



Possible interaction between exposure to environmental contaminants and nutritional stress in promoting disease occurrence in seabirds from French Guiana: a review

Manrico Sebastiano^{1,2} · David Costantini¹ · Marcel Eens² · Kevin Pineau³ · Paco Bustamante^{4,5} · Olivier Chastel⁶

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Abstract

Environmental contaminants pose a global threat to humans and biodiversity conservation worldwide. Yet little is known about contaminant levels in tropical seabird communities located in key biodiversity points. French Guiana is a hotspot of biodiversity and is one of the regions experiencing a rampant increase in mercury (Hg) contamination. This review has the objective to summarize the results of (i) previous work on Hg contamination in seabirds from French Guiana and (ii) already published work on other environmental contaminant sources as persistent organic pollutants (POPs). Furthermore, previous research on Grand Connétable island, a key breeding site for Caribbean seabirds, reported high blood Hg concentrations in several seabirds, reaching the threshold of possible health concern for some species, particularly for the magnificent frigatebird *Fregata magnificens*. Because frigatebirds are experiencing massive mortality events of chicks caused by a herpesvirus disease that first appeared in 2005, this review further discusses a potential synergistic or additive interaction between food availability and Hg exposure in determining the recurrent disease outbreaks, a topic that has been often neglected in the literature. Here, we (i) summarize already published results from several years of research on this topic and (ii) suggest a potential connection between the occurrence of infectious diseases and cumulative effects of environmental stressors in marine top predators including birds, which clearly deserves further investigations. We also highlight the lack of studies on other sources of local pollution rather than Hg, and the need to take into consideration the cumulative effects of stressors on the health status of organisms, rather than focus on individual stressors or specific contaminants.

Keywords Seabirds · Cumulative effects · Environmental contaminants · Disease · French Guiana · Mercury · Food shortage

Introduction

Exposure to environmental contaminants represents a global threat to humans and wildlife. The growing awareness of the detrimental effects of certain compounds has consequently led to the regulation of their release into the environment. For instance, the Stockholm Convention, adopted in 2001,

regulates the release of Persistent Organic Pollutants (POPs) into the environment. Similar to the Stockholm Convention on POPs, the Minamata Convention, an international agreement adopted in 2013, has the objective “to protect human health and the environment from the adverse effects of mercury”. When contaminants are regulated, their environmental concentrations rapidly decline although they remain detectable for decades after being banned (Hung et al. 2016; Wong et al. 2018). Despite being under regulatory measures of emission in most industrialized countries, some contaminants including POPs are still found at very high concentrations in wildlife tissues (Muir et al. 2019). Similarly, mercury (Hg) remains amongst the major dangerous chemicals for public health (WHO 2017) and wildlife (Whitney and Cristol 2017; Wolfe et al. 1998).

Hg emissions have been regulated worldwide, but recent estimates indicate that anthropogenic emissions of

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✉ Manrico Sebastiano
manrico.sebastiano@mnhn.fr

Extended author information available on the last page of the article

Hg increased about 20% from 2010 to 2015 alone (UNEP 2019), likely due to an increase in artisanal and small-scale gold mining (hereafter ASGM) (Eagles-Smith et al. 2018). Several contaminants including POPs and methyl-mercury (MeHg), the organic toxic form of Hg, bioaccumulate in organisms' tissues and biomagnify through food webs, showing increasing concentrations from lower to higher trophic levels (Catry et al. 2008; Lavoie et al. 2013). Predatory birds including seabirds are therefore generally exposed to high levels of environmental contaminants (Rowe 2008) and are considered excellent sentinels of the status of the marine environment (Burger and Gochfeld 2004; Rowe 2008). Only very few published studies have investigated the occurrence of environmental contaminants in the tropics, and even less work has been carried out in the Guyana shield, a region in north-eastern South America which includes French Guiana (an overseas department of France), Guyana (also known as the British Guiana), and Suriname (also known as Dutch Guiana). Thus, the use of seabirds as bioindicators appeared suitable to assess the contamination of the marine environment in French Guiana (Furness and Camphuysen 1997).

