Research Paper

Seabird predation effects and population viability analysis indicate the urgent need for rat eradication from Europa Island, western Indian Ocean

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ABSTRACT. Rats are among the worst invasive alien predators. They prey upon eggs, chicks, and sometimes adults of seabirds, leading to the decline of many populations. Rats have invaded 93% of the islands in the western Indian Ocean, which is an avian biodiversity hotspot. Europa Island, Mozambique Channel, is a major seabird breeding site, where at least 1,000,000 pairs bred at the end of 20th century, including the endemic white-tailed tropicbirds (*Phaethon lepturus europae*). This species and the red-tailed tropicbird (*Phaethon rubricauda*) are vulnerable to predation by black rat (*Rattus rattus*), barn owl (*Tyto alba*), and pied-crow (*Corvus albus*) on Europa Island. In this study, we estimate the current population sizes of these tropicbird species and their breeding success. The impact of predators on tropicbird nests was quantified with camera traps. Finally, we model the dynamics of these populations under three management scenarios (no action, complete rat eradication, and targeted control of rats around nests). In 2019, 1,027 pairs of red-tailed and 100 pairs of white-tailed tropicbirds bred on Europa Island, which indicates an annual decline of 5% and 17% since 2009, respectively. Breeding success of red-tailed tropicbirds and white-tailed tropicbirds was extremely low (0.08 ± 0.07 and 0.06 ± 0.03 respectively). Rats were detected at most surveyed nests and were the main predators of eggs and chicks. Pied-crows and barn owls also depredated nests occasionally. Population viability analysis projected a local extinction in 32–85 years for the red-tailed tropicbird, and in 11–50 years for white-tailed tropicbirds without conservation intervention. The complete eradication of rats would result in a rapid recovery of both populations. Rat control around nests only would result in population recovery only if 74% of the nests of white-tailed and 63% of the nests of red-tailed tropicbirds are free of rats.

Une analyse des effets de la prédation des oiseaux de mer et de la viabilité de la population révèle un besoin urgent d'éradication des rats dans l'île Europa, dans l'ouest de l'océan Indien

RÉSUMÉ. Les rats font partie des prédateurs étrangers les plus invasifs. Ils se nourrissent d'œufs, d'oisillons et parfois d'oiseaux de mer adultes, ce qui provoque le déclin de nombreuses populations. Les rats ont envahi 93 % des îles de l'ouest de l'océan Indien, qui est un haut lieu de biodiversité aviaire. L'île Europa, dans le canal du Mozambique, est un site majeur de reproduction des oiseaux, puisqu'au moins un million de couples s'y reproduisaient à la fin du XXe siècle, notamment le phaéton à bec jaune (*Phaethon lepturus europae*). Cette espèce, ainsi que le phaéton à brins rouges (*Phaethon rubricauda*) est vulnérable à la prédation par le rat noir (Rattus rattus), la chouette effraie(*Tyto alba*) et le corbeau-pie (*Corvus albus*) sur l'île Europa. Dans cette étude, nous estimons la taille des populations de ces espèces d'oiseaux tropicaux et le succès de leur reproduction. L'impact des prédateurs sur les nids de phaétons a été quantifié à l'aide de pièges photographiques. Enfin, nous modélisons la dynamique de ces populations dans trois scénarios de gestion (aucune action, éradication complète des rats et contrôle ciblé des rats autour des nids). En 2019, 1 027 couples de phaétons à brin rouge et 100 couples de phaétons à bec jaune se sont reproduits sur l'île Europa, ce qui correspond respectivement à un déclin annuel de 5 % et de 17 % depuis 2009. Le succès de la reproduction des phaétons à brin rouge et des phaétons à bec jaune était extrêmement faible (0,08 ± 0,07 et 0,06 ± 0,03 respectivement). Des rats ont été détectés autour de la plupart des nids surveillés et étaient les principaux prédateurs d'œufs et d'oisillons. Les corbeaux-pie et les chouettes effraie détérioraient parfois également les nids. L'analyse de viabilité de la population projetait une extinction locale d'ici 32 à 85 ans pour le phaéton à brin rouge et d'ici 11 à 50 ans pour le phaéton à bec jaune sans intervention de conservation. L'éradication complète des rats entraînerait le rétablissement rapide des deux populations. Pour que le contrôle des rats à proximité des nids permette le rétablissement de la population, il faudrait que 74 % des nids de phaétons à bec jaune et 63 % des nids de phaétons à brin rouge soient débarrassés des rats.

Key Words: *conservation; eradication; management; population viability analysis; predation; seabird*

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INTRODUCTION

Seabirds are among the most threatened group of birds (Butchart et al. 2004, Croxall et al. 2012, Dias et al. 2019). In 2018, 31% of seabird species were classified as globally threatened (BirdLife International 2018). In 2019, 47% of seabird species were suspected to decline (BirdLife International 2019) because of threats acting on land and at sea, with cumulative effects on population dynamics. Invasive alien predators, fishery by-catches and climate change are the worst threats to seabirds (Dias et al. 2019). Invasive alien mammals are responsible, directly (by predation) or indirectly (e.g., by facilitation of other predators), for 42% of bird extinctions on islands (Atkinson 1985, Jones et al. 2008). Rats (*Rattus rattus*, *Rattus exulans*, and *Rattus norvegicus*) have been introduced and have invaded more than 80% of the island groups of the world (Atkinson 1985). They are among the worst invasive alien predators of seabirds (Jones et al. 2008). They reduce breeding success by eating eggs and chicks (Atkinson 1985, Thibault 1995, Pascal et al. 2008). They can also prey upon adults of small seabird species like storm petrels (all species of the families Hydrobatidae and Oceanitidae) and noddies (*Anous* spp.) (Atkinson 1985, Elst and Prŷs-Jones 1987, Jones et al. 2008).

