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Ch 77. Tick and tick-borne disease circulation in a changing marine ecosystem

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1. Expert opinion

One may wonder how ticks and tick-borne disease could be present in marine ecosystems. It is true that ticks do not live underwater (although they can survive immersion) and do not exploit fish. However, ticks do feed on other vertebrates that are marine animals, in particular those that spend part of their lives on land, predominantly seabirds. Indeed, at least 30 tick species occur regularly in this ecosystem, and can be found across the globe, including the most extreme areas of both hemispheres (Table 1).

As in terrestrial systems, high infestations by ticks can reduce seabird body condition and lower reproductive success, which in turn can affect seabird population dynamics (Boulinier and Danchin, 1996; Gauthier-Clerc *et al.*, 1998; Mangin *et al.*, 2003). The impact of tick exploitation can be especially important under marine conditions, where thermal stress and the physiological demands of foraging can be arduous. Hyper-infestations by *Ixodes uriae*, resulting in blood loss and hypothermia, was, for example, implicated as a direct cause of death of breeding adult King penguins, *Aptenodytes patagonicus* (Gauthier-Clerc *et al.*, 1998). According to attachment site preferences, heavy infestations can also directly impair locomotion, leading to starvation or predation (Fig. 1a). Even lighter tick infestations have been associated with lower reproductive success and colony abandonment (Bergstrom *et al.*, 1999; Monticelli *et al.*, 2008; Sanz-Aguilar *et al.*, 2020); this can be due to direct impacts on young birds or irritation that perturbs normal feeding and vigilance behaviours in adults. Tropical seabirds are reported to shift colony locations as a means of avoiding the buildup of large numbers of ticks, such as *Ornithodoros capensis* (Fig. 1b; Duffy, 1983; Feare, 1976).

In addition to these direct effects, general surveys of marine ticks have shown that a range of infectious agents are present and circulating in these systems, including diverse bacteria, viruses, and protozoan parasites (Table 1). Some of these agents are known pathogens for humans and/or

their domestic animals, such as the bacterial agents of Lyme disease, carried by *Ixodes uriae*, or of African tick-bite fever (*Rickettsia africae*) found in *Amblyomma loculosum*. The impact of these agents on seabirds (or on ticks, for that matter) remain largely unknown. However, it is likely that the presence of these organisms is of some consequence for seabird health and population ecology. For example, the Soldado virus (Hughes serogroup) has been isolated from sick birds, and experimentally shown to kill chickens (Converse *et al.*, 1975). Infection by *Babesia peircei* has been associated with higher mortality rates in certain seabirds brought to rehabilitation centres, particularly penguins (Parsons *et al.*, 2018, 2017). More generally, quantifying the impact of infection on seabirds, as in other wild populations, is extremely difficult when pathogenicity is chronic in nature and acts in concert with other sources of environmental stress (e.g., food availability, predators, etc).

It is evident that current global changes will alter interactions between ticks and their marine hosts, with subsequent consequences for the circulation of infectious agents. This may occur via several possible mechanisms:

(i) Marine ticks can only exist where their hosts breed. The presence of breeding colonies is dependent on both suitable nesting habitat and adequate food resources for nestlings. The distribution of seabird species has been dynamic over evolutionary time, shifting with changes in climate. For example, the formation of the Antarctic Polar Front during the Miocene led to the formation of a region of extremely high biodiversity, favouring its use by a large diversity of seabirds (Bost *et al.*, 2009). The discovery of fossilized nests on Bermuda showed that albatross bred within the North Atlantic up until approximately 400,000 years ago, likely going extinct during an interglacial period when sea water levels and storm surge were maximised (Olson and Hearty, 2003). Climate-driven changes in gyres where seabirds feed are regularly noted and known to affect adult survival (Fluhr *et al.*, 2017). Current rapid changes will therefore certainly result in the displacement or extinction of certain colonies. Indeed, as warming waters cause thermal expansion and ice sheets to melt, sea levels will rise and will eliminate low-lying colonies. Increases in water column stratification, deoxygenation, and salinity, along with shifts in ocean circulation patterns, will accompany increasing sea surface temperatures and affect the availability of local food sources for birds (Hoegh-Guldberg *et al.*, 2018). Increasing distances between established nesting sites and food sources will put hatchlings at risk (Jenouvrier *et al.*, 2015) and may lead to colony abandonment. Some seabird species may respond rapidly to such changes, particularly if replacement zones for reproduction and foraging can be found. For example, warmer conditions in high latitudes may allow some species to expand their ranges poleward (Péron *et al.*, 2010). However, some species will not have this opportunity and will need to adapt to a warmer world. Given the 'slow pace' of life of

