i> White 1952	Holarctic, Antarctic, Australian, Neotropical, Paletropical (Circumpolar distribution)	>60 Alcidae, Diomedidae, Hydrobatidae, Laridae, Pelecanoididae, Phalacrocoracidae, Procellariidae, Spheniscidae, Stercorariidae, Sulidae	Viruses from KEM (mainly Great Island viruses complex), SAK, HUG, UUK, S-TBFV, and NG serogroups, <i>Rickettsia</i> -like organism, <i>Borrelia</i> spp. ( <i>B. garinii</i> , <i>B. burgdorferi</i> s.s., <i>B. lusitanae</i> )	56, 57, 58, 59, 60, 61, 62, 63, 106
<i>Amblyomma loculosum</i> <sup>b</sup> Neumann 1907	Australian, Indian Ocean, Paleotropical (Seychelles, Madagascar, Indian Ocean, Australia)	>10 <i>Fregata ariel</i> , <i>F. minor</i> , <i>Anous stolidus</i> , <i>A. minutus</i> , <i>Phaethon lepturus</i> , <i>Puffinus pacificus</i> , <i>P. puffinus</i> , <i>Sterna fuscata</i> , <i>S. dougalli</i> , <i>Sula sula</i> , <i>S. leucogaster</i> , <i>S. dactylatra</i>	HUG: Soldado virus, NG: Aride virus	64, 65, 66, 67, 68, 69

Observations refer to the biogeographical zone where the tick was recorded. For the host range, we provide a complete list of all recorded host species, except for *I. uriae*, for which only family names are included. The references associated with host and pathogen observations can be found in the Appendix at the end of this article.

<sup>a</sup>The acronyms for viral groups are as follows: S-TBFV, seabird tick-borne flaviviruses; KEM, Kemerovo; SAK, Sakhalin; HUG, Hughes; UUK, Uukuniemi; NYM, Nyamanini; QRF, Quarantini; UPO, Uppolu; NG, nongrouped viruses.

<sup>b</sup>Occasionally found on nonseabird species.

ticks, three species are not considered as truly specific to seabirds because of their apparent extended host range: *Ixodes auritulus* and its sub-species *I. auritulus zealandicus*, which have also been recorded from land birds, and *A. loculosum*, which is also known to exploit goats, lizards, and humans although these hosts are incidental and this only occurs on seabird islands (Table 1). Other tick species have been recorded from seabird colonies but are considered here as accidental records and are thus not included in Table 1. For example, *Haemaphysalis punctata* and *Hyalomma marginatum*, which are usually parasites of mammals or land birds, have been recorded on *Larus* and *Sterna* species (Andreev and Shcherbina 1975, Hubálek et al. 1982, Guiguen et al. 1986). These ticks transmit numerous pathogens of medical and veterinary interest (e.g., tick-borne spotted typhus, Q fever, babesiosis, theileriosis, and Crimean-Congo hemorrhagic fever virus). Therefore, although their importance for seabirds is minor, their presence on these hosts may favor long-distance dispersal events of these ticks and their pathogens (see below).

Hard seabird ticks fed on all the avian families considered here, except pelicans for which no observations have been recorded (Fig. 2). At least two hard tick species have been found in each family with the highest tick species richness for petrels and shearwaters (Procellariidae), which are parasitized by 10 different hard tick species. The number of ticks species recorded in each seabird family is positively correlated with the specific richness of the family (Pearson's correlation:  $r = 0.77$ ,  $p = 0.00132$ ). This correlation means that, after correcting for species richness, the different seabird families seem to harbor the same approximate tick species diversity. However, it is difficult to generalize about tick species richness among seabird families at this point. Sampling effort for different seabird species/family is difficult to quantify, particularly given that publications are biased to cases when tick

species are found, and this effort can be correlated with the number of parasite species recorded (Hughes and Page 2007).

In relation to the observed host range, seabird colonies in higher latitudes tend to be infested by hard ticks (Fig. 3). The main example is *Ixodes uriae*, which is the most important species in terms of its geographical and host species range. *I. uriae* is the only tick recorded both in the Northern and Southern hemispheres, and more than 60 species, from 10 different families, are considered as potential hosts (Table 1; Fig. 3). Other hard tick species are found in more restricted areas (i.e., *I. eudyptidis* around the Australian region, *Ixodes Philipi* in Japan, and *Ixodes rothschildi* along the British and French coasts; Fig. 3). Interesting exceptions to the polar distribution of hard seabird ticks are *Ixodes laysanensis* and *Ixodes amersoni* described in the Hawaiian Islands, and *A. loculosum*, which parasitizes seabirds across the Indian and Pacific Oceans. For some species, the true extent of their geographical distribution is unknown because the species description was based on a single observation (i.e., *I. diomedea* on Nightingale Island, Tristan Da Cunha; *Ixodes kohlsi* in New South Wales, Australia; *I. murreleti* in Los Coronados Island, Mexico).

### Soft seabird ticks

There are currently 12 described species of soft tick associated specifically with seabirds, all belonging to the *Argas* and *Carios* genera (Table 2). Three other species have been recorded, but we consider these occurrences as accidental or a result of a misidentification. For example, *A. cooleyi* (usually an ectoparasite of cliff swallows) was collected at Mono Lake, California, from *Larus californicus* nests. However, only adult ticks were used for identification and it is well known that the best characters for separating species of *Argas* come from larvae (Sonenshine et al. 1962). Later, observations of larvae from the same island described the new species *A. monolakensis* and suggested that the presence of *A. cooleyi* could have been a misidentification (Schwan et al. 1992). Likewise, *A. robertsi* and *A. arboreus* usually fed on Ciconiiforms, but have also been recorded on cormorants (Hoogstraal et al. 1979).