The Western Indian Ocean (WIO) is a stronghold for tropical seabirds with 31 breeding seabird species, totaling about 7.4 million pairs of breeding adults (Le Corre et al. 2012, Danckwerts et al. 2014). Although 93% of island groups of the WIO are invaded by rats (Russell et al. 2016), few data are available on the demographic impacts of rats on seabirds of the region (but see Le Corre et al. 2015, Ringler et al. 2015). Europa (3059 ha, 22° 22′S, 40°22′E), a French island of the Mozambique Channel (Fig. 1) administrated by Terres Australes et Antarctiques Françaises (TAAF), is one of these invaded islands. The first inhabitants of Europa were probably castaways, who were wrecked because the exact location of the island was mistaken for Bassas da India (21° 29′10″S, 39°40′51″E), a submerged atoll of the southern Mozambique Channel (Paulian 1950). Although this part of Europa's history is poorly documented (but see Le Corre and Jouventin 1997), it is likely that black rats (*Rattus rattus*) were introduced before 1860 on the atoll, during one of these wrecks (Russell and Le Corre 2009). Indeed, when the first voluntary inhabitants settled on the island to fish and hunt turtles, rats were already present (Le Corre and Jouventin 1997, Russell and Le Corre 2009). Rats are now very abundant on Europa (average density of 8–65 rats/ha^{-1}, depending on the seasons and habitats; Russell et al. 2011, Ringler et al. 2015, 2021). Currently, the only human occupancy of Europa consists of a military detachment, TAAF rangers, and scientists representing 15–20 people living on the island with a turnover every 45–60 d.

At the end of the 20th century, eight seabird species, representing at least 1,000,000 pairs, were breeding on Europa (Le Corre and Jouventin 1997) (Append. 1). Europa was classified as a Nature Reserve in 1975 by prefectural decree (no. 13/DG/IOI). It has been considered an international sanctuary for seabirds since 1997 (Le Corre and Jouventin 1997) and identified as an Important Bird Area since 2001 (IBA RE012, Le Corre and Safford 2001). The island was also designated as a Ramsar site in 2011 (Ramsar no. 2073). These protection statutes identify Europa as a globally important site for biodiversity conservation, providing a remarkable terrestrial and marine biological diversity,

particularly for seabirds (Le Corre and Jouventin 1997). However, seabird populations on the island are exposed to several threats, the most important being predation by rats (Le Corre and Jouventin 1997, Ringler et al. 2015).

Fig. 1. Geographic location and characteristics of Europa Island.
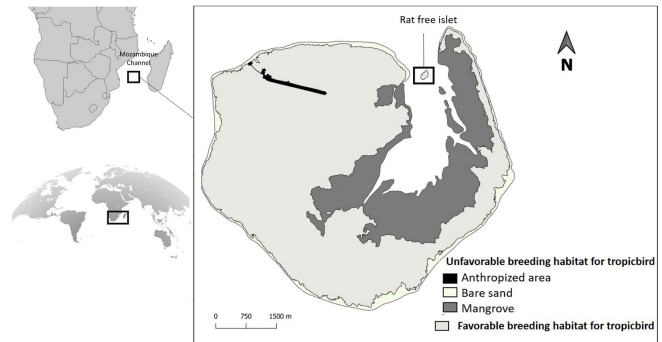
This paper focuses on the two tropicbird species that breed on Europa: the red-tailed tropicbird (*Phaethon rubricauda*) and the white-tailed tropicbird (*Phaethon lepturus europae*). Both species are ground-nesting seabirds and are thus particularly vulnerable to rat predation. The white-tailed tropicbird (WTTR) is represented on Europa by a critically endangered endemic subspecies (Le Corre and Jouventin 1999). A recent study including all subspecies of WTTR in the world confirmed the endemic status of this small population and demonstrated a very strong genetic isolation of the birds of Europa (Humeau et al. 2020).

In addition to black rats, two land birds, the barn owl (*Tyto alba*) and the pied-crow (*Corvus albus*), can also depredate nests of tropicbirds (Ringler et al. 2015). It is not known if barn owls were introduced on Europa by early inhabitants to control the rat population, as in the Seychelles and Hawaii (e.g., Tomich 1962, Au and Swedberg 1966) or if the population is native. However, their presence is undoubtedly facilitated by the presence of rats, which are now the main prey of barn owls (Ringler et al. 2015). The introduction of rats benefited barn owls, which probably increased in number, leading to a possible increase of barn owl predation on seabirds, the so-called hyperpredation process (Courchamp et al. 2000, Ringler et al. 2015). The pied-crow population is probably native to the island, but this anthropophilic species has benefited from the permanent settlement of humans since 1970 because they take advantage of waste and freshwater tanks provided by people (Le Corre and Jouventin 1997, Le Corre and Safford 2001). Their current population is thus probably favored by human settlement. We estimate that 100–200 pairs of pied-crows (*unpublished data*, authors) and 15–20 pairs of barn owls currently breed on Europa (*unpublished data*, authors).

The breeding success of both tropicbird species is very low on Europa (Ringler et al. 2015). Although predation by rats, pied-crows, and barn owls is the main cause of this very low breeding success (Le Corre and Jouventin 1997, Ringler et al. 2015), the impact of each of these predators has never been properly quantified. It is important to identify the role of each of these potential predators to implement adapted conservation actions.

Furthermore, the long-term impact of such a low breeding success on the viability of the populations remains unknown.

