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LETTER

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Food supplementation protects Magnificent frigatebird chicks against a fatal viral disease

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Abstract
Outbreaks of wildlife diseases are occurring at an unprecedented rate. In French Guiana, recurrent episodes of frigatebird chicks' mortality due to a viral disease that first appeared in 2005 have recently turned into massive mortality episodes (85–95%) of chicks. One of the suggested hypotheses behind the appearance of the disease is food limitation due to the recent decline of local shrimp fishery boats on which frigatebirds rely for opportunistic feeding. We therefore experimentally fish-supplemented frigatebird chicks with and without clinical signs of the disease. Food supplementation protected all chicks from the appearance of clinical signs of the disease and increased survival perspectives of sick chicks. These results suggest that food shortage might decrease resistance of chicks to infectious diseases and that using a specifically tailored food supplementation regime could be a complimentary tool to protect frigatebirds and other endangered birds from disease outbreaks threatening them with extinction.

KEYWORDS
avian diseases, avian glucocorticoid, emerging infectious diseases, food limitation, frigatebirds, seabirds

1 | INTRODUCTION

There is growing recognition that infectious diseases impact negatively wildlife (Smith, Sax, & Lafferty, 2006). Much effort has been dedicated to emphasize the role of infections in species endangerment (Smith et al., 2006) and to develop protective procedures against pathogens (Bourret et al., 2018). Yet, outbreaks of infectious diseases are occurring at an unprecedented rate due to global changes (Altizer, Ostfeld, Johnson, Kutz, & Harvell, 2013; Cunningham, Daszak, & Wood, 2017). Understanding the factors that favor the activity of infectious diseases is thus a critical priority in conservation biology.

Food shortage causes physiological stress (Kitaysky, Piatt, & Wingfield, 2007) and reduces immune function (Gasparini, Roulin, Gill, & Boulinier, 2006), which might make organisms less resistant to infections. Previous work has investigated how the nutritional status of the host can influence the outcome of the infection (e.g., Becker, Streicker, & Altizer, 2015; Murray, Becker, Hall, & Hernandez, 2016; Tollington et al., 2015; Sánchez et al., 2018). Recent meta-analyses showed that food provisioning results in highly heterogeneous infection outcomes that depend on pathogen type (Becker et al., 2015; Sánchez et al., 2018). Becker et al. (2015) also showed that the effects of food provisioning on viral infections are underrepresented as compared to other pathogens (e.g., helminths, protozoans). Also, limited information is available for specific taxa, such as seabirds. Seabirds aggregate at high densities during the breeding season, thus are strongly susceptible to changes in food availability (Velando, Ortega-Ruano, & Freire, 1999) and disease outbreaks (Schoombie et al., 2017; Weimerskirch, 2004). Seabirds are also currently facing a strong decline in food resources due to climate change (Cahill et al., 2013) and overfishing (Wagner & Boersma, 2011), and are among the most threatened avian groups (Croxall et al., 2012).

Grand Connétable is a small rocky island located near the coasts of French Guiana (South America), which hosts approximately 1,300 reproductive pairs (unpublished data) of Magnificent frigatebird *Fregata magnificens* (described in Sebastiano et al., 2017a). This frigatebird population is considered as one of the most important along the Atlantic coast of South America (Nuss, Caio, Ignacio, & Nelson, 2016). In recent years, recurrent episodes of frigatebird chicks' mortality due to disease outbreaks that first appeared in 2005 (de Thoisy et al., 2009) have turned into massive mortality episodes (85–95% of chicks) that occur annually (Sebastiano et al., 2017b). The disease is characterized by the appearance of visible clinical signs (i.e., skin crusts) that can rapidly spread all over the chicks' body, giving in most cases no chances of recovery (Sebastiano et al., 2017c; Sebastiano et al., 2018). Microscopic evaluation of skin lesions, attempts of bacterial cultures, viral screening and PCR analyses of skin crusts and cloacal swabs identified the presence of a herpesvirus with up to several million copies of viral DNA in sick individuals (de Thoisy et al., 2009; Sebastiano et al., 2017b). These analyses also excluded the presence of ectoparasites, poxvirus, and avian influenza (de Thoisy et al., 2009; Sebastiano et al., 2017b), suggesting that the clinical signs are most likely only due to the herpesvirus activity.