Soft seabird ticks have been described from 12 different seabird families (Fig. 2); no observations have been recorded from diving-petrels and skuas. As for hard ticks, there is a significant correlation among seabird species richness within a family and the diversity of ticks exploiting that family (Pearson's correlation:  $r = 0.65$ ,  $p = 0.01135$ ); tropicbirds are parasitized by a single soft tick species (*C. capensis*), whereas gulls, petrels, and shearwaters harbor the highest soft tick species richness compared to other families (respectively eight and seven different ticks). Different patterns of tick species richness among seabird families could be linked to differences in their ecology. For example, the high species richness of soft and hard ticks observed in Procellariidae could be explained by the fact that these birds are mainly burrow-nesting species with long periods of nest-site occupancy. They may therefore represent attractive hosts because of the duration of feeding opportunities for ticks and the humid and relatively warm conditions within the burrow. Other possible factors that could intervene in this pattern include their wide geographic distributions, large body sizes, and high longevity. However, these traits vary among species; thus, a fuller understanding of patterns of tick diversity would require a more indepth

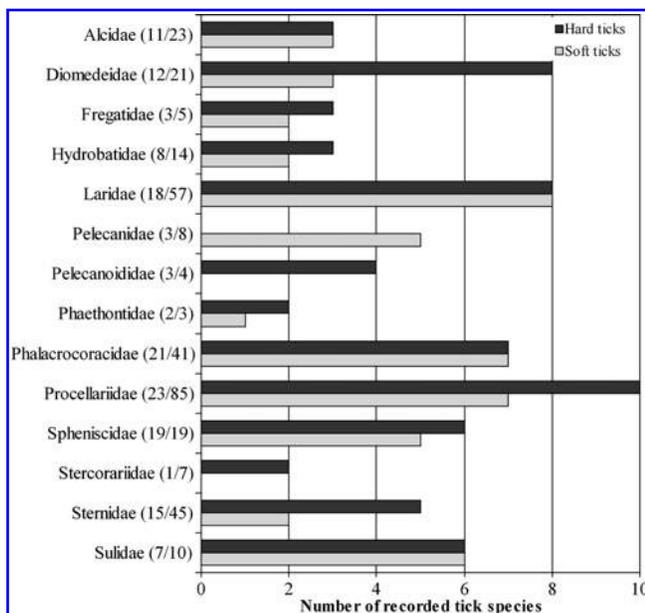


FIG. 2. Tick species richness among seabird families. The ratio in parentheses refers to the number of seabird species found parasitized by ticks (hard and soft) over the total number of species in the family.

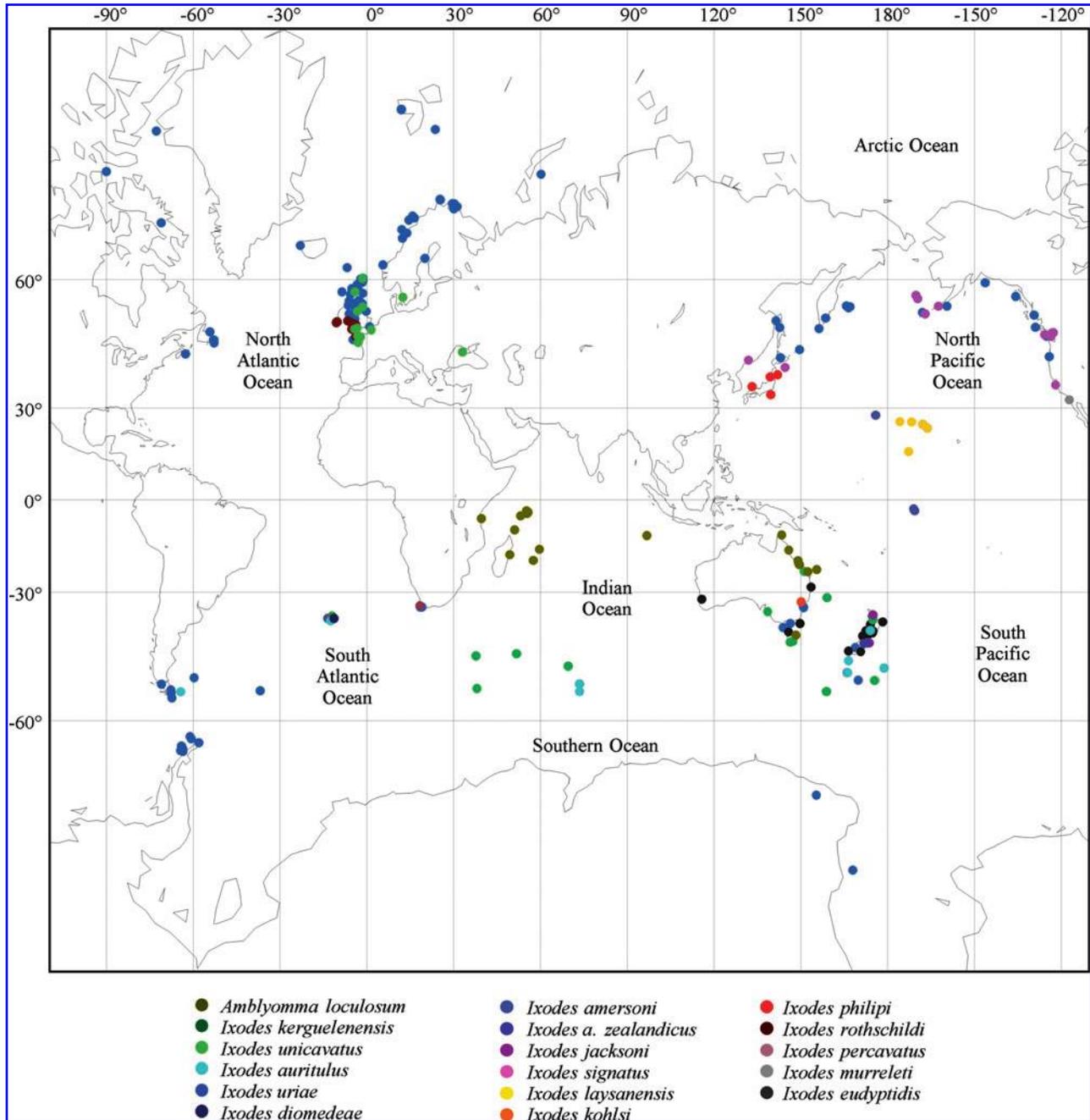


FIG. 3. Distribution of hard ticks associated with seabirds.