The goals of our study were thus (1) to quantify the relative impact of the different predators on tropicbird nests by coupling camera trap surveys with monitoring of the breeding success; (2) to estimate the current population sizes of both species, and (3) to perform a population viability analysis (PVA; Boyce 1992) to project the future of these two populations. We will also use the PVA to predict the demographic impacts of three management options: (1) no action, (2) complete rat eradication, and (3) targeted rat control at nests (Jones 2010, Towns et al. 2013, Jones et al. 2016). The last scenario was explored because rat eradication is not immediately possible, so we explored an interim option controlling rats at only a certain proportion of nests. The goal of this specific analysis is to determine the proportion of controlled nests required to avoid decline of the tropicbird populations.

METHODS

Study Species and Site
Europa is a coralline island of about 3,059 ha of which 836 ha is mangrove. There are two seasons on Europa: a dry and cool season during austral winter (April to October), and a warm and wet season during austral summer (November to March; Le Corre and Jouventin 1997). All terrestrial habitats of the island (except sandy beaches, rocky shore, and mangrove) are used as breeding habitats by both species of tropicbird. This represents 2,246 ha of favorable breeding habitat. Europa is invaded by rats and also by goats (*Capra hircus*), which are known to have a negative impact, especially on the vegetation (Le Corre and Jouventin 1997).

In 1974 and 1997, the population size of WTTR was estimated to be more than 1,000 pairs (Barré and Servan 1988, Le Corre and Jouventin 1997). Although the current population size is not known, recent data suggest that the population is decreasing (*personal communication*, TAAF, and see Results). This declining trend is confirmed by genetic analyses, which showed an undated reduction of population size (Humeau et al. 2020). According to the genetic isolation and rapid population decline, the WTTR of Europa is regarded as a critically endangered endemic sub-species and needs urgent conservation actions to avoid the loss of an entire and unique gene pool (Humeau et al. 2020). On Europa, the WTTR breeds in crevices within the ancient coral substrates, between tree roots, or under dead trees. It breeds asynchronously all year round (Le Corre 2001).

The red-tailed tropicbird (RTTR) is an Indo-Pacific species (Marchant and Higgins 1993). In 1997, the population size on Europa was estimated between 3,000 and 4,000 pairs, making it the largest RTTR colony of the WIO (Le Corre and Jouventin 1997). Recent observations suggest that the population has strongly declined over the last few decades (*personal communication*, TAAF, and see Results), but the current population size is not known. The RTTR breeds synchronously during austral summer at Europa (Le Corre 2001). It breeds under bushes of *Pemphis acidula* and *Suriana maritima*, under dense tussocks of *Sclerodactylon macrostachyum*, or under uprooted silver thickets (*Euphorbia stenoclada*). Red-tailed tropicbirds lay one egg per clutch, incubation period is 42 d, and mean chick rearing period is 89 d (Fleet 1972).

Identification of Seabird Predators by Camera Trap Survey
From 25 July 2019 to 7 August 2019, 12 December 2019 to 27 January 2020, and 4 June 2020 to 26 July 2020, we monitored tropicbird nests with infrared camera traps (Bushnell Aggressor and Stealth Cam) in photographic mode (24 h/d, motion detection activated with high sensitivity, medium LED Control, three pictures per occasion, and 10 sec until a new detection). Thirteen WTTR nests were surveyed: eight in incubation stage and five in chick-rearing stage. Eighteen RTTR nests were surveyed: all in incubation stage (five of them were also surveyed after hatching, thus during the first part of the chick rearing).

All pictures were visually analyzed. We noted each animal observed—with special attention to species—that interacted at least once with tropicbirds. The number of observations of each of these species was noted. The behavior of each potential predator was then described as follows: approaching the nest, visiting the nest (i.e., going inside the nest), and attacking or attempting to attack the adult, the chick, or the egg. We also defined a "suspected predation" as an observation of a potential predator entering where immediately after the nest subsequently failed, but with no clear image showing the predation. For all statistical analysis, "suspected predation" has been considered as predation. We compared the observation frequency of species other than tropicbirds with two log-linear (Poisson) generalized linear models. The response variable is the number of times an animal was seen in the photos, and the explanatory variables are (1) predator species, and (2) predator's behavior. We did not test the effect of breeding stage on predator behavior or number of visits because too few nests were surveyed until hatching.

In order to assess whether the success of a given nest was related to the number of rats observed at this nest during the camera trap survey, we tested the influence of the number of rats observed on the fate of all RTTR nests surveyed with camera traps and for which the breeding outcome was known (n = 18 nests). For these nests, we tested the relationship between the number of visits and approaches by rats and the breeding success of the nest with two logistic regressions (one regression for the hatching success and one regression for the fledging success), separating visits and approaches by rats. For each nest, the duration of the survey (in days) was used as a covariate to control for observation effort. We did not test the influence on breeding success of the number of pied-crows and barn owls visiting the nest, because they visited few nests.

Seabirds, and particularly tropicbirds, occasionally neglect their eggs or very young chicks for a few minutes or hours (e.g., Vanderwerf and Young 2014). This increases the risk of predation as eggs or chicks are left unattended. We noted all neglect behaviors to assess whether this increased the risk of predation by rats or other predators.

Estimation of the Demographic Parameters

Breeding success
The breeding success of RTTR nests in the absence of rats was estimated during the breeding season 1995–1996, on a 2.65 ha islet of Europa, in the inner lagoon, where rats were eradicated. The breeding success of RTTR nests in the presence of rats was estimated on the main island (invaded by rats) by surveying nests

Table 1.. Breeding success of white-tailed tropicbirds and red-tailed tropicbirds at Europa Island from 1994 to 2020. *n* is the number of surveyed nests. Data from 1994 to 1996 from Le Corre (1998).