One way to increase the survival of infected animals in the wild is to create vaccines (Bourret et al., 2018). However, the feasibility of this approach may be very limited to some specific wildlife pathogens (Bourret et al., 2018) and could prove useless when the environmental conditions that contribute to disease outbreaks remain unchanged. It is therefore of crucial importance to identify and manage the environmental factors that underlie infectious disease outbreaks. As in other seabird species, frigatebirds can adopt an opportunistic feeding behavior during the breeding season that enables them to benefit from fishery discards (Calixto-Albarran & Osorno, 2000; Martinet & Blanchard, 2009). In French Guiana, the first outbreaks of the disease overlapped with a strong decline in the shrimp fishery activity. Right after the shrimp fishery decline, some frigatebirds were struggling to feed their chicks (Martinet & Blanchard, 2009). Hence, one of the suggested hypotheses behind the appearance of these clinical signs in frigatebirds is food limitation (Martinet & Blanchard, 2009), although direct evidences are so far lacking.

Here, we tested whether food availability constrains the capacity of Magnificent frigatebird chicks to cope with a fatal viral disease. We supplemented birds either with or without clinical signs of the disease with fish. Unsupplemented birds either with or without clinical signs were used as controls. Of each bird, we measured the body condition (i.e., body mass normalized by body size) and the plasma concentration of the avian glucocorticoid corticosterone (CORT) before and after the supplementation. The quantification of CORT was carried out because baseline CORT may reflect food availability (Kitaysky et al., 2007), a decrease in food supply is associated with an increase in CORT (Kitaysky et al., 2007), and a chronic exposure to CORT can be immunosuppressive (Shini, Huff, Shini, & Kaiser, 2010) and might thus increase the susceptibility to viral infection. This experimental design enabled us to investigate whether: (i) food supplementation protects healthy chicks from the appearance of clinical signs; (ii) food supplementation increases resilience and survival of sick birds; and (iii) CORT production is one endogenous mechanism linking food availability to the progress of the disease. If the appearance of clinical signs is tied to food shortage, we should expect an increased capacity to cope with the disease in food-supplemented birds.

2 | MATERIALS AND METHODS

The study was conducted in 2017 on Grand Connétable island (4°49′30N; 51°56′00W). Frigatebird chicks (25 without and 35 with clinical signs) approximately 4 months old were randomly selected and captured on the nest. A blood sample was collected within 3 minutes from capture. Body mass and beak length (proxy of body size) were also measured, and an aluminum ring was used for individual recognition. At the end of the food-supplementation experiment (please see Supplementary Material for detailed information), a second sample of blood was taken and body mass and beak length were measured again. Blood was used to measure plasma levels of the stress hormone corticosterone (CORT, expressed as ng/mL) following a previous protocol (Lormée, Jouventin, Trouve, & Chastel, 2003). Two pictures of each bird were taken from the same distance and same position before the start and at the end of the experiment. The pictures were used to classify the chicks based on severity of visible clinical signs ("*no signs*," "*mild*," and "*severe*;" Figure 1), which are important to assess the progress of a herpesvirus-induced disease (e.g., Thomas, Hunter, & Atkinson, 2007) and are associated with diverse physiological markers of health status (Sebastiano et al., 2017b,c). This approach enabled us to determine any changes in chicks' health status: did not have any clinical signs at the beginning of the experiment but showed them at the end of the experiment ("*new sick*"); never showed clinical signs ("*always healthy*"); showed a

FIGURE 1 Frigatebird chick classification based on the severity of visible clinical signs of the disease: (a) "no signs," (b) "mild," and (c) "severe."

decrease in clinical signs over the experiment ("*better condition*"); did not show any changes in the severity of visible clinical signs ("*same severity*"). All statistical models about the body mass included the beak length as a covariate to adjust the body mass for the body size, thus providing an estimate of the body condition (García-Berthou, 2001). Similar outcomes were obtained when body size was not included as a covariate (data not shown). Two general linear models were used to test whether there were any differences among groups in pretreatment values of body condition and CORT: (i) among chicks classified on the severity of clinical signs (*no signs*, *mild*, and *severe*); and (ii) among chicks classified according to the progress of the disease (*always healthy*, *new sick*, *better condition*, *same severity*, including chicks that did not survive over the course of the experiment, hereafter "*did not survive*"). To test the effect of food-supplementation, linear mixed models with a repeated measure design were used. The body mass and CORT were included as dependent variables, respectively. Experimental group, sampling period (pre- or posttreatment), treatment (supplemented or not), and their interactions (including the three-way interaction) were included as fixed factors and the factor individual was included as a random factor. The beak size was included as a covariate in the model about body mass (García-Berthou, 2001). For each variable, we ran two linear mixed models. The first model (Model 1) included four experimental groups: unsupplemented healthy; unsupplemented sick; food-supplemented healthy; food-supplemented sick chicks (Table S1). The second model (Model 2) also included four groups: always healthy; new sick; better condition; same severity. Both general and linear mixed models including chicks classified according to the progress of the disease were only run on control individuals. This is because the treatment influenced the probability to show clinical signs, of a decrease in visible clinical signs, or death (tested with generalized linear models with a binomial error distribution and a logit link function, Likelihood-ratio test LRT). Finally, CORT values were square-root transformed to achieve normality of residuals. Data points were considered outliers and removed from the models when their standardized residual exceeded ± 3 SD (e.g., Tukey, 1977). Outcomes of models were unchanged if outliers were included in the model (Supplementary Material). All analyses were performed in R v.3.3.1.