examination of these factors, where differential sampling effort among seabird families could be controlled for.

Contrary to hard ticks, soft ticks typically infest seabird colonies in the tropics and subtropics (Fig. 4). *Carios capensis* is the most widespread species. Its host range includes more than 35 different seabird species (from the 12 families) from across the Pacific, Atlantic, and Indian oceans. This species is also found in Paleotropical, Neotropical, and Australian regions (Fig. 4). *C. maritimus* also parasitizes a wide range of seabird species, but its distribution is localized to European coasts (Fig. 4 and Table 2). As for hard ticks, several soft tick species have been described from a single observation; *A. cucumerinus* was described in Peru from cliffs used by

pelicans (Clifford et al. 1978) and *C. cheikhi* was identified from terns in Mauritania (Vermeil et al. 1997) (Table 2).

#### Habitat versus host specificity

An alternate off-host/on-host life cycle requires ticks to deal with very diverse natural selection pressures from the two habitat types (Needham and Teel 1991). During the off-host phase, which generally represents 90% of the life cycle, seabird ticks have to face the abiotic conditions of the nest area habitat of their host. It is well known that ticks are sensitive to local climatic conditions (e.g., temperature and relative humidity) (Sonenshine 1991, Gern et al. 2008). On the basis of

TABLE 2. SOFT TICKS ASSOCIATED WITH SEABIRDS

<i>Species</i>	<i>Observations</i>	<i>Seabird host species</i>	<i>Pathogens</i>	<i>References (see Appendix)</i>
<i>Argas cucumerinus</i> Neumann 1901	Neotropical (Peru)	1 <i>Pelecanus thagus</i>	Unknown	70, 71
<i>Argas macrostigmatus</i> Filippova 1961	Palaearctic (Corsica, Crimea)	1 <i>Phalacrocorax aristotelis</i>	Unknown	59, 72
<i>Argas monolakensis</i> Schwan 1992	Neotropical (California)	1 <i>Larus californicus</i>	KEM: Mono Lake virus, <i>Coxiella</i> sp.	73, 74
<i>Carios amblus</i> Chamberlain 1920	Neotropical (Peru, Chile)	<10 <i>Larosterna inca</i> , <i>Pelecanus thagus</i> , <i>Phalacrocorax bougainvilli</i> , <i>P. gaimardi</i> , <i>Spheniscus humboldti</i> , <i>Sula variegata</i> , <i>S. nebouxii</i> , <i>Morus capensis</i>	KEM: Huacho virus, HUG: Punta salinas virus	75, 76, 77, 78, 79, 80, 81, 82
<i>Carios capensis</i> Neumann 1901	Nearctic, Palaearctic, Neotropical, Paleotropical, Australian, Indian ocean (Globally distributed around equator line)	>35 Alcidae, Diomedidae, Fregatidae, Hydrobatidae, Laridae, Pelecanidae, Phaethontidae, Phalacrocoracidae, Procellariidae, Spheniscidae, Sternidae, Sulidae	HUG: Hughes, Soldado, Farallon viruses, UPO: Upolu and Aransas Bay viruses, S-TBFV: Saumarez Reef virus, NYM: Midway and Horita viruses, QRF: Johnson Atoll and Abal viruses, <i>Rickettsia</i> spp., <i>Coxiella</i> sp., <i>Borrelia lonestari</i>	2, 55, 56, 57, 58, 59, 62, 70, 83, 84, 85
<i>Carios cheikhi</i> Vermeil, Marjolet & Vermeil 1997	West Palaetropical (Mauritania)	1 <i>Sterna</i> sp.	Unknown	86
<i>Carios denmarki</i> Kohls, Sonenshine & Clifford 1965	Nearctic, Neotropical and Australian (Hawaii islands, Peru, Mexico, Jamaica, Martinique, Florida, Australia, New Zealand)	>10 <i>Uria aalge</i> , <i>Diomedea irrorata</i> , <i>Larus occidentalis</i> , <i>Sterna fuscata</i> , <i>Anous stolidus</i> , <i>Pelecanus occidentalis</i> , <i>Phalacrocorax penicillatus</i> , <i>Puffinus lermieri</i> , <i>P. pacificus</i> , <i>Sula dactylatra</i> , <i>S. leucogaster</i>	HUG: Hughes, Soldado, Farallon-like, Frazer Point and Raza viruses, NYM: Midway virus, QRF: Johnston Atoll virus	2, 56, 87, 88, 89, 90, 91, 92, 93, 94
<i>Carios maritimus</i> Vermeil & Marquet 1967	Palaearctic (British islands, France, Spain, Portugal, Morocco)	>35 Alcidae, Fregatidae, Laridae, Pelecanidae, Phalacrocoracidae, Procellariidae, Spheniscidae, Sternidae, Sulidae	KEM: Essaouira, Kala Iris, Baku and Moellez viruses, HUG: Soldado, Great Saltee, Pettico Wick and Puffin Island viruses, S-TBFV: Meaban virus, NG: Caspian virus, West Nile virus, <i>Rickettsia</i> - like organism	55, 57, 59, 62, 95, 96, 97
<i>Carios muesebecki</i> Hoogstraal 1969	Palaetropical (Arabian sea)	<10 <i>Sterna bengalensis</i> , <i>S. repressa</i> , <i>S. anaethetus</i> , <i>S. bergii</i> , <i>Phalacrocorax nigrogularis</i> , <i>Sula dactylatra</i>	HUG: Zirqa virus	98, 99, 100
<i>Carios sawaii</i> Kitaoka & Suzuki 1973	East Palaearctic (Japan)	2 <i>Oceanodroma monorhis</i> , <i>Calonectris leucomelas</i>	<i>Rickettsia</i> sp., <i>Borrelia</i> sp.	83, 101, 102