seabirds and the relative speed of current changes, many of these species will likely be driven to extinction, along with their parasites and pathogens (Grose *et al.*, 2020).

(ii) Climate changes may directly impact the presence and abundance of ticks in coastal marine environments. Marine ticks are only found on their hosts for the time of the bloodmeal and have adapted to a range of climates, with only the very coldest and driest polar regions seemingly unoccupied at present. Increasing temperatures and modified humidity regimes will change this distribution. Indeed, studies have shown that many terrestrial tick species are currently expanding their distributions northward due to milder winters that enable tick establishment (see references in Léger *et al.*, 2013). Surveys now suggest the same pattern holds true for marine ticks. For example, *Ixodes uriae* seems to be increasingly present in high Arctic seabird colonies due to milder temperatures (Descamps, 2013). However, as the current distribution of marine ticks is still only partially known, such changes will be difficult to quantify. More importantly, *if ticks expand in some ranges, will they actually retract in others? How plastic are ticks to changing conditions, and is the current rate of change too fast for adaptation to follow?* We know that marine ticks can survive under extreme conditions. For example, *I. uriae* has the largest temperature tolerance range known in ticks, from -30 °C to +30 °C, but is almost absent from seabird colonies in latitudes between 43 °N and 45 °S. Is this due to temperature/humidity interactions (Benoit *et al.*, 2007) or to some other environmental or ecological factor (e.g., competition)? Ticks seem to have large, highly repetitive genomes (Ullmann *et al.*, 2005). This may enable rapid adaptation to changing environmental conditions and shifts in host species use, ensuring their survival. Such a mechanism has been hypothesized to explain the worldwide distribution and broad host range of *I. uriae* (Dietrich *et al.*, 2014b).

(iii) The impact of ticks and their infectious agents can be exacerbated by the concurrent influence of other environmental factors, such as extreme weather conditions, reduced food resources, pollution, and the presence of predators or coinfecting parasites/pathogens. It is the combination of these different individual factors which may have the greatest impact on marine vertebrate populations (Dias *et al.*, 2019), and as a consequence on their interactions, with ticks and tick-borne infectious agents. These additional sources of stress are augmenting rapidly. For example, by-catch and competition with fisheries for depleting stocks have increased over time, leading to seabird population declines (Grémillet *et al.*, 2018). Pollutants are ubiquitous in the marine environment and have reached even the most untouched zones of the planet via ocean currents (Cózar *et al.*, 2017). Indeed, massive accumulations of plastics have formed, destroying foraging and breeding habitats for marine animals and bioaccumulating along trophic food chains with potential chronic toxicity effects (Auta *et al.*, 2017). Climate change is rapidly modifying access to habitats and

food resources used by marine animals, and destabilising populations via an increasing number of extreme weather events (Jenouvrier *et al.*, 2015).