Season (November–March)	White-tailed tropicbird		Red-tailed tropicbird	
1995–1996 (islet, rat free)	-	-	0.79	*n* = 43
1994–1995 (main island)	-	-	0.06	*n* = 97
2008–2009 (main island)	0.069	*n* = 43	0.082	*n* = 120
2009–2010 (main island)	-	-	0.05	*n* = 87
2011–2012 (main island)	-	-	0.02	*n* = 50
2016–2017 (main island)	0.055	*n* = 36	0.223	*n* = 103
2017–2018 (main island)	0.089	*n* = 45	0.035	*n* = 114
2018–2019 (main island)	0.018	*n* = 54	0.033	*n* = 88
2019–2020 (main island)	-	-	0.15	*n* = 73
Mean±Standard error on the main island	0.058±0.03		0.081±0.071	

from incubation to fledging or failure from 1994 to 2020 (but not every year, see Table 1). Breeding success of WTTR was estimated by surveying nests between 2008 and 2012 and between 2016 and 2020 on the main island only, as no WTTR breed on the islet. For both species, nests were geolocated, marked with ribbon, and visited every 15–25 d to observe the status of the nests: incubation, brooding, rearing a chick, chick about to fledge, or failure. The influence of year, location (islet or main island), and species on breeding success was analyzed using a logistic generalized linear model.

During the 2009–2010 breeding season, 128 nests of RTTR were monitored every 3–5 d from incubation until failure, fledging or the end of the fieldwork. We used these data to estimate the daily survival rate of nests with a nest survival model (Rotella et al. 2004). We tested the effect of the age of the nest on the daily nest survival to determine when most breeding failures occurred. For each nest, we considered the day of hatching as the day when a chick was first observed, considering an accuracy of about 3–5 d matching our visitation frequency. The age of a nest is defined as the number of days since egg laying. We calculated the laying date of all nests for which the hatching date was known by subtracting 42 d from the date of hatching (the duration of incubation is 42 d in RTTR; Fleet 1972). The age of the nests that failed before hatching (68 nests) was considered the mean age of nests of known age (60 nests). We ran two models: one with constant daily nest survival rate and another with nest daily survival rate dependent on the age of the nest. We considered the best model as the model with the lowest AIC (Burnham and Anderson 2002).

Demographic rates
The only demographic parameter estimated from our study populations is the breeding success. We did not estimate the survival rates of the adult tropicbirds of Europa because the capture–mark–recapture data were insufficient. Therefore, we used estimates of adult and juvenile survival ranging from the highest to the lowest values published in the literature (Append. 2). We hypothesized that the survival rates of Europa tropicbirds were situated within these ranges, as there are no environmental specificities on Europa that could impact adult or juvenile survival more than those observed at other study sites. In particular, there are no introduced cats on Europa, which would have a strong impact on adult survival (Le Corre 2008). We defined two scenarios for survival rates: an optimistic scenario using survival

rates at the upper limit of their range and a pessimistic scenario with survival rates at the lower limit of their range. We also used age-specific breeding probabilities and individual breeding frequency from the literature (Doherty et al. 2004 for RTTR and Catry et al. 2009 for WTTR; see Append. 2). Adult RTTR were assumed to breed every year (as in Doherty et al. 2004 for a RTTR population on Johnston atoll) and adult WTTR every 7.5 months (as in Catry et al. 2009 for a WTTR population on Aride island) (Append. 2).

Population size
The number of breeding pairs of RTTR and WTTR was estimated in austral summers 2009–2010, 2012–2013, and 2019–2020. In 2009, 72 quadrats of 1 ha (100 m x 100 m) were systematically located in all favorable habitats of the island (Append. 3). In 2009, 2012, and 2019, all quadrats were surveyed, except those inaccessible due to high vegetation density (dense thickets of *Pemphis acidula*). One quadrat was not surveyed in 2009, 13 in 2012, and 6 in 2019. Each quadrat was exhaustively searched for WTTR and RTTR nests during 15–40 min by one or two people. Survey duration varied among quadrats because some were more difficult than others to move around in. However, all surveys were done following the same systematic pattern, to minimize bias.

We defined the type of habitat for each quadrat following the nomenclature of Boullet et al. (2020). We calculated the mean nest density and 95% confidence interval (CI95) for each type of habitat and for each species and year. We then calculated the total number of pairs in each habitat by multiplying the mean nest density per habitat by the total surface of each habitat. Finally, we estimated the total breeding population size for each species and each year by adding the number of nests for all habitats.

We calculated the observed population growth rates with the following equation [1], where N_t is the number of breeding pairs at the end of the interval, N_{t0} the number of breeding pairs at the beginning of the interval, t0 the starting year (first census), and t the ending year (last census):

$$\lambda_{obs} = \left(\frac{N_t}{N_{t_0}} \right)^{\frac{1}{t-t_0}} \tag{1}$$

Population Viability Analysis

Matrix Population Model
Population viability analyses are powerful tools to estimate extinction probabilities and time to extinction (Beissinger and McCullough 2002). They are based on matrices used to calculate population growth, assess the sensitivity of the population growth to changes in each vital rate, and test the best management options for population recovery (Hunter and Gibbs 2006). To study the dynamics of the populations, and following Doherty et al. (2004) for tropicbirds, we built a female-only, age- and stage-classified post-breeding census matrix population model (Caswell 2001) with six age classes and two stages for both populations (Append. 4). In order to take into account interannual variability in demographic parameters, we built an environmental stochastic matrix population model. Environmental stochasticity was included by sampling yearly values of survival rates and breeding success from a beta distribution with mean and variance equal to those estimated or obtained from the literature.