(continued)

TABLE 2. (CONTINUED)

Species	Observations	Seabird host species	Pathogens	References (see Appendix)
<i>Carios spheniscus</i> Hoogstraal, Wassef, Hays & Keirans 1985	Neotropical (Peru)	1 <i>Spheniscus humboldti</i>	Unknown	81
<i>Carios yunkerii</i> Kierans, Clifford & Hoogstraal 1984	Neotropical (Galapagos)	<10 <i>Diomedea irrorata</i> , <i>Sterna lunata</i> , <i>Phalacrocorax harrisi</i> , <i>Spheniscus mendiculus</i> , <i>Sula dactylatra</i> , <i>S. nebouxii</i>	Unknown	78, 103

Observations refer to the biogeographical zone where the tick was recorded. For the host range, we provide a complete list of all recorded host species, except for *C. capensis* and *C. maritimus*, for which only family names are included. The references associated with host and pathogen observations can be found in the Appendix at the end of this article. See Table 1 for viral group abbreviations.

their geographical distributions, hard and soft seabird ticks have evolved adaptations to different environments and thus different types of habitat specificities. Hard ticks are more resistant to cold climates and require a reasonable moisture level, whereas soft ticks are restricted to warmer and often drier environments (Nuttall 1911). For example, *I. uriae* resists desiccation in its off-host phase by selecting moisture-rich microhabitats and by forming aggregations (Benoit et al. 2007).

Contrary to the off-host phase, the on-host phase is relatively short in time but can be intense in nature. The tick–host interface is characterized by intimate and complex interactions that involve both specific and nonspecific immune pathways and a rich assembly of biologically active molecules, adaptations which have likely played a key role in the evolution of tick–host specificity (Brossard and Wikel 2004, Francischetti et al. 2009). As we have seen above, seabird ticks may vary widely in their host use (Tables 1 and 2). The majority are associated with several host species, suggesting that most seabird ticks are host generalists. However, genetic studies have shown that host specialization may arise in *a priori* generalist tick species. This is the case for *I. uriae*, for which host-associated races have been found in both the Northern and Southern hemispheres (McCoy et al. 2001, 2005b, Kempf et al. 2009). However, given the fragmentary nature of host records and a general lack of genetic studies on these species, it is difficult to characterize host specificity in this group at this time.

#### Tick dispersal

The exploitation of seabirds imposes certain constraints on their parasites. In particular, many seabirds are pelagic, meaning that they are only on land a few months per year during the breeding season. As it seems unlikely that ticks can remain on their hosts for the long period at sea, tick dispersal among isolated seabird colonies can be spatially limited and largely restricted to host movements during the breeding season (McCoy et al. 2003). However, certain antiparasite strategies adopted by seabirds may be beneficial for ticks in the long term. That is, infested birds that desert their breeding colony to avoid tick parasitism may move further than uninfested breeders, and thus may favor tick dispersal by carrying infesting ticks to new locations. Likewise, immature birds or failed breeders may visit other colonies to prospect for future reproduction, and may be particularly important

for this type of dispersal (Danchin 1992). As the feeding time of soft ticks is shorter than that of hard ticks, dispersal of soft ticks via the host may be more limited and may occur at only very local spatial scales (Heath 1987).

#### Effects of ticks on seabird populations

Ticks can have both direct and indirect effects on their seabird hosts. Heavy infestation by ticks may lead to abnormal mortality or to delays in the nestling development (e.g., Ramos et al. 2001, 2005, Monticelli et al. 2008). Field observations suggest a direct relationship between seabird death and heavy tick infestations, even for adult birds (Gauthier-Clerc et al. 1998). At sublethal levels, ticks may deplete resources crucial for normal postnatal development, resulting in reduced rates of wing growth and altered fledgling periods (Morbey 1996). However, this effect is likely resource dependent (McCoy et al. 2002, Mangin et al. 2003). Localized tick infestations can cause serious lesions to seabirds with indirect consequences on seabird predation and reproduction (Feare and Gill 1997). For instance, some tick species tend to attach mainly to legs and feet (e.g., *A. loculosum* and *C. capensis* in Bird Island, Seychelles), causing irritations and rendering the birds more wary and more likely to leave the nest when disturbed. This could interfere with incubation and thus affect hatchability and cause egg loss via predation. Eggert and Jodice (2008) found a positive relationship between *C. capensis* infestation and both growth rates and hatching success of brown pelican nestlings, in South Carolina. These results suggest that the consistent exposure of nestlings to ticks can induce behavioral and/or physiological modifications that limit their negative effects (e.g., trade-off in energy allocation and increased begging rates).