3 | RESULTS

Of the 25 chicks without clinical signs at the start of the experiment, seven unsupplemented chicks showed the appearance of clinical signs at the end of the experiment. Of the 35 sick chicks, three were found dead (all unsupplemented), and 12 had a reduction of their visible clinical signs (5 unsupplemented, 7 food-supplemented). Five chicks without clinical signs and two sick chicks were not found at the end of the experiment, thus were not included in the models about the progress of the disease because we could not know their final health status.

Before the start of the experiment, chicks divided on the severity of clinical signs had similar CORT levels (all $t < 1.04$, all $P > 0.56$, Table 1) and similar body condition (all $t < 1.62$, all $P > 0.25$, Table 1). Before the start of the experiment, unsupplemented chicks that were found dead at the end of the experiment had a significantly lower body condition than the ones that survived (all $t > 3.10$, $P < 0.04$, Table 1), while all chicks divided on the progress of the disease had similar CORT levels (all $t < 2.27$, all $P > 0.19$, Table 1).

Unsupplemented healthy chicks had a strong decrease in their body condition over the experiment (Model 1: $t = 3.63$, $P = 0.016$; Table 2, Figure 2a), whereas the body condition of the other groups did not change significantly (Model 1: all $t < 0.52$, all $P > 0.99$; Table 2). There were no differences in the reduction of the body condition among the groups classified according to the progress of the disease (Model 2: group*period, $F = 2.43$, $P = 0.095$; Table 2), indicating that both the chicks that showed the appearance of clinical signs and the ones that did not show a similar reduction of the body condition. CORT levels increased in sick supplemented chicks (Model 1: $t = -3.34$, $P = 0.032$; Figure 2b, Table 2).

Unsupplemented chicks had a higher probability to show the appearance of clinical signs (LRT = 9.60, $P = 0.002$, Figure 3a) and to die (LRT = 5.09, $P = 0.024$, Figure 3c) than food-supplemented chicks. The probability to show a decrease in visible clinical signs did not differ between supplemented

TABLE 1 Linear models on the body condition (expressed as marginal means of body mass (in grams) extracted from models with body size as a covariate) and sqrtCORT (ng/mL) of the birds before the start of the experiment. The model based on the progress of the disease (groups: *always healthy, new sick, better condition, same severity, did not survive*) included only unsupplemented birds. Birds that were not found at the second sampling period are also included. One outlier for body condition was found and excluded from the model based on the severity of clinical signs. Groups that share the same letter showed nonsignificant differences. CI = 95% confidence interval

		Body condition (g)					sqrtCORT (ng/mL)				
	Group	Mean	*n*	Lower CI	Upper CI	Comparison	Mean	*n*	Lower CI	Upper CI	Comparison
Severity of clinical signs	No signs	1355	25	1298	1412	a	4.16	25	3.29	5.02	a
	Mild	1389	19	1323	1456	a	4.22	19	3.04	5.41	a
	Severe	1303	15	1225	1382	a	3.40	16	2.34	4.47	a
	Group	Mean	*n*	Lower CI	Upper CI	Comparison	Mean	*n*	Lower CI	Upper CI	Comparison
Progress of the disease	*Always healthy*	1430	5	1309	1551	a	3.77	5	2.66	4.88	a
	New sick	1348	7	1250	1446	a	3.78	7	2.16	5.40	a
	Better condition	1413	5	1297	1530	a	2.26	5	1.72	2.80	a
	Same severity	1388	7	1288	1485	a	3.06	7	0.99	5.13	a
	Did not survive	1061	3	896	1225	b	5.72	3	2.88	8.56	a