Management Options
For each species, we projected the population growth using two management options in relation to rats. The first option implies no action (no rat eradication or control). For this option, we used the observed breeding success on the main island for the two populations. The second option consists of eradicating rats from the entire island. Here, we used the breeding success obtained on the rat-free islet of Europa for RTTR and 0.66 ± 0.07 for the WTTR population, corresponding to breeding success of *Phaethon lepturus catesbyi* from Bermuda before rat introduction (Wingate and Talbot 2003). The other vital rates (pre-breeding and adult survival, age at first breeding, individual breeding frequency) remained the same for both options. Each option was modeled using the two survival scenarios (optimist and pessimist) previously described. We did not change adult survival rates between management options because rats do not prey upon adult tropicbirds.

Population Viability and Extinction Risk
For both populations, we ran 1,000 Monte Carlo simulations for 200 yr, with an escape threshold of 100 pairs and three extinction thresholds of 5, 10, and 20 pairs, to estimate population growth, probability of extinction and time to extinction according to the two management options. For each model, t0 is year 2019.

Proportion of Nests Controlled
Another solution to avoid tropicbird population decline is to locally control rats, i.e., kill rats around tropicbird nests with lethal traps. We applied the following equation [2] to estimate how many nests should be locally rat-controlled to avoid population decline. Let BS_t be the total breeding success of a population consisting of a mixture of controlled and uncontrolled nests. BS_c is the breeding success of the controlled nests. BS_{nc} is the breeding success of the non-controlled nests. α is the proportion of nests that are controlled (thus 1 - α is the proportion of nests that are not controlled). $BS_t = \alpha \times BS_c + (1-\alpha) \times BS_{nc}$. Thus:

$$\frac{BS_t - BS_{nc}}{BS_c - BS_{nc}} = \alpha \qquad (2)$$

In order to estimate α as the proportion of nests required to maintain a stable or increasing population, we used the minimal value of BS_t for each species, which resulted in a population growth rate >1 for the pessimistic scenario (see Results).

Statistical Analysis
Statistical analyses were made with R (R Core Team 2019). For both species, matrix population models were developed using the package "pop.bio" in R (Stubben and Millingan 2007) and the software ULM (Unified Life Models; Legendre and Clobert 1995). We analyzed daily survival rates of the nests with the package RMark (Laake 2013).

RESULTS

Camera Trap Monitoring of the Nests and Breeding Success
Each RTTR nest was monitored from 3–35 d (14.9 ± 10.2 d, *n* = 18 nests). We recorded 623 images with animals other than tropicbirds (Table 2). The majority of observations were hermit crabs (*Coenobita perlatus*) (50%), rats (28%), and pied-crows (16%). The only potential predators observed at RTTR nests were rats, which were observed on 15 nests, and pied-crows observed on two nests. Rats were detected approaching nests on 168 images and visiting them 84 times (Fig. 2) with an average of 0.37 ± 0.47 observations/d/nest (Table 2). Pied-crows were detected 90 times approaching nests and seven times visiting them (Fig. 2, Table 2), including 96 interactions with only one nest (Table 2). They were observed on average 0.46 ± 2.00 observations/d/nest (Table 2). We suspected one predation event on chicks and one on eggs by rats. Clear predation events by rats were observed on two eggs (Fig. 3, Append. 5). We observed a collective attack on a RTTR nest by two pied-crows: a first pied-crow attacked the incubating adult while the other took the egg. Hermit crabs were observed at 13 nests (72%) and clearly disturbed adults in seven nests without any predation. Hermit crabs were observed more frequently than other species on RTTR nests (Tables 2, 3). Crabs (*Cardisoma carnifex*) were detected in three nests (17%) (Table 2), and two interacted quickly with the adult, without predation.

Fig. 2. Percentage of red-tailed tropicbird (*Phaethon rubricauda*) and white-tailed tropicbird (*Phaethon lepturus europae*) nests approached or visited by hermit crabs (*Coenobita perlatus*), crabs (*Cardisoma carnifex*), rats (*Rattus rattus*) and pied crow (*Corvus albus*). Numbers in plots represent the numbers of nests.
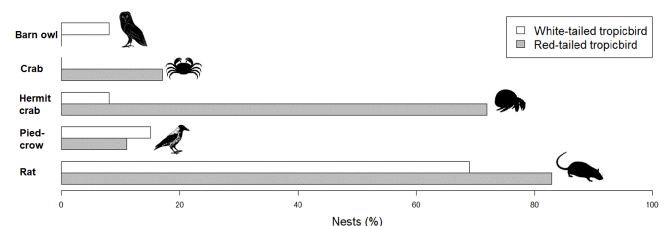
Each WTTR nest was monitored from 2–31 d (22.2 ± 22.3, *n* = 13 nests). We observed animals other than tropicbirds on 520 images (Table 2). The most frequent observations were goats (48%), which did not interact with tropicbirds, and rats (43%)

Table 2. Summary of observations from camera traps deployed on 18 red-tailed tropicbird and 13 white-tailed tropicbird nests at Europa