Via their effects at the individual level, ticks are likely an important element in the ecology of colonial seabirds and may explain some part of their population dynamics (Duffy 1983, Proctor and Owens 2000). High densities of ticks can directly affect the breeding success of seabirds by causing nest desertions, as seen in the case of massive infestations of *C. capensis* in colonies of sooty terns (*Sterna fuscata*), guanay cormorants (*Phalacrocorax bougainvillii*), peruvian boobies (*Sula variegata*), and brown pelicans (*Pelecanus occidentalis*) (Feare 1976, King et al. 1977a, 1977b, Duffy 1983). Even in less extreme cases, seabirds—particularly young birds—may disperse from heavily infested colonies, thereby altering local

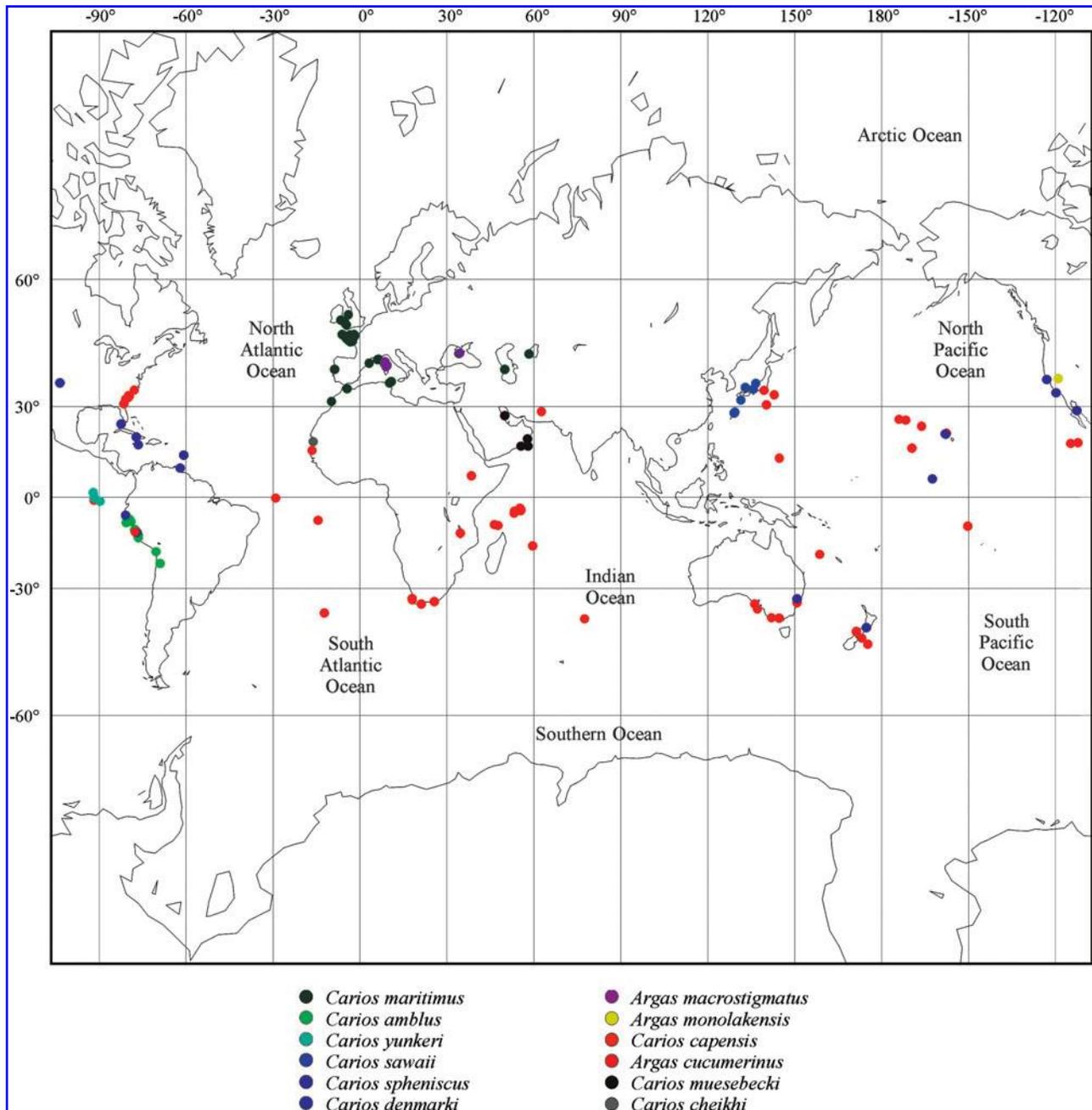


FIG. 4. Distribution of soft ticks associated with seabirds.

return and recruitment rates (Boulinier et al. 1996, 2001). As seabirds are long-lived and site faithful, these changes will have long-term consequences for the dynamics of these populations and the large scale functioning of seabird metapopulations (Boulinier et al. 2001).

Heavy infestation of ticks may also result in habitat modifications, with potential consequences for the dynamics of seabird populations. For example, on Bird Island, Seychelles, massive tick infestations seem to be linked with repeated seabird colony desertions (Feare 1976), which can result in the subsequent colonization and development of new vegetation types (e.g., woodland) (Gillham 1961, Norton et al. 1997). Such habitat changes may then have long-term consequences for the birds by rendering the habitat unsuitable for future

recolonization. However, heavy infestations of ticks do not appear to be self-sustaining, and the factors involved in the periodicity of these outbreaks remain unknown. Future studies on these factors might enable us to better understand the causes of tick outbreaks and the consequences for the seabird community.

#### Pathogens Associated with Seabird Ticks

##### Diversity

Seabird ticks are involved in the circulation of a wide diversity of pathogens, including diverse bacteria and viruses (see Tables 1 and 2). Among these, viruses have been the most frequently recorded. In contrast, parasites such as *Babesia*

species have never been isolated from seabird ticks, although their presence has been reported in the blood of different seabird species (Peirce 2000, Yabsley et al. 2009). In general, the abundance of certain pathogens may largely reflect the degree of sampling effort, rather than true patterns of species diversity and abundance, and this is particularly true for viruses (Labuda and Nuttall 2004). As a consequence, our current information on pathogen diversity should be interpreted with caution.