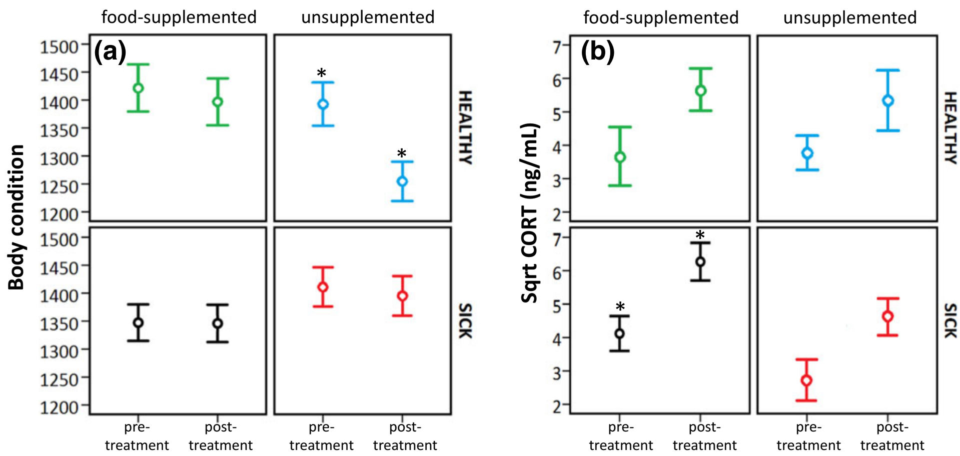

FIGURE 2 Results of the linear mixed model that includes the birds divided on the presence/absence of clinical signs (Model 1) on (a) the body condition (expressed as marginal means of body mass (in grams) extracted from models with body size as a covariate) and (b) sqrtCORT (ng/mL). Experimental groups: food-supplemented healthy (green, $n = 8$); food-supplemented sick (black, $n = 18$); unsupplemented healthy (blue, $n = 12$); and unsupplemented sick (red, $n = 12$). Asterisks indicate that a significant increase/decrease occurred over the course of the experiment (pre- to posttreatment). Three outliers for body condition and one outlier for CORT were found and removed from the model. Data are shown as mean ± standard error

and control chicks (38.9% vs 33.3%, LRT = 0.11, $P = 0.74$, Figure 3b).

4 | DISCUSSION

Chicks that were supplemented with fish had a lower probability to develop an infection, as indicated by the lack of clinical signs, and a higher probability to survive to the disease as compared to chicks that did not receive extra fish. These results provide a clear indication that chicks exposed to reduced food availability might be more susceptible to the considered infectious viral disease.

Food shortage has been identified as one of the main causes of chicks' mortality (de Jong, van Riel, Lourens, Bracke, & van den Brand, 2016; Velando et al., 1999). Nutritional stress compromises immune function of birds (Alonso-Alvarez & Tella, 2001; Gasparini et al., 2006), a mechanism that may be mediated by the action of CORT, which is released when there is food shortage in some bird species (Kitaysky et al., 2007). However, we found no evidences in support of this hypothesis in our study species. Baseline CORT increased slightly in supplemented sick birds. Given that frigatebird chicks experience regularly short periods of fasting during the entire growth period (Osorno, 1996), it might be that they do not need to upregulate production of CORT to cope with episodes of food

TABLE 2 Outcome of the linear mixed models (Model 1 and 2) performed on body condition (expressed as marginal means of body mass (in grams) extracted from models with body size as a covariate) and sqrtCORT (ng/mL) of those birds for which we had two measurements (pre- and posttreatment) (coefficient estimates are reported in Table S1). The mixed model based on the progress of the disease (Model 2: groups *always healthy*, *new sick*, *better condition*, *same severity*) was only run on unsupplemented birds. Significant *P*-values are shown in bold