One of the few investigations of environmental contaminants in the Guyana shield is represented by the "Sentinel" project supported by the CNRS (French National Centre for Scientific Research). This project enabled to investigate the presence of trace elements and legacy POPs in six seabird species breeding in Grand Connétable island, a key breeding site for several seabird species. In particular, because the Magnificent frigatebird *Fregata magnificens* is affected by annual outbreaks of a viral disease with yearly mortality episodes of chicks (up to 90%, personal observations and monitoring studies made by the Groupe d'Etude et de Protection des Oiseaux en Guyane GEPOG), the project was further implemented to investigate the physiological mechanisms underlying the emergence and progress of the disease, and to identify the factors that may be involved in the appearance of clinical signs in this species. In recent years, ecologists and ecotoxicologists are assessing the impact of multiple stressors on the health status of wild animals (Marcogliese and Pietrock 2011), and the above-mentioned research project has further explored this possibility. The idea that multiple stressors can act in synergy and have a cumulative effect is increasingly being accepted and demonstrated (Jacobson et al. 2003; Marcogliese and Pietrock 2011). In particular, there is growing interest in testing whether the damaging effects of pathogens on hosts may be exacerbated by concomitant exposure to other stressors.

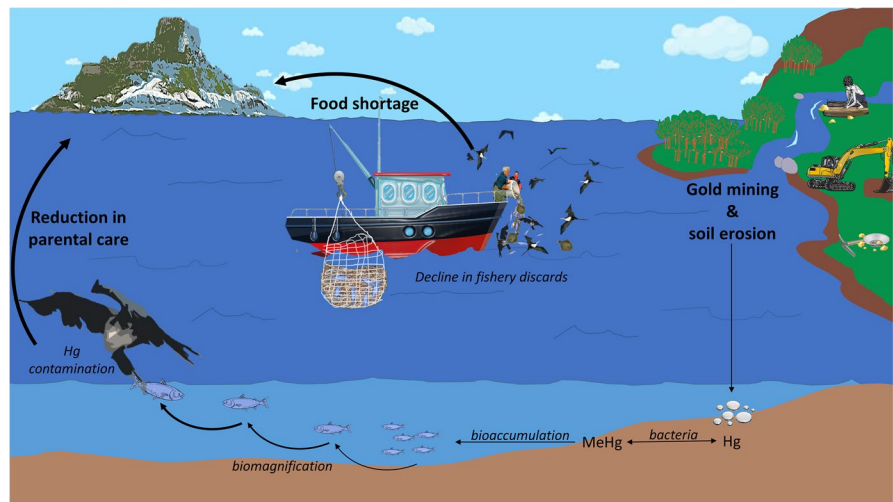
This review has the objective to illustrate one research question: Does exposure to environmental stressors exacerbate the action of pathogens and promote disease outbreaks in wild populations? To address this question, the review is divided into four main parts. First, it summarizes already published results from several years of research on

Hg contamination in French Guiana and the surrounding countries. The second part reports the results of studies that have analysed other environmental contaminants rather than Hg in the region, and how likely species will be under pressure in the next years. The third part of the review reports detailed information on the occurrence of disease outbreaks in seabirds from French Guiana, further discussing the possible underlying physiological mechanisms. Finally, the last part attempts to clarify the hypotheses that might explain the reported disease outbreaks, suggesting a potential cumulative effect of exposure to environmental contaminants and food shortage in promoting the occurrence of outbreaks of a viral disease in a seabird species (Fig. 1). By doing so, this review stresses how ecotoxicological studies are lacking in this highly biodiversity-rich region, identifies knowledge gaps on the relationship between contaminant exposure and disease occurrence in wildlife, and suggests the use of a "one health approach", which may be beneficial for the environment and the organisms that inhabit it.

High mercury contamination in humans and wildlife in the Guianas

The Guiana Shield represents a region of dense and intact tropical forest that covers all of the Guianas (Guyana, Suriname and French Guiana), parts of northern Brazil, southern Venezuela, and eastern Colombia. The region's biodiversity and ecological integrity are, however, threatened by the rampant growth of gold mining in the region. The impact of artisanal and small-scale gold mining is widespread and long lasting. Not only does ASGM cause deforestation and disruption of natural environments, which take decades to recover, but it also represents the major cause for Hg release into the environment, which is likely a main driver of long-lasting damages to local biodiversity (Cordier et al. 1998; Legg et al. 2015; Lemaire et al. 2021a). Large quantities of Hg are used to amalgamate gold particles; then the amalgamate is burned to separate the Hg from the gold, resulting in its release to the atmosphere and hydrosphere (UNEP 2012). In gold-producing countries from South America, ASGM accounts for 20 to 60% of gold production (Hammond et al. 2013); therefore, they are experiencing a rapid increase of Hg release into the environment. Although there are no recent detailed studies on trends in Hg contamination in French Guiana, recent work found increasing Hg concentrations from year to year in the piscivorous wolf fish *Hoplias aimara* (Brachet et al. 2020). Hg use was banned from 2006 in legal gold mines, but recent mining exploitations and soil erosion on the same sites imply a higher risk of re-mobilizing Hg (Hellal et al. 2020). Hg is still massively used in illegal gold mines, and recent work estimated that the number of gold mining sites in the Guiana shield is still growing over the past years (Dezecache et al. 2017).