During recent years, much interest has focused on the Lyme borreliosis bacteria complex, *Borrelia burgdorferi* sensu lato. This is known to circulate in *I. uriae* and has been found in *C. capensis* from brown pelicans on the east coast of North America (Olsén et al. 1993, Reeves et al. 2006, Duneau et al. 2008). More recently, Takano et al. (2009) found a relapsing fever spirochete, closely related to *Borrelia turicatae*, in the Japanese tick *C. sawaii*. Among other bacteria, *Rickettsia* agents are occasionally associated with seabird ticks and have been isolated from *I. uriae*, *C. maritimus*, *C. capensis*, and *C. sawaii* (Chastel et al. 1993, Kawabata et al. 2006, Reeves et al. 2006). Recently, a *Coxiella* sp., genetically close to the species responsible for Q fever, has also been isolated in the soft ticks *C. capensis* and *A. monolakensis* (Reeves et al. 2006, Reeves 2008).

About 60 viruses or variants have been isolated from seabird ticks (reviewed by Clifford 1979, Chastel 1980, Nuttall 1984). In some cases, it has been shown that these viruses are transmitted to seabirds (e.g., Nunn et al. 2006a). Virus names often correspond to the location from which the ticks were collected, resulting in a growing number of viral names and some confusion about the distinctness of these different viruses. The majority of these viruses are classified into eight serogroups: Sakhlin and Hughes (Bunyaviridae: Nairovirus), Uukuniemi (Bunyaviridae: Phlebovirus), Upolu (Bunyaviridae: not yet assigned to an order), Kemerovo (Reoviridae: Orbivirus), Quarantil [Orthomyxoviridae: Quarjavirus; classification recently proposed by Presti et al. (2009)], Nyamanini [Nyavirus; classification proposed by Mihindukulasuriya et al. (2009)], and the seabird tick-borne flaviviruses, namely Saumarez reef, Meaban, Gadgets Gully, and Tyuleniy viruses (Flaviviridae: Flavivirus). Other viruses remain unclassified.

Among these viruses, Soldado virus (Hughes) is the most widely distributed. It has been found in all intertropical and warm temperate regions, except the Far East. Soldado virus is mainly associated with the soft tick *C. capensis*, and to a lesser extent with *C. maritimus*, *C. denmarki*, and the hard tick *A. loculosum*. Similarly, viruses of the Great Island complex (Kemerovo) are the most important viruses harbored by hard ticks. They have been isolated from across the Northern hemisphere and from one site in Australia (Macquarie Island), reflecting the bipolar distribution of *I. uriae*. This tick is the most well-studied species and the majority of hard tick viruses are therefore associated with this tick (Table 1) (Doherty et al. 1975, Nuttall et al. 1981, 1984). Other tick species have been found to harbor viruses, but to a lesser extent. It is the case for the soft ticks *C. amblus* in Peru and Chile, *A. monolakensis* in California, the Arabian tick *C. muesebecki*, and the hard ticks *I. rothschildi*, *I. signatus*, and *I. eudyptidis* (Tables 1 and 2).

### Specificity of pathogens

The type of virus infecting ticks in a seabird colony appears to vary according to the local tick species (Nuttall 1984,

Nuttall et al. 1984). Thus, viruses of the Sakhlin and Uukuniemi serogroups have only been isolated from hard ticks, whereas the Hughes, Quarantil, Nyamanini, and Upolu groups have been essentially found in soft ticks (with the exception of the Soldado virus, which has also been isolated from *A. loculosum*; see above). When the geographical distribution of soft and hard ticks overlap, different types of viruses can be found sympatrically, but virus–tick specificity seems to be maintained. For instance, on Great Saltee Island, Ireland, seabirds host both hard (*I. uriae*, *I. rothschildi* and *I. unicavatus*) and soft ticks (*C. maritimus*). In this region, Nuttall (1984) showed that *I. uriae* and *I. rothschildi* harbor only Uukuniemi serogroup viruses, whereas only Hughes serogroup viruses are present in *C. maritimus*. In contrast, viruses of the Kemerovo group are found in both *I. uriae* and *C. maritimus*, suggesting that virus–tick specificity varies among viral serogroups.

In many cases, it is difficult to assess the respective role of geography and tick specificity in pathogen divergence. For example, the Soldado virus is composed of numerous antigenic variants with a clear separation between the strains isolated from *C. capensis* and *C. denmarki* in the New World (Trinidad, Texas, and Hawaii) and from *C. maritimus* sampled in the Old World (Ireland, France, and Morocco) (Chastel et al. 1983). The observed relationship may be due to the geographic isolation of seabird hosts and/or tick vectors (i.e., viruses never encounter other tick species), or to interspecific differences in tick competence (i.e., tick's ability to support viral replication) (Nuttall 1984). Further studies are now required to address such issues. For example, Soldado viral strains have been isolated from both *A. loculosum* and *C. capensis* in the Seychelles (Hoogstraal and Feare 1984). Are these strains identical or have they specifically adapted to each of the tick species? With only limited information on the viral strains, we cannot yet answer this question.

Pathogen differentiation may be due to adaptation to a particular seabird host and specificity in the tick–host interface. Variable patterns of tick infestation among different seabird species will alter exposure to pathogens, and different hosts may vary in their response to exposure (i.e., seroprevalence: Gasparini et al. 2001, Nunn et al. 2006a, 2006b). Moreover, via cascading effects, tick–host specificity may affect rates of pathogen transmission and replication among host types. For example, *Borrelia* prevalence in *I. uriae* varies among sympatric seabird hosts and different host species show also different antibody responses to the bacterium (Duneau et al. 2008, Staszewski et al. 2008). Nunn et al. (2006a) also found that susceptibility to infection can vary among sympatric seabird species: only guillemots had neutralizing antibodies against Great Island virus, even though both guillemots and kittiwakes were infested by infected ticks.