		Pretreatment body condition (g)			Posttreatment body condition (g)				
	N	Mean	Lower CI	Upper CI	Mean	Lower CI	Upper CI	Diff.	*P*-value
Model 1									
Unsupplemented healthy	12	1395	1325	1464	1256	1187	1326	–139	**0.016**
Unsupplemented sick	12	1411	1341	1481	1394	1324	1464	–17	0.99
Food-supplemented healthy	8	1422	1336	1508	1398	1311	1484	–24	0.99
Food-supplemented sick	16	1348	1290	1407	1347	1287	1407	–1	0.99
Model 2									
Always healthy	5	1434	1312	1556	1221	1098	1343	–213	0.10
New sick	7	1357	1256	1459	1273	1171	1376	–84	0.85
Better condition	5	1426	1304	1547	1332	1211	1452	–94	0.88
Same severity	7	1395	1293	1496	1430	1328	1531	+35	0.99
		Pretreatment sqrtCORT (ng/mL)			**Posttreatment sqrtCORT (ng/mL)**				
Model 1									
Unsupplemented healthy	12	3.78	2.48	5.07	5.34	4.04	6.64	+1.57	0.46
Unsupplemented sick	12	2.73	1.43	4.03	4.62	3.32	5.92	+1.89	0.23
Food-supplemented healthy	8	3.66	2.07	5.25	5.65	4.07	7.24	+1.99	0.41
Food-supplemented sick	17	4.12	3.06	5.18	6.24	5.15	7.32	+2.12	**0.032**
Model 2									
Always healthy	5	3.77	1.67	5.86	6.68	4.58	8.77	+2.91	0.35
New sick	7	3.78	2.01	5.55	4.39	2.62	6.16	+0.61	0.99
Better condition	5	2.26	0.16	4.35	4.37	2.27	6.46	+2.11	0.71
Same severity	7	3.06	1.29	4.83	4.79	3.02	6.56	+1.73	0.74

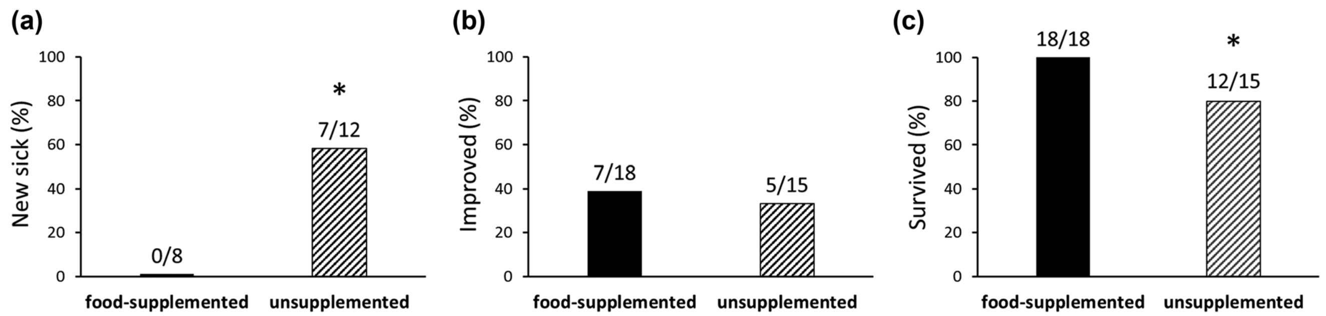

FIGURE 3 Effect of food supplementation on the percentage of birds that: (a) showed the appearance of clinical signs at the end of the experiment; (b) had a reduction of their visible clinical signs; and (c) survived over the course of the experiment. Asterisks indicate a significant difference between the experimental groups (tested with generalized linear models with a binomial error distribution)

shortage. CORT is also not dependent on the time of sampling in our species (Sebastiano et al., 2017c). Blood was collected within three minutes in all birds, thus CORT reflected baseline levels (Romero & Reed, 2005). However, we cannot exclude that our repeated manipulation of chicks increased basal production of CORT. It might also be that sick chicks had a dysregulated activity of their hypothalamic–pituitary–adrenal (HPA) axis, which may occur when being exposed to chronic stress (Rich & Romero, 2005). Increased food intake might have helped them to restore the HPA axis function, causing an increased release of CORT. Further studies will be needed to test the above explanations. It will also be important to test the response of immune and inflammatory markers to the food supplementation (i.e., white blood cells; Davis, Maney, & Maerz, 2008).

Our results provided evidence that nutritional stress might reduce the capacity of offspring to cope with a viral disease. If the disease were responsible for a reduction in the chicks' body condition, we would have expected a decrease in body condition to occur only in birds that showed the appearance of clinical signs over the experiment. However, we also observed a reduction in body condition in individuals that did not show the appearance of clinical signs, indicating that the loss of individual's body condition might be a cause rather than a consequence of the disease. These results open to two possible scenarios. A first scenario suggests that during the developmental period local food resources are limited and adult frigatebirds struggle to feed their chicks. In addition to the decline in shrimp fishery activity, illegal fishing is also leading to the decline of large marine predators (Artero et al., 2015; IUCN, 2017), to which frigatebirds may rely on for opportunistic feeding. A second scenario points out a potential very variable investment of the male into reproduction (18–161 days; Osorno, 1996), which would make some females in trouble to provide enough food to their offspring after the male abandons the nest. Both scenarios, however, do not explain why the reduction in chicks' body condition did not also occur in unsupplemented sick birds, thus further investigations are warranted.