	Interactions					Without interaction			
	Predators			Non-predators					
	Rats	Pied crows	Barn owls	Hermit crabs	Land crabs	White-eyes	Dimorphic egrets	Goats	Eurasian whimbrels
Red-tailed tropicbird nests (monitored during 297 d with 8,987 images)									
Total number of observations (percentage from pictures with animal detection)	170 (28%)	97 (16%)	0 (0%)	310 (50%)	8 (1%)	4 (0.6%)	1 (0.2%)	33 (5%)	0 (0%)
Number of nests with interactions (percentage of the surveyed nests)	15 (83%)	2 (11%)	0 (0%)	13 (72%)	3 (17%)	-	-	-	-
Number of observations of predators per day and per nest (mean± standard error)	0.37 ± 0.47	0.46 ± 2.00	0	-	-	-	-	-	-
White-tailed tropicbird nests (monitored during 258 d with 32,163 images)									
Total number of observations (percentage from pictures with animal detection)	224 (43%)	23 (4%)	4 (0.8%)	3 (0.6%)	0 (0%)	0 (0%)	0 (0%)	249 (48%)	11 (2%)
Number of nests with interactions (percentage of the surveyed nests)	9 (69%)	2 (15%)	1 (8%)	1 (8%)	0 (0%)	-	-	-	-
Number of observations of predators per day and per nest (mean± standard error)	0.56 ± 0.80	0.05 ± 0.12	0.02 ± 0.06	-	-	-	-	-	-

(Table 2). Rats, but also pied-crows and barn owls, seem to be potential predators. Rats were observed at 69% of the nests (Table 2, Fig. 2) and, for all nests, with an average of 0.56 ± 0.80 observations/d/nest. They were observed 161 times approaching the nest, and 68 times visiting it (Fig. 3). We did not observe clear predation events but we suspected one predation on an egg and another one on a chick. Barn owls were observed, 0.02 ± 0.06 observations/d/nest at one nest (8%) (Table 2, Fig. 2) and four times close to nests: three times approaching and one time with one leg in the nest. During this last event, we suspected a predation of the chick, as the chick was absent in the following survey. Pied-crows were observed 0.05 ± 0.12 observations/d/nest at two nests (15%) (Fig. 2), 22 times close to nests: 21 times approaching, and one time entering the nest (Fig. 3). We observed a fight between an adult WTTR protecting its nest and a pied-crow (Append. 5). Although the pied-crow tried to enter the nest, no predation was recorded. Hermit crabs were observed on only one nest (8%) (Table 2, Fig. 2).

Fig. 3. Number of interactions of potential predators with red-tailed tropicbirds (*Phaethon rubricauda*) (on the top) and white-tailed tropicbirds (*Phaethon lepturus europae*) (on the bottom) during incubating and chick-rearing stages.
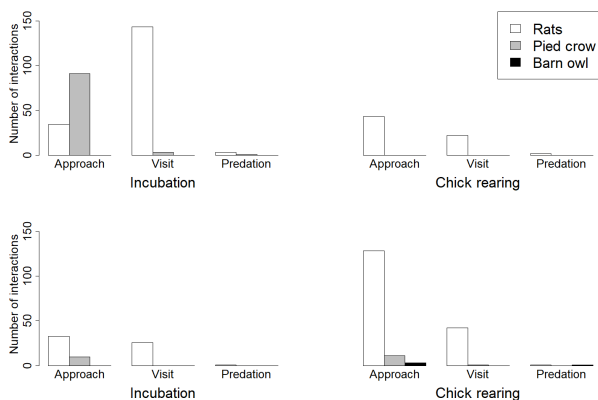

Table 3. Results from the generalized linear model for the number of interactions between red-tailed and white-tailed tropicbirds nests and other species on Europa

Covariate	Estimate	Standard Error	P value
Red-tailed tropicbirds:			
Intercept	-0.940	0.378	0.012
Pied crow	2.639	0.391	<0.001
Hermit crab	4.070	0.381	<0.001
Rat	3.196	0.386	<0.001
White-tailed tropicbirds:			
Intercept	-1.179	0.500	0.018
Pied crow	1.705	0.544	0.002
Rat	4.007	0.505	<0.001

For both tropicbird species, rats were the most frequently observed predator at the nests, and barn owls the least frequently observed (Tables 3, 4).

Table 4. Quasi-Poisson generalized model results for interactions between potential predators and tropicbird nests (RTTR: red-tailed tropicbirds)

Coefficients	Estimate	Standard Error	P value
Intercept	-0.508	1.283	0.693
Owls	-1.188	2.626	0.651
Rats	2.898	1.309	0.004
Predating	-3.808	0.620	0.029
Visit	-0.979	0.447	0.046

Egg and Chick Neglect Behaviors in Tropicbirds

We observed egg neglect on 14 occasions on six nests of RTTR (Table 5). Two of them were probably followed by predation by

Table 5. Summary of parental neglect on red-tailed (RTTR) and white-tailed (WTTR) tropicbird nests

	Species	Start	End	Duration	Status	Predation
Nest 1	RTTR	25/12/19 4:07 AM	25/12/19 5:55 AM	1:48	1-d-old chick	
		26/1912/ 5:58 AM	26/12/19 8:00 AM	2:02	2-d-old chick	
		4/1/20 5:55 AM	4/1/20 2:33 PM	8:38	10-d-old chick	
		4/1/20 6:40 PM	5/1/20 9:59 AM	15:19	10-d-old chick	presumed by rat
Nest 2	RTTR	25/12/19 9:20 PM	25/12/19 11:29 PM	2:09	egg	by rat
Nest 3	RTTR	30/12/19 4:27 PM	30/12/19 6:52 PM	2:25	egg	presumed by rat
Nest 4	RTTR	21/12/19 8:50 AM	21/12/19 10:00 AM	1:10	chick	not observed
Nest 5	RTTR	28/12/19 5:07 AM	28/12/19 6:15 AM	1:08	egg	
		30/12/19 1:00 PM	30/12/19 2:00 PM	1:00	egg	
		1/1/20 9:55 AM	1/1/20 5:17 PM	7:22	egg	not observed
Nest 6	RTTR	22/1/20 7:50 AM	22/1/20 9:18 AM	1:28	chick	
		23/1/20 8:56 AM	23/1/20 10:37 AM	1:41	chick	
		26/1/20 12:33 PM	26/1/20 1:27 PM	0:54	chick	not observed
Nest 7	WTTR	4/8/21 12:00 AM	5/8/21	all night long	chick	not observed

a rat (Table 5): an egg was left unattended at night, at 9:20 p.m. A rat came immediately and depredated the egg at 11:29 p.m. Another egg was left unattended on the afternoon and was presumably depredated by a rat 2 h later.