### Persistence of infection

Repeated isolation of pathogens from ticks collected in seabird colonies indicates that seabird populations can be persistent foci for pathogen circulation (e.g., Nuttall et al. 1981). Because of their longevity, ticks can carry pathogens over prolonged periods of time and may therefore not only be vectors, but also act as reservoir hosts. Pathogen persistence in ticks depends on their ability to survive the diapause stage (Nuttall 1984). For example, viruses have been known to remain active in ticks for more than 2 years (Lvov et al. 1979).

Survival strategies of pathogens also include trans-stadial and trans-ovarial transmission. The isolation of orbi- and bunyaviruses from adult male *I. uriae* indicates that trans-stadial transmission likely occurs in this species since males do not feed in the adult stage (Nuttall et al. 1981). Likewise, observations of unfed larvae of *C. capensis*, infected with *Rickettsia* and *Coxiella*, suggest that trans-ovarial transmission readily occurs (Reeves et al. 2006). However, the presence and frequency of trans-ovarial and trans-stadial transmission may vary widely among pathogens and tick species and remain untested in many systems.

The reintroduction of pathogens through the movement of infectious vectors and/or seabird hosts may also help to maintain the circulation of pathogens. Gylfe et al. (2000) showed that migratory passerines are able to carry *Borrelia* spirochetes as latent infections for several months, and that infections could be reactivated and transmitted to ticks as a result of migratory restlessness (i.e., agitation and stress related to the approach of the migration period). This phenomenon may also occur in seabirds, leading to an annual boom in pathogen transmission to ticks at the start of the breeding season of birds and the maintenance of high prevalence within colonies.

#### *Pathogen dispersal*

Seabirds generally form isolated breeding groups within colonies; thus, infections can remain localized to these patches. However, seabird colonies in widely separated geographical locations have been shown to harbor related pathogens, suggesting that seabirds transport and disperse pathogens from one colony to another (Clifford 1979, Moss and Nuttall 1984, Nuttall 1984). In the case of *Borrelia* spp., the same pathogenic species (*B. garinii*) can be found in both the Southern and Northern hemispheres, raising the question of the role of migratory seabirds in the transportation of pathogens over large distances (Olsén et al. 1995a, 1995b). The details and dynamics of these movements are poorly known but may become more accessible with the advent of new tracking technologies and the development of intrinsic markers for birds (Ramos et al. 2009). Finally, indirect studies on tick and pathogen population structure may also improve our knowledge on seabird movements. For example, genetic studies on *I. uriae* population structure have led to a better understanding of kittiwake movements in the Atlantic Ocean during the breeding season (McCoy et al. 2005a).

#### *Pathogenic effects on seabirds and ticks*

The effects of tick-borne infections on the health of seabird populations are poorly understood. Despite direct detection of pathogens in seabird tissues, no pathologic studies have yet tested the direct effects of pathogens on seabird fitness (Main et al. 1976, Nuttall et al. 1981, Gylfe et al. 1999). In the field, it is difficult to determine whether behavioral and pathological disorders are the result of tick infestation and/or of tick-borne infection (e.g., Converse et al. 1976a, Feare 1976). Some laboratory investigations have shown that seabird tick viruses are often of low virulence for standard laboratory animals and cell cultures, evoking only minimal antibody responses, and failing to induce viraemia in a wide variety of vertebrates (e.g., Clifford et al. 1971, Converse et al. 1976b, Chastel 1988, Chastel et al. 1993). However, field-based tests on the specific

seabird species involved are called for to address this question in a more direct way.

As seabirds are long-lived species, the presence and persistence of specific antibodies against pathogens may be a mechanism of ecological and epidemiological importance, by affecting the long-term dynamics of infection within seabird colonies. The maintenance of these antibodies can provide an advantage against future pathogen exposition and may allow females to confer an early and passive protection to their young via the transfer of maternal antibodies to the egg (Gasparini et al. 2001, Staszewski et al. 2007, Pearce-Duvet et al. 2009). Specific immunity may also lead to high selective pressure and account for the antigenic variation of pathogens (Nuttall et al. 1984). It may therefore play a key role in the virulence evolution of these pathogens, rendering them more dangerous to naive hosts (Mackinnon and Read 2004).

Although some studies suggest that vector-borne pathogens cause little if any damage to their vectors (e.g., Hogg and Hurd 1997), few studies, to date, have explicitly tested these effects. Pathogen infection can cause direct damage to vectors, resulting in a reduction in arthropod survival and/or fecundity (e.g., Niebylski et al. 1999, Watt and Walker 2000, Ross and Levin 2004, Gray and Bradley 2006). In other cases, changes in resource allocation, immunity costs, behavioral modifications, or alteration of gene expression may affect the biology of the vector (Ferguson and Read 2002, Ramamoorthi et al. 2005). Despite little direct evidence on this matter, such phenomena may have ecological and epidemiological significance by modifying seabird-tick interactions, tick population dynamics, and pathogen transmission rates.