Although seabirds are among the most vagile creatures on earth, most show strong migratory and breeding site fidelity, limiting their movements to within well-defined limits. Exploratory movements only tend to occur when individuals prospect for new locations to breed. This is seen in young birds during the period between fledgling and first reproduction, but also in adult birds that have failed a reproductive attempt. As the proportion of local nest success declines within a colony, the probability that a given breeding pair will leave to prospect increases (Boulinier *et al.*, 2008). Failed birds in colonies with widespread failure will thus show reduced site fidelity the following year, and will have a higher probability of changing breeding partners. This behaviour sets-up a feedback loop in which breeding failures (caused by a combination of potential factors), leads to unstable spatio-temporal population dynamics and a higher probability of dispersal. This, in turn, increases the probability of dispersing parasites (ticks) and infectious agents harboured by the birds, allowing the invasion of new locations and novel hosts. Therefore, the combined effect of different environmental stresses can alter the nature and outcome of host-parasite interactions and result in large-scale changes to the ecological and evolutionary pathways taken by these species. As global changes increase pressure on marine birds, this phenomenon may become more frequent, resulting in the large-scale homogenization of ticks and infectious agents across ranges of suitable ecological conditions.

2. Future predictions

So can we make any concrete predictions? This is a difficult question to answer in a complex and rapidly changing marine ecosystem. However, I expect that certain opportunistic tick species, such as *A. loculosum* and *O. capensis* *sl*, will expand their distributions and explode in numbers. Other, more specialist species, and particularly polar species such as *Ixodes signatus* and *I. kerguelenensis*, will likely follow the dynamics of their hosts, and decline in prevalence and abundance. Still other, more plastic, species like *I. uriae*, may be able to maintain the status quo, shifting their distributions to the limits of their physiological capacities and adapting to those host species available locally. What is sure is that these changes will interplay with other environmental factors that affect seabird community dynamics, patterns of colony use, and dispersal. This, in turn, will feedback on the interaction to alter the spread of ticks and the infectious agents these ticks and their host birds carry. As competition for limiting marine resources continue to intensify, contact between humans and wildlife are likely to increase, opening new links between marine and terrestrial tick and tick-borne disease systems. In this light, a better understanding of what limits the spatial distribution of

marine ticks, along with more basic information on the infectious agents they carry, seem essential first steps for predicting future impacts of ticks and tick-borne disease on marine ecosystems and beyond.

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Table 1. Known tick species from the marine ecosystem and associated infectious agents. Updated from Dietrich *et al.* (2011) with only new references included.

Tick genera	Species	Recorded Hosts	Known distribution	Infectious agents
<i>Argasidae</i>				
<i>Argas</i>	<i>cucumerinus</i>	<i>Pelecanus thagus</i>	Peru	unknown
	<i>macrostigmatus</i>	<i>Phalacrocorax aristotelis</i>	Corsica, Crimea	unknown
	<i>monolakensis</i>	<i>Larus californicus</i>	California	Mono Lake virus (Orbivirus, Kemerovo serogroup)
<i>Ornithodoros</i> (<i>Carios/Alectorobius</i>)	<i>amblus</i>	< 10; Suliformes, Charadriiformes, Sphensiformes ¹	Peru, Chile	Huacho virus (Orbivirus, Kemerovo serogroup), Punta salinas virus (Nairovirus, Hughes serogroup)
	<i>capensis</i>	> 35; diverse Procellariiformes, Suliformes, Charadriiformes, Sphensiformes, Phaethontiformes, Pelecaniformes	Globally distributed across tropical/subtropical regions	Soldado, Farallon viruses (Nairovirus, Hughes serogroup); Upolu, Aransas Bay viruses (Thogotovirus), Saumarez Reef virus (Flavivirus), Midway virus (Nyamivirus), Johnson Atoll virus (Quarantavirus); Adenoviruses (group B); <i>Rickettsia bellii</i> ; <i>R. hoogstraalii</i> ²
	<i>cheikhi</i>	<i>Sterna</i> sp.	Mauritania	Unknown
	<i>denmarki</i>	> 10; diverse Procellariiformes, Suliformes, Charadriiformes, Sphensiformes	Hawaii islands, Peru, Mexico, Jamaica, Martinique, Florida, Australia, New Zealand	Soldado virus (Nairovirus, Hughes serogroup), Farallon-like (Nairovirus, Hughes serogroup), Frazer Point and Raza viruses; Midway virus (Nyamivirus), Johnson Atoll virus (Quarantavirus)
	<i>maritimus</i>	> 35; diverse Procellariiformes, Suliformes,	British Isles, France, Spain, Portugal, Morocco	Essaouira, Kala Iris, Baku, Moellez viruses (Orbivirus, Kemerovo serogroup); Soldado,