We observed very young chick neglect on three RTTR nests and on one WTTR nest. One of the RTTR chicks was left unattended for the first time the day after it hatched and then three other times. Although we did not formally observe predation, this chick was certainly depredated by a rat before the adults came back, as the nest was found empty later, and this nest was visited 0.44 times per day by rats before the chick disappeared, and no other predators were observed at this nest. Another chick was neglected for just over 1 h, but no predation occured. The WTTR chick was left unattended during an entire night, but no predation was observed (Table 5).

Breeding Success
On the main island, the breeding success from 2008 to 2012 and from 2016 to 2020 was on average 0.08 ± 0.07 for RTTR and 0.06 ± 0.03 for WTTR (Table 1). The breeding success of RTTR in 1995 on the rat-free islet was 0.79 ± 0.04 (Table 1). There was no significant difference in breeding success between years and between species. The RTTR breeding success varied only according to location (main island vs. rat-free islet, Table 6).

Table 6. Results of the binomial generalized linear model relating breeding sucess to year, location, and species of tropicbirds on Europa

	Estimate	Test statistic	P value
Year	-0.045	-0.592	0.554
Species	-196.783	-1.244	0.213
Location	1.747	3.328	0.001
Year*Species	0.098	1.249	0.212

During the 2009–2010 breeding season, the mean daily survival rate of RTTR nests was 0.96 ± 0.03, but this rate significantly changed with age of the nest (Append. 6), from 0.99 ± 0.002 at day 1 to 0.91 ± 0.05 at day 56. We observed a strong decline of daily nest survival rate during the hatching period (Fig. 4). Ultimately, 64% of the surveyed nests failed during brooding and

26% during incubation. Indeed, nests containing eggs were surveyed on average for 21.0 ± 11.7 d (1–42 d), and those containing chicks were monitored on average for 7.9 ± 5.2 d (2–22 d) until failure. This reinforces the hypothesis that most failures occurr during the first days after hatching, with chicks surviving on average only 7.9 ± 5.2 d.

Fig. 4. Daily nest survival rate of red-tailed tropicbird (*Phaethon rubricauda*) as a function of age of the nest according to the best model (Append. 6).
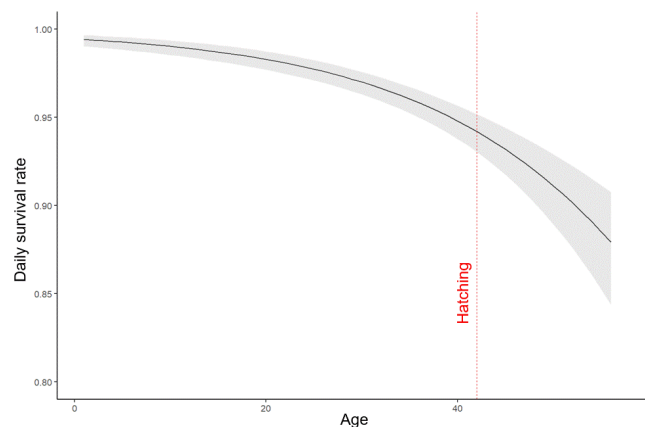
The number of interactions by rats had no significant effect on hatching or fledging success of RTTR (Table 6).
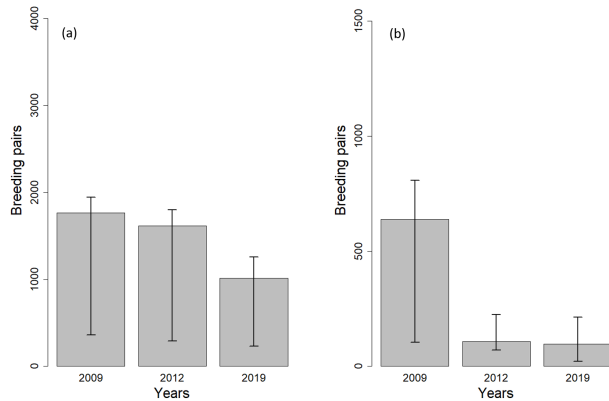
Population Sizes
In 2009, RTTR estimated population size was 1,766 pairs (CI 95%= [363;1,944]). In 2012, it was 1,614 (CI 95%= [293;1,799]), and in 2019, it was 1,027 pairs (CI 95%= [232; 1,256]) (Fig. 5).

In 2009, WTTR population size was 638 pairs (CI 95% = [105; 807]). In 2012, it was 108 pairs (CI 95% = [70; 225]), and in 2019, it was 96 pairs (CI 95% = [21; 213]) (Fig. 5).

The observed mean annual population growth rate for RTTR and WTTR between 2009 and 2019 was 0.95 and 0.83, respectively. Thus, both populations are rapidly declining, at an annual rate of -5% and -17% for RTTR and WTTR respectively.

Fig. 5. Number of breeding pairs of red-tailed tropicbirds (*Phaethon rubricauda*) (a) and white-tailed tropicbirds (*Phaethon lepturus europae*) (b) estimated with quadrats in 2009, 2013, and 2019. The black bars correspond to the IC95%.