Fig. 1 Graphic representation of the stress factors from French Guiana. Hg from gold mining and soil erosion is converted into MeHg, which bioaccumulates and biomagnifies within food webs. Adult frigatebird exposed to high Hg contamination may suffer its toxic effects at the physiological level (e.g. reduced parental care). Furthermore, frigatebirds are likely facing food shortage due to the decline in discards associated with shrimp trawlers and may struggle to provide food to their chicks



Once in the environment, Hg can be methylated by microorganisms into MeHg. Because it is highly bioavailable for biota, MeHg is easily assimilated via food intake and biomagnifies within food webs, occurring at increasing concentrations from lower to higher trophic level organisms. Therefore, long-lived top predators, including seabirds, are often exposed to high Hg concentrations (Becker et al. 2016; Burger and Gochfeld 2004; Cherel et al. 2018).

The potential increase in environmental contaminants in tropical regions is a topic that remains largely overlooked. Despite the rampant increase in Hg contamination in the region, most studies focused on the relationship between freshwater fish consumption and Hg contamination in local Amerindian communities. For instance, Frery et al. (2001) found high Hg concentrations in hair samples of four different Amerindian villages in French Guiana, suggesting that their excessive exposure is related to the consumption of contaminated fish. Similarly, a previous work on Amerindians between 2004 and 2009 found a significant association between hair Hg concentration and fish consumption (Fujimura et al. 2012). Fish consumption is therefore the major exposure pathway as fish in French Guiana is contaminated and Amerindians tend to have preferences towards the more contaminated piscivorous species such as the barred catfish *Pseudoplatystoma fasciatum* and the wolf fish (Frery et al. 2001; Fujimura et al. 2012). In a previous study, 14.5% of the 270 fish collected from 48 species exceeded the safety limit applied in the USA, Canada and Brazil of 500 ng/g of fresh weight or 2500 ng/g of dry weight, mostly exceeded by piscivorous species (Frery et al. 2001). As an example, Durrier et al. (2005) showed that there is a probability of 93% to catch a piscivorous wolf fish that exceeds the WHO safety limits for Hg, confirming the high Hg contamination in the region.

In French Guiana, up to a few years ago, there was nearly no information on the levels of environmental contaminants

in local marine wildlife, except a study on the maternal transfer of organic contaminants in the leatherback turtles *Dermochelys coriacea* (Guirlet et al. 2010). But in 2013, a research project collected hundreds of blood samples in both adults and chicks of the six seabird species breeding on Grand Connétable Nature Reserve (Magnificent frigatebirds, royal terns *Thalasseus maximus*, cayenne terns *Thalasseus eurygnathus*, sooty terns *Onychoprion fuscatus*, laughing gulls *Leucophaeus atricilla*, brown noddies *Anous stolidus*; i.e. “Sentinel” project) to assess the concentrations of 14 trace elements, including Hg and POPs (Sebastiano et al. 2016, 2017a). The authors documented that Hg concentrations in adults of the laughing gull, the royal tern and the magnificent frigatebird were similar or higher than those recorded in highly contaminated populations of diverse seabird species from other geographic regions (Sebastiano et al. 2017a). Other elements considered toxic at high concentrations (e.g. cadmium, copper, nickel, lead) occurred at low concentrations, so that they might not pose a danger to this seabird community (Sebastiano et al. 2017a). Frigatebirds were the most exposed birds to Hg contamination, likely owing to the higher trophic position they occupy in comparison to the other species breeding on Grand Connétable (Sebastiano et al. 2017a).

The high biodiversity of French Guiana and the presence of high environmental Hg concentrations represent an excellent framework for ecotoxicological investigations in wild animals, yet the number of studies remains scarce. Except for the above-mentioned studies on seabirds (Sebastiano et al. 2016, 2017a) and on fish species (Brachet et al. 2020; Durrier et al. 2005; Frery et al. 2001), Hg in vertebrates was only further studied and documented in leatherback turtles (low Hg concentrations likely owing to the high pelagic nature of leatherbacks, Guirlet et al. 2008), black caimans *Melanosuchus niger* (Hg was associated with body size and trophic position of caimans, Lemaire et al. 2021a),

spectacled caimans *Caiman crocodilus* (Hg was related to disruption of osmoregulation (sodium levels), hepatic function (alkaline phosphatase levels) and endocrine processes (corticosterone levels), Lemaire et al. 2021b) and neonate smooth-fronted caimans *Paleosuchus trigonatus* (reduced body size in neonates characterized by elevated Hg concentrations, Lemaire et al. 2021c). Despite the available data suggest high Hg contamination and possible health concerns for local wildlife, these studies are outnumbered by human-oriented studies, which report Hg in soil, invertebrates, and humans. If Hg contamination remains high or continues to increase in the next years, species that occupy the top of their food webs (e.g. seabirds, marine mammals) may be at risk, and future studies should focus on such species for early detection of environmental pollution.