		Charadriiformes, Phaethontiformes, Pelecaniformes, Spheniformes		Great Saltee, Pettico Wick, Puffin Island viruses (Nairovirus, Hughes serogroup); West Nile, Caspiy, Meaban viruses (Flavivirus), <i>Rickettsia</i> spp., <i>Borrelia</i> spp, <i>Babesia</i> spp. ³
<i>muesebecki</i>	< 10;	Charadriiformes, Suliformes	Arabian sea	Zirqa virus (Nairovirus, Hughes serogroup)
<i>sawaii</i>	2 species;	Procellariiformes	Japan	<i>Rickettsia</i> sp., <i>Borrelia</i> sp.
<i>spheniscus</i>		<i>Spheniscus humboldti</i>	Peru	Unknown
<i>yunkerii</i>	< 10; certain	Procellariiformes, Suliformes, Charadriiformes, Spheniformes	Galapagos	Unknown

Ixodidae

<i>Ixodes</i>	<i>amersoni</i>	> 5 species: Procellariiformes (Diomedeidae), Suliformes (Sulidae), Charadriiformes (Laridae)	Central Pacific Ocean	unknown
	<i>auritulus</i>	>35 species : diverse Procellariiformes, Suliformes, Charadriiformes, Spheniformes	Southern circumpolar region	unknown
	<i>diomedea</i>	1 species: Procellariiformes (Diomedeidae)	Tristan da Cunha	unknown

<i>eudyptidus</i>	>10 species : diverse Procellariiformes, Suliformes, Charadriiformes, Spheniformes	Australia, New Zealand	Saumarez Reef virus (Flavivirus)
<i>jacksoni</i>	1 species: Suliformes	Australia, New Zealand	unknown
<i>kerquelenensis</i>	>10 species : diverse Procellariiformes (Diomedeidae, Procellariidae)	Southern circumpolar region	unknown
<i>kohlsi</i>	>5 species : Procellariiformes, Suliformes, Charadriiformes, Spheniformes	Australia	unknown
<i>layanensis</i>	10 species : Procellariiformes, Suliformes, Charadriiformes, Phaethontiformes	Central Pacific ocean	unknown
<i>murreleti</i>	1 species: <i>Synthliboramphus hypoleucus</i>	Mexico	unknown
<i>percavatus</i>	2 species: Procellariiformes (Diomedeidae), Spheniformes	Tristan da Cunha	unknown
<i>philipi</i>	2 species: Procellariiformes	Japan	unknown
<i>rothschildi</i>	>10 species : diverse Procellariiformes, Suliformes, Charadriiformes	North-eastern Atlantic	Phlebovirus (Uukuniemi group)

	<i>signatus</i>	~4 species : Suliformes, Charadriiformes	North Pacific Ocean	Orbivirus (Kemerovo group); Orthonairovirus (Sakhalin group), Phlebovirus (Uukuniemi group)
	<i>unicavatus</i>	2 <i>Phalacrocorax</i> spp.	Eastern north Atlantic, Baltic sea	unknown
	<i>uriae</i>	> 60 species: diverse Procellariiformes, Suliformes, Charadriiformes, Spheniformes	Circumpolar (both hemispheres)	Orbivirus (Kemerovo group); Orthonairovirus (Sakhalin and Hughes groups); Phlebovirus: (Uukuniemi group); Flaviviruses; <i>Borrelia burgdorferi</i> sl (<i>B. garinii</i> , <i>B. bavariensis</i> , <i>B. burgdorferi</i> ss, <i>B. lusitaniae</i>) ⁴
<i>Amblyomma</i>	<i>darwini</i>	1 : <i>Amblyrhynchus</i> <i>cristatus</i> (iguana) ⁵	Galapagos	unknown
	<i>loculosum</i>	>10 species : diverse Procellariiformes, Suliformes, Charadriiformes, Phaethontiformes	Australia, Indian Ocean	Soldado virus (Nairovirus, Hughes serogroup) <i>Rickettsia africae</i> . ²
	<i>nitidum</i>	Sea snakes (<i>Laticauda</i>) ⁶	South western Pacific Ocean	unknown