#### **Implications for Human Health**

Few reports of seabird tick bites to humans have been documented. Most are likely unreported and may not have resulted in illness. However, when symptoms are observed, the relative roles of the tick bite and pathogen infection in the production of these symptoms are unknown (Johnson and Casals 1972, Varma et al. 1973, Converse et al. 1976a, Chastel et al. 1981). For instance, in Australia, St. George et al. (1977) reported human febrile illness after bites of *I. eudyptidis* infected with Saumarez Reef virus. In Peru, bites by *C. amblus*, infected with Punta Salinas virus, have been suggested to be responsible for a human illness similar to that caused by *C. muesebecki* infected with Zirqa virus in Arabia (Converse et al. 1976a). In Atlantic Islands, puffin hunters can be exposed to Lyme disease spirochetes from tick bites, and prevalence of *Borrelia* spp. in ticks can be high (Gylfe et al. 1999, Duneau et al. 2008). Nevertheless, seabird ticks are not major bridging vectors for human disease and the risk of direct pathogen transmission to humans remains limited to people in close contact with seabird colonies (e.g., hunters, ornithologists, and field biologists).

Even if seabird tick systems and their pathogens are relatively restricted to marine ecosystems, the existence of a link between marine and terrestrial tick systems, *a priori* considered as independent, has been raised. The accidental use of nonseabird host species by seabird ticks, or in turn the parasitism of seabirds by nonseabird ticks can have important consequences for the global epidemiology of tick-borne pathogens and their impact for human health. For example, evidence of recombination between marine and terrestrial

*Borrelia* strains suggests that Lyme disease bacteria are exchanged between these two enzootic cycles (Bunikis et al. 1996, Duneau et al. 2008). Areas where seabird ticks co-occur with other tick species that are important vectors of human and animal pathogens (e.g., *Ixodes ricinus*, *I. persulcatus* or *I. scapularis*) represent possible contact zones for pathogen transmission. However, it is still unclear where and how frequently contact occurs. More generally, increasing evidence suggests that we must change our current view about the circulation of tick-borne pathogens in avian systems and include a wider range of potential pathogens while surveying these systems to provide a more complete picture of the epidemiology of the associated diseases and the possible risk to humans.

### Conclusions and Future Directions

Ticks associated with seabirds are characterized by a large diversity of species and seabird hosts, and cover the entire globe. Nonetheless, many questions remain open. More detailed investigations are needed to validate single host–tick observations and to better define the geographic extent and host range of each species. Difficulties in the identification of closely related tick species are added to the fact that the number of available specimens is often low or from a single host individual. In this sense, the application of genetic tools should allow us to better understand the phylogeographic and taxonomic relationships among seabird tick species. Further, most publications on seabird ticks to date only provide descriptive data about the presence of ticks, whereas information on the prevalence and/or intensity of ticks is limited or simply absent. Field investigations therefore need to focus on obtaining samples that enable us to estimate these parameters and thus determine the importance of these species for seabird ecology and disease transmission.

As seabird ticks encounter both seabird hosts and the nesting habitat during their life cycle, ecological adaptations of ticks to both these environments may play an important role in tick ecology and evolution (Klompen et al. 1996). Recent studies have raised this issue and show that both host and habitat influence host specificity in *I. uriae* (e.g., McCoy et al. 2005b, Benoit et al. 2007). An increasing number of population genetic studies that take into account the host species should enable us to better evaluate the relative importance of these two factors in tick evolution.

As outlined above, tick infestation can have important consequences for the individual survival and breeding biology of the seabird host. In this way, the presence and abundance of ticks within a colony are of utmost importance for species of conservation concern. Long-term studies on seabird–tick interactions would provide a better understanding on the effects of tick infestation on seabird population dynamics, and should be integrated in the development of monitoring programs for seabird conservation.

Seabird ticks harbor a large diversity of pathogens; however, our knowledge on their associations, circulation, transmission, and effects remains limited. Combined with improvements in the detection and characterization of pathogens (e.g., genetic tools), systematic screening in natural populations is needed to better document pathogen diversity and prevalence, along with host–vector associations. Experimental approaches in the laboratory could also enable us to

explore these questions. Tick rearing represents an interesting tool to investigate vector competence, specificity, pathogen transmission (trans-stadial and trans-ovarial), and virulence. However, due to the high host specificity of many seabird ticks, finding an efficient system of artificial feeding in the laboratory may represent a significant challenge.

Current evidence suggests that several pathogens of medical and veterinary importance circulate in seabird populations and that seabird ticks may act as competent vectors (e.g., Lyme disease bacteria and *I. uriae*). However, our knowledge on the role of seabirds and their ticks in the circulation and maintenance of these tick-borne pathogens remains limited. Due to their high vagility, seabirds can potentially transport pathogens across large spatial scales. Moreover, the adaptation of some seabird species to urban habitats (e.g., gulls) may increase the potential for the exchange of these infectious agents between terrestrial and marine systems. However, before we can make clear predictions on the role of seabirds and their ticks on the global epidemiology of zoonotic diseases, further studies on the prevalence and distribution of seabird ticks and their pathogens will be required. When combined with accumulating knowledge on the movements of seabirds over large spatial scales (i.e., geolocator tracking tools) (Grémillet and Boulinier 2009), predictions on the spread of pathogens over space and time should become possible.

In recent years, there is growing concern on the effects of global climate change in the emergence of zoonotic diseases. Global climate change and human activities may indeed affect the circulation of pathogens by modifying the current distribution of seabirds and their ticks. For instance, local stresses, such as reduced food availability, can lead to increase seabird dispersal and thus to the transmission of local pathogens to new areas. Similarly, studies of other vector-borne systems have suggested that global changes can impact the physiology of vectors (e.g., tick survival) and the phenology of vertebrate hosts (e.g., breeding season and fledging period of birds), with potential implications for the epidemiology of vector-borne diseases (e.g., Crick and Sparks 1999, Kovats et al. 2001, Purse et al. 2005). To predict these potential impacts, increased knowledge on how these host–parasite systems function in space and time via multidisciplinary and integrative approaches (taxonomy, ecology, and epidemiological studies) will be required.

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## Appendix

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