Other contaminants in the Guianas potentially affecting wildlife

French Guiana and the surrounding countries may also be experiencing an increase in the use of POPs, including per- and polyfluoroalkyl substances (PFAS). POPs are amongst the major contaminants currently found in wildlife, of which polychlorinated biphenyls remain the most prevalent class of POPs detected despite they have been banned more than 30 years ago (Tartu et al. 2015a). In French Guiana, 41 different organic contaminants were also analysed in frigatebirds, cayenne terns and brown noddies (Sebastiano et al. 2016, 2017a). Most of the analysed contaminants were either not detectable or showed low levels compared to literature values and therefore are unlikely to pose a threat to this seabird community (Sebastiano et al. 2016, 2017a). However, given the (unclear) sub-lethal effects that POPs may have on organisms even at a low concentration (Elskus 2014), additional work is needed to monitor the occurrence of these contaminants in the region.

Additional work is also necessary to assess the occurrence of PFAS, as to date, there are no studies on the presence of PFAS and other emerging contaminants in French Guiana. This is particularly important considering that in Brazil, the insecticide sulfluramid is used in plantations for the control of leaf-cutting ants (Nascimento et al. 2018). Brazil, a major global agricultural producer, has massively used sulfluramid in the past years, corresponding to approximately 30 tonnes per year of EtFOSA (a PFAS precursor abundant in sulfluramid) between 2004 and 2015 (Gilljam et al. 2016). Because of their high volatility and long-range oceanic and atmospheric transport, PFAS may reach remote areas and accumulate in areas where there are not-known point sources of PFAS, as previously documented (Sebastiano et al. 2020a, 2021). Further work on other emerging pollutants, including PFAS, is strongly warranted to clarify whether they threaten the French Guianese marine ecosystems, and whether they

represent confounding factors for the interpretation of the results (as described in Sebastiano et al. 2022).

Furthermore, during the last few years, French Guiana has also experienced a considerable increase of plastic debris close to the study area. The negative consequences resulting from interactions between wildlife and plastic debris are diverse and often visually striking and can include nutritional deprivation, entanglement and damage to or obstruction of the gut (e.g. perforations and ulcers), as described in a previous study (Provencher et al. 2018). To date, there is only one study documenting plastic debris in wildlife from French Guiana (Plot and Georges 2011), and it has been carried out 10 years ago. This study reported an adult female leatherback turtle expelling 2.6 kg of plastic debris from her cloaca while nesting in French Guiana, highlighting the need for effective waste management in the region (Plot and Georges 2011). Seabirds often confound plastic debris for prey; therefore, they are amongst the most threatened groups of wild animals. Plastic pollution is an exponentially increasing global issue (Wilcox et al. 2015), but to date, we do not know almost anything on the occurrence of plastic debris and potential detrimental effects of plastic pollution in French Guiana. Frigatebirds seem to be less prone than other species to ingest plastic litter (Rapp et al. 2017). However, considering that plastic debris is a trap for POPs (Rios et al. 2007), this may act as an additional source of contaminants or as another stressor to frigatebirds and other species from the region. We strongly warrant future studies to determine whether seabirds and other marine animals are being affected by the increasing plastic pollution in French Guiana.

Outbreaks of a viral disease in seabirds from French Guiana

In 2005, clinical cutaneous signs associated with mortality episodes were recorded for the first time in chicks of magnificent frigatebirds on Grand Connétable island. Chicks showed proliferative skin lesions on the neck and legs, body crusts, hyperkeratosis of eyes and bone frailty, likely associated with a novel alphaherpesvirus (de Thoisy et al. 2009). Herpesviruses are DNA viruses found in many animal species (Davison 2010) which are often associated with latent infections. However, in certain conditions, some herpesviruses can cause severe harm to their host and lead to massive mortality events (Brand and Docherty 1988; Long et al. 2016).

Since the first appearance of clinical signs in 2005, annual monitoring programs for frigatebirds and the other species that breed sympatrically in the natural reserve were carried out by the GEPOG, an association that manages the study area. In 2009, several dead or dying adult sooty terns showing similar clinical signs of frigatebirds were found to be infected by a novel alphaherpesvirus distinct from that of

frigatebirds (Sebastiano et al. 2020b). While the expression of clinical signs was reduced in the sooty tern, about 90% of frigatebird chicks died each year due to the disease. Although herpesviruses are amongst the most common infectious pathogens, our knowledge on the physiological consequences they have on wild animal populations remains very limited.