¹ Llanos-Soto *et al.*, 2019

² Dietrich *et al.*, 2014a

³ Dupraz *et al.*, 2017; Gomard *et al.*, 2020; Sanz-Aguilar *et al.*, 2020

⁴ Munro *et al.*, 2017

⁵ Schulze, 1936

⁶ Kwak *et al.*, 2020

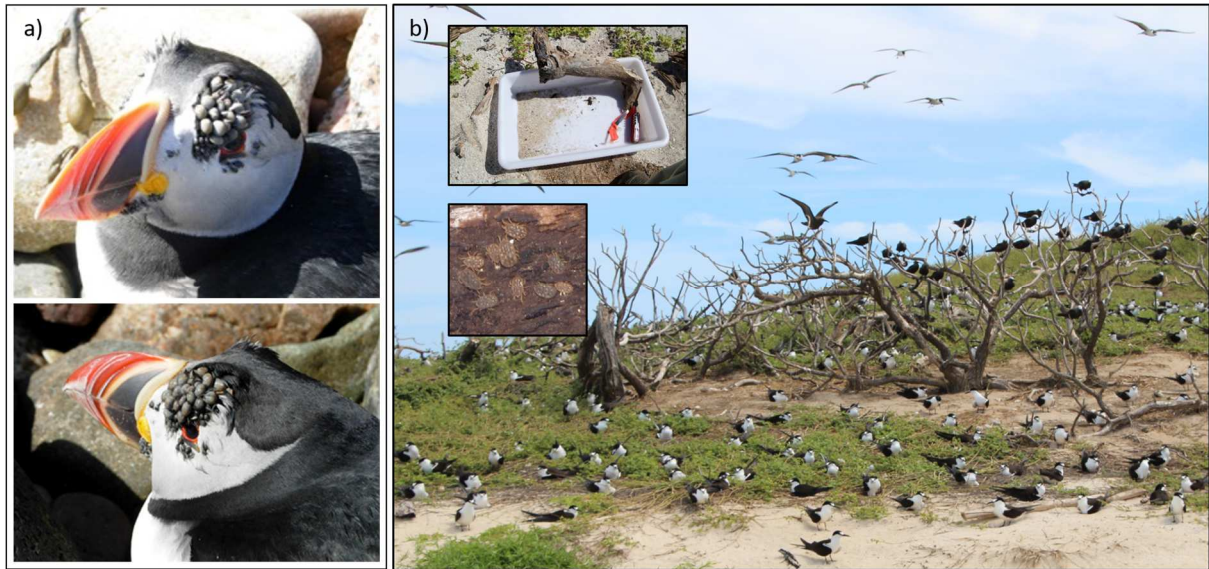


Fig. 1. Marine ticks can pose significant problems for breeding seabirds in cases of heavy infestations and via the transmission of infectious agents. While infestations by ixodid ticks are relatively easy to quantify, as seen by this massively infested Atlantic puffin *Fratercula arctica* (a), those by argasid ticks are much more difficult. Indeed, soft ticks can be present in significant numbers within tropical and temperate seabird colonies, such as in this Sooty tern, *Onychoprion fuscatus*, colony on the Ile de Lys, Iles Eparses (b), but only leave shelters in the vegetation for their short bloodmeal during the night (insets: sampling of *Ornithodoros capensis*). Photo credits: (a) D. Playle used with permission from A. Spellman (www.mullbirds.com); (b) K.D. McCoy.