It is unclear whether the beneficial effects of food supplementation in preventing the progress of the disease are long-lasting and whether there may be long-term benefits of food supplementation beyond increasing the survival probability until fledging. If the effect of food supplementation is limited to improving the fledging rate, the question then is whether this stabilizes the population. This is very important for the frigatebird population in Grand Connétable. First, although no apparent decline in the breeding population size has been observed yet, the massive mortality events of chicks that have occurred over the past years make the viral outbreaks as the most immediate threat for its long-term viability. In long-lived birds with low fecundity and a lifespan above 30 years as is the case for Magnificent frigatebirds, even a small chick mortality has been recently proved to have important negative demographic effects (Finkelstein, Doak, Nakagawa, Sievert, & Klavitter, 2010). Second, the frigatebird population in Grand Connétable functions as a bridge for gene flow among the frigatebird populations breeding in Brazil and in the Caribbean (Nuss et al., 2016). The current exchange of individuals among those populations is fundamental to maintain genetic connectivity and likely moderates the negative effects associated with chicks' mortality. Thus a population collapse in Grand Connétable might reduce gene flow across frigatebird populations, leading to genetic isolation and, possibly, reduction of genetic variation. However, exchange of individuals might also facilitate the spread of the viral disease, which stresses the need to further study exposure to herpesviruses in potentially connected seabird populations (Niemeyer et al., 2017). Visible clinical signs of the disease have been recorded in breeding males and females in both French Guiana and Barbuda in 2017 (unpublished data), providing evidence that the virus is already present in other populations. However, neither visible clinical signs nor mortality events in chicks have been yet recorded in Barbuda and in other areas, which further emphasizes the importance of looking at local environmental factors that favor the appearance and progress of the disease. Given the central role of the Grand Connétable population, improvement of future conservation plans and laws that regulate local fishing activities will be fundamental. GPS-tracking of adult frigatebirds also showed that they forage in the southern waters along the coasts until Brazil, covering a distance of over 200 km on average (Sebastiano et al., 2016). The northern Brazilian coasts would therefore be a target hotspot for the creation of multiple marine protected areas, where fishing is strictly regulated to provide enough foraging territory and food for frigatebirds. These actions might be implemented through the Brazilian Blue Initiative by the Brazilian Ministry of Environment and the Federal Protected Areas Agency (ICMBio—Chico Mendes Institute).

Avian herpesviruses have a worldwide distribution and, when outbreaks occur, the mortality can be massive (e.g., Thomas et al., 2007). Our work makes the point that research on herpesvirus infections should be part of health monitoring programs for wild birds, which is rarely done (Niemeyer et al., 2017; Thomas et al., 2007). The worrying conservation status of many seabird species has prompted numerous agreements and laws, such as the Marine Strategy Framework Directive of the European Union, the Convention for the Protection of the Marine Environment of the North–East Atlantic or the Agreement on the Conservation of Albatrosses and Petrels. Our work points out that conservation strategies might be more effective when implementation of a sustainable development of fisheries will take into account more strongly the relevance of particular stages of the bird life cycle, such as the chick rearing period where food availability and predictability of food abundance are dramatically important. Scaling up food supplementation as a management tool to other species groups might also prove important, but a refined understanding of feeding ecology is needed. For example, many seabirds accept easily food and do not need to be forced fed. Also, many birds of prey use supplementary feeding stations. Food provisioning during critical stages of life and, possibly, food enrichment with antiviral molecules (Sebastiano et al., 2018) may improve conservation actions further. Food supplementation might also be particularly important as a complimentary tool in vaccination programs for other pathogens to increase the nutrients needed to sustain the immune system and to protect those birds that do not produce any antibodies (Klasing, 2007).

In conclusion, our work showed that food shortage might be one relevant environmental factor that favors the viral outbreak in our frigatebird population. It also identified a potential way of increasing resistance of chicks to develop a disease. A longer-term treatment would prove useful to understand whether food supplementation has long-term consequences for mitigating infection risk. Our approach will be relevant for the conservation of this and other species suffering outbreaks of herpesviruses and, possibly, other pathogen strains. Thus, our work should be of particular relevance for both governmental and nongovernmental organizations involved in the regulation of sustainable exploitation of marine resources and conservation of animals threatened by infectious diseases.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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