Previous clinical studies suggest that oxidative stress may represent one important physiological mechanism underlying the activation of certain viruses (Hu et al. 2017; Li et al. 2011). By comparing values of a number of oxidative status biomarkers between chicks with and without clinical signs of the disease, Sebastiano et al. (2017b) found that visible clinical signs are associated with changes in several of these markers and that oxidative damage is negatively associated with the survival of chicks (Sebastiano et al. 2017b). The authors further demonstrated that a supplementation experiment with resveratrol, a powerful antioxidant, corroborated the hypothesis that dietary molecules might constrain the capacity of animals to face a viral disease (Sebastiano et al. 2018a).

As the immune system is crucial for the progress of the disease, Sebastiano et al. (2017c) measured some biological markers that are used as indices of the immune response. The concentrations of the inflammatory protein haptoglobin and that of nitric oxide, and the capacity to agglutinate and lyse exogenous blood, change significantly in response to an inflammatory stimulus such as infection and disease (Quaye 2008), and reflect immunocompetence (Matson et al. 2005). When investigating the difference in plasma concentrations of haptoglobin, the authors found this protein to be greatly increased during the progress of the disease and to predict the short-term probability of survival of frigatebird chicks (Sebastiano et al. 2017c), while such results were not found with the other markers of immunocompetence and of DNA damage including telomere length (Sebastiano et al. 2017c).

In birds, elevated concentrations of the stress hormone corticosterone (i.e. the main avian glucocorticoid) have detrimental effects on chick growth and immunity (Kitaysky et al. 2003; Rubolini et al. 2005). Therefore, glucocorticoids may link environmental stress to the appearance of the disease through their negative effects on the individual immunocompetence. However, the authors found no indication that corticosterone is associated with the occurrence of clinical signs in this species, suggesting that corticosterone levels may vary due to other factors rather than clinical signs of the disease (Sebastiano et al. 2017c). The manifestation of clinical signs owing to a viral outbreak suggests that the affected birds might be exposed to severe sources of stress. However, although Sebastiano et al. (2017b, c) found that some markers of physiological stress are associated with disease outbreaks in frigatebird chicks, it is not yet clear which factors are responsible for these outbreaks, and several hypotheses have been formulated.

Do environmental stressors exacerbate the action of pathogens and promote disease outbreaks?

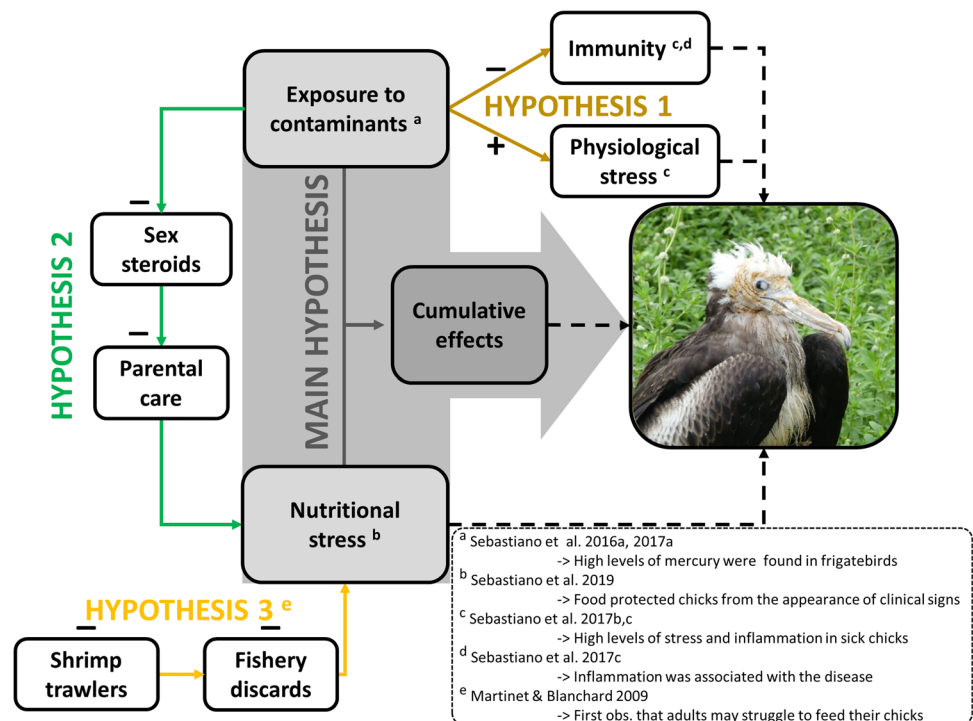
Over the past few years, as a result of the ongoing research projects and experiments aimed at understanding the causes of the viral outbreaks in French Guianese wildlife, several hypotheses have been formulated.

Hypothesis 1: Hg directly affects the immune function and the physiological status of exposed birds

Hg exposure is a global threat to humans and wildlife because its accumulation in the body may impair neurobehavioural, reproductive and immune functions (Chételat et al. 2020; Evers 2017). Recent work provided evidence of the detrimental effect of Hg on diverse physiological and fitness-related traits in 72% of field studies and 91% of laboratory studies on birds (Whitney and Cristol 2017). The high Hg concentrations in frigatebirds raise the important question of whether Hg might favour the appearance of clinical signs in populations exposed to viral strains (HYPOTHESIS 1, Fig. 2).

As an example, a greater rate of bacterial infection was observed in captive common loons *Gavia immer* experimentally dosed with Hg in their diet (Kenow et al. 2007), suggesting that Hg may facilitate the spread of infectious pathogens. Similarly, gastrointestinal parasite loads in European shag *Phalacrocorax aristotelis* females increased strongly with decreasing Se:Hg molar ratios (Carravieri et al. 2020). Hg may therefore represent a factor favouring the appearance of clinical signs in populations exposed to viral strains. While analysing the presence of trace elements in the six species that nest on Grand Connétable island, Sebastiano et al. (2017a) found that frigatebirds had the highest concentrations of Hg but also showed much lower concentrations of Se than the other species. The relationship between the concentrations of Hg and Se is of a great importance to describe Hg toxicity. Se protective effect against Hg toxicity is presumed to involve selenoproteins such as selenoenzyme and selenoprotein P enabling the sequestration of Hg, thereby preventing its harmful effects (El Hanafi et al. 2022; Manceau et al. 2021a; Manceau et al. 2021b). However, the high affinity between Hg and Se also results in Hg binding to selenoproteins, thus compromising biological functions and availability of Se (Ralston and Raymond 2010). Se plays an important regulatory role in the immune response (Hoffmann and Berry 2008), and its deficiency has been associated with an increased susceptibility to diseases (Gomez et al. 2002; Wang et al. 2009). But to date, there is still very little evidence to support a possible association between Hg exposure (and the possible decrease in Se bioavailability) and outbreaks of infectious diseases (Eagles-Smith et al.

Fig. 2 Schematic representation of the hypotheses that might explain the occurrence of clinical signs of a viral disease in this population. Contaminants may directly affect the health status of chicks by decreasing immunity and increasing physiological stress (HYPOTHESIS 1). Nutritional stress caused either indirectly by the effect of environmental contaminants on parental care of adults (HYPOTHESIS 2) or directly due to the decrease in fishery discards from shrimp trawlers (HYPOTHESIS 3). However, the most probable explanation is that frigatebirds are under a cumulative effect of nutritional stress and exposure to environmental contaminants (MAIN HYPOTHESIS). The letters in the box refer to what has already been done in previous years



2018), and we are very much in need of targeted studies to fully explore this hypothesis.

Hypothesis 2: Hg interferes with the action of hormones that control parental care in adults

In birds, one of the most widely investigated and reported consequences of Hg exposure is a decreased reproductive success (Tartu et al. 2013; Whitney and Cristol 2017) and the detrimental effects on population dynamics (Goutte et al. 2015, 2014). Furthermore, one of the main effects of Hg exposure described in the literature is the negative association with parental care. Common loons and American kestrels *Falco sparverius* exposed to Hg spent less time incubating (Albers et al. 2007; Evers et al. 2008). Carolina wrens *Thryothorus ludovicianus* nesting on contaminated sites were more likely to abandon their nests than co-specifics nesting on reference sites with low Hg concentrations (Jackson et al. 2011). Similarly, Tartu et al. (2015b) found that snow petrels *Pagodroma nivea* males with higher Hg concentrations were more likely to neglect their egg.

In birds, incubation and chick brooding behaviours are primarily controlled by the pituitary hormone prolactin (Angelier et al. 2016), and previous research conducted in polar seabirds supports the hypothesis for a major role of Hg in disrupting the secretion of prolactin (Tartu et al. 2015b; Tartu et al. 2016; Tartu et al. 2013). In magnificent frigatebirds, males show a highly variable commitment to chick-rearing (19 days–5 months) as compared to that of females,

which lasts 9 to 12 months (Osorno 1996), but the reasons for such variability are yet to be elucidated. However, because larger chicks have a higher probability of survival until fledging, males that abandon their chick earlier might jeopardize their survival because of the reduced parental care. A possible follow-up of this research would be to test the hypothesis that males exposed to higher concentrations of Hg either (i) provide less parental care (spend less time at the nest, supply less food to their chicks) or (ii) abandon the chick earlier during the breeding season, leaving the female with the arduous task of providing for the chick alone, behaviours that would make chicks more susceptible to the disease (HYPOTHESIS 2, Fig. 2).

Hypothesis 3: Outbreaks of disease are tied to an ongoing nutritional stress

As stated above, the relationship between the concentrations of Hg and Se is of a great importance to describe Hg toxicity, and Se deficiency might represent one of the detrimental effects of Hg exposure on this population. Although not carried out in French Guiana, a very recent study described unusual mortality events of Guiana dolphins *Sotalia guianensis* in Southeastern Brazil as a result of a morbillivirus outbreak (Manhães et al. 2021). The authors found high Hg concentrations and showed that all Se was complexed as HgSe, implying that Se was not available for important biological functions such as the regulation of the oxidative status and the animal's health

(Manhães et al. 2021). The authors further suggested a possible cumulative effect of Hg toxicosis and Se deficiency on the severity of *Morbillivirus* infections in cetaceans (Manhães et al. 2021).

In seabirds, fish represent the major dietary source of Se. In 2009, the paper that first described the appearance of clinical signs in the frigatebird population pointed to nutritional stress as a possible cause of the appearance of clinical signs (de Thoisy et al. 2009). During the same year, a study on the fishery activity in the region reported that some frigatebird pairs seemed unable to provide for the needs of their chicks (Martinet and Blanchard 2009), pointing to the recent rapid decline in shrimp fishing activities and their discards, highly beneficial for frigatebirds (Martinet and Blanchard 2009). In addition, examination of the carcasses of some dead sick chicks showed classic signs of malnutrition (de Thoisy et al. 2009).

Declines in natural populations of marine predators are often attributed to nutritional stress. In birds, food shortage causes physiological stress with increased corticosterone production (Kitaysky et al. 2007). Food availability during the breeding season influences the immune function of birds (Gasparini et al. 2006), which might make organisms less resistant to infections. But to date, there is no evidence for an association between declining nutritional resources and the appearance of viral diseases.

For this reason, an experiment was carried out on the same population with the intention to test whether food availability constrained the capacity of frigatebird chicks to cope with this fatal viral disease (Sebastiano et al. 2019). Food supplementation was carried out in both healthy and sick chicks for several consecutive weeks (Sebastiano et al. 2019). Seven out of twelve un-supplemented healthy chicks (58%) showed the appearance of clinical signs over the study period, while none of the food-supplemented healthy chicks showed the appearance of any clinical signs of the disease (Sebastiano et al. 2019). Furthermore, none of the food-supplemented sick chicks died, while three out of fifteen un-supplemented sick chicks (20%) died during the experiment (Sebastiano et al. 2019), supporting the nutritional stress hypothesis (HYPOTHESIS 3, Fig. 2).

Hypothesis 4: Diverse sources of stress act in combination to promote viral outbreaks

The results of the food supplementation experiment in frigatebirds suggested that nutritional stress might be one of the factors that affect the health status of chicks (Sebastiano et al. 2019). Thus, Hg is not the only source of environmental stress to which frigatebirds are potentially exposed, and a cumulative effect of different stressors may be in place.

During the food supplementation experiment, Sebastiano et al. (2019) reported that frigatebird chicks were fed with non-local fish with a very low Hg content and high Se. Therefore, the authors did not exclude that food supplementation has also diminished the negative effects of assimilating contaminated fish or that chicks benefited from the subsequent increase in the bioavailability of Se (Sebastiano et al. 2019). If Hg decreases the availability of Se for important biological functions, Se might act as a limiting factor of the immunocompetence of chicks. Therefore, nutritional stress and the lower intake of Se through the diet might increase the susceptibility of chicks to pathogens. The results of Sebastiano and colleagues indicate that frigatebird chicks might be exposed to a strong nutritional deficiency and high Hg contamination (and, possibly, other pollution sources), suggesting that they can have combined negative effects (e.g. synergistic or additive) that led to the appearance of clinical signs in this species (MAIN HYPOTHESIS, Fig. 2).

This hypothesis is supported by previous work on birds that found that environmental contaminants may have different effects on organisms' health in combination with other stressors (Bustnes 2006; Leung and Furness 2001). Specifically related to pathogens, several examples have been reported in birds and fish species. For instance, common eiders *Somateria mollissima* exposed to Hg suffer the effect of a parasitic infection in a more pronounced manner when they are in poor condition (Provencher et al. 2017). Similarly, juvenile chinook salmon *Oncorhynchus tshawytscha* infected with trematodes showed impaired immune function and disease resistance, but the combination with contaminant exposure had a greater negative effect on salmon health (Jacobson et al. 2003). Furthermore, parasites enhanced the detrimental effects of organic contaminants in the glaucous gulls *Larus hyperboreus* (Bustnes et al. 2006).

Anthropogenic emissions of Hg and of other contaminants expose wildlife to novel stressors that require physiological and genetic adaptations. The research carried out so far on this population of frigatebirds suggests that exposure to environmental contaminants in combination with other sources of stress (e.g. food shortage or nutritional deficiency) might trigger disease outbreaks in populations exposed to viral strains or pathogens. This may be particularly important for piscivorous species experiencing nutritional stress and contaminant exposure simultaneously, given that the high concentration of Se contained in fish may protect organisms from detrimental effects of Hg exposure. Experimental work on this subject (i.e. showing that the effect of environmental contamination is greater when individuals are subjected to other stressors) is of paramount importance because it could lead to the tightening of current regulations on emissions of chemicals, which would help preserve protected areas and the conservation of species.

Conclusions

The literature cited in this review suggests a potential connection between the occurrence of infectious diseases and Hg exposure in marine top predators, including birds. In marine animals and, especially, top predators exposed to Hg, food shortage might further compromise their health status owing to the lower Se intake and the consequent lower protection against Hg, resulting in cumulative stress. In this context, the community of seabird species breeding in French Guiana offers an unprecedented opportunity to investigate how species respond to the current and increasing contamination at the population, species and ecosystem level. Given the scarcity of information on other contaminants, which may either enhance or reduce toxicity by antagonistic, additive or synergic effects (Kortenkamp and Faust 2018), we suggest continued investigation on contaminants in the region and on the potential cocktail effects that would impact on the health of seabirds. The outbreaks of disease in French Guiana make the studied population highly suitable to experimentally investigate this potential relationship between contaminant exposure, nutritional stress and viral outbreaks in wild animals, which has never been investigated in the wild.

For conservation purposes, we reiterate that the mortality of frigatebird chicks remained high in recent years, and sporadic episodes of viral outbreaks were also found in other species breeding sympatrically with frigatebirds (annual monitoring program from GEPOG; Sebastiano et al. 2020b). The breeding population of frigatebirds is still large; therefore, there has not been apparently a decline in the number of pairs breeding on the island. However, considering that the high mortality of chicks is a driver of population decline in seabirds (Finkelstein et al. 2010), the number of breeding pairs might collapse in the following years unless the immigration rate from other colonies will compensate for adult mortality (or adults that cease breeding). Additional work is therefore needed to identify colonies that have an exchange of individuals with French Guiana to assess the possible occurrence of a source-sink dynamics and to early detect a possible spread of the virus to other colonies (as discussed in Sebastiano et al. 2018b). Seabirds are amongst the most threatened bird groups (Vo et al. 2011; Wagner and Boersma 2011; Wilcox et al. 2015), so that we call for an urgent need to better understand the mechanisms that underlie their decline to develop appropriate strategies of mitigation of the long-lasting negative effects on population viability.

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Authors and Affiliations

Manrico Sebastiano^{1,2}  · David Costantini¹ · Marcel Eens²  · Kevin Pineau³ · Paco Bustamante^{4,5}  · Olivier Chastel⁶

¹ UMR 7221 CNRS/MNHN, Physiologie Moléculaire Et Adaptation Group, Muséum National d'Histoire Naturelle, 7 rue Cuvier, 75005 Paris, France

² Behavioural Ecology and Ecophysiology Group, Department of Biology, University of Antwerp, Universiteitsplein 1, 2610 Wilrijk, Belgium

³ Groupe d'Etude et de Protection Des Oiseaux en Guyane (GEPOG), 431 route d'Attila Cabassou, 97354 Remire-Montjoly, French Guiana, France

⁴ Littoral Environnement et Sociétés (LIENSs), CNRS & La Rochelle Université, 2 rue Olympe de Gouges, 17000 La Rochelle, France

⁵ Institut Universitaire de France (IUF), 1 rue Descartes, 75005 Paris, France

⁶ Centre d'Etudes Biologiques de Chizé (CEBC), CNRS & La Rochelle Université, F-79360 Villiers-en-Bois, France