In 1997, the RTTR population size was 3,500 breeding pairs and about 750 breeding pairs for the WTTR (see median in Append. 1). Thus, the annual population growth between 1997 and 2019 was 0.95 for RTTR and 0.92 for WTTR.

Population Viability Analysis

Sensitivity analyses showed that population growth rates of both RTTR and WTTR were more sensitive to variation in adult survival rate than to changes in breeding success (Fig. 6). However, to obtain a positive population growth with the current breeding success, adult survival would need to be over 0.985 for both populations, which is extremely high and very unlikely for these species (see Schreiber and Burger 2001).

Option 1: No Rat Eradication

The annual stochastic population growth rates estimated with our optimistic scenarios are very close to the annual observed population growth between 1997 and 2019. Indeed, for RTTR, with the current breeding success, the stochastic population growth rate is 0.94 ± 0.001 for the optimistic scenario and 0.88 ± 0.000 for the pessimistic scenario (Fig. 7a). For WTTR, the population growth rate is 0.95 ± 0.001 for the optimistic scenario and 0.88 ± 0.001 for the pessimistic scenario (Fig. 7b). With no rat eradication, the probability of extinction before 100 yr was one for both species, whatever the scenario and for the three different extinction thresholds. However, time to extinction differed according to the extinction thresholds and scenarios (Table 7). For the optimistic scenario, time to extinction for RTTR was between 65 ± 0.2 and 85 ± 0.4 yr (Fig. 7a, Table 7). For the pessimistic scenario, it was between 32 ± 0.1 and 43 ± 0.1 yr (Fig. 7a, Table 7). For WTTR, according to the optimistic scenario, time to extinction was between 30 ± 0.1 and 50 ± 0.2 yr. The population would be extinct between 11 ± 0.03 and 18 ± 0.03 yr for the pessimistic scenario (Fig. 7b; Table 7).

Fig. 6. Population growth rate landscape from a sensitivity analysis including adult survival, pre-breeding survival, and breeding success according to the pessimistic (gray dotted line) and the optimistic (gray full line) scenario. Adult survival for (a) red-tailed tropicbirds (*Phaethon rubricauda*), and (c) white-tailed tropicbirds (*Phaethon lepturus europae*). Pre-breeding survival for (b) red-tailed tropicbirdsand (d) white-tailed tropicbirds. The gray circle represents the situation according to the actual breeding success.
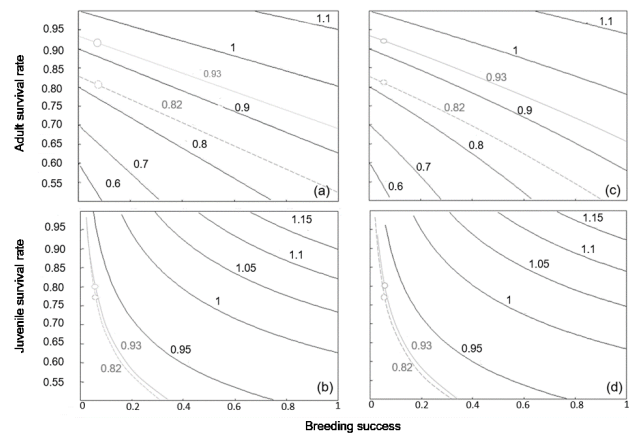

Fig. 7. Breeding pairs of red-tailed tropicbirds (*Phaethon rubricauda*) (a), and white-tailed tropicbirds (*Phaethon lepturus europae*) (b) as a function of year for the optimistic and pessimistic scenarios and according to actual breeding success and breeding success estimated for the rat eradication scenario.
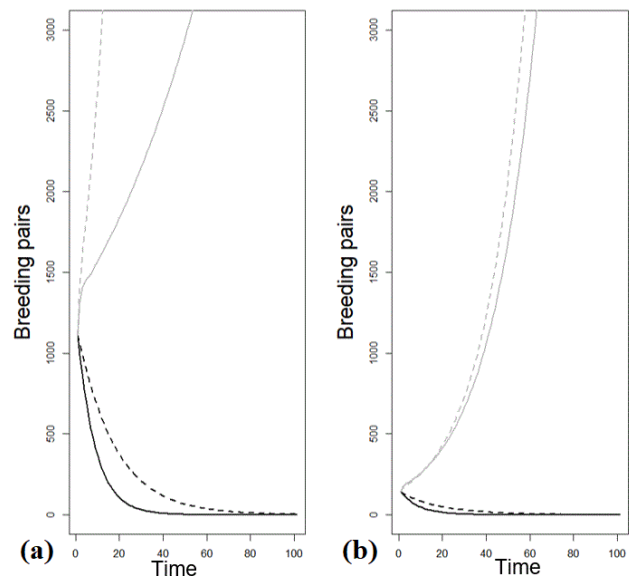
Table 7. Time to extinction of tropicbird populations on Europa according to two scenarios (rat eradication, no management) and three extinction thresholds (5, 10, and 20 breeding pairs)

	White-tailed tropicbirds	Red-tailed tropicbirds
Rat eradication		
Optimistic scenario	No extinction	No extinction
Pessimistic scenario		
Extinction threshold: 5 pairs	No extinction	No extinction
Extinction threshold: 10 pairs	No extinction	No extinction
Extinction threshold: 20 pairs	No extinction	No extinction
No management		
Optimistic scenario		
Extinction threshold: 5 pairs	50±0.15 yr	85±0.4 yr
Extinction threshold: 10 pairs	40±0.13 yr	75±0.2 yr
Extinction threshold: 20 pairs	30±0.11 yr	65±0.18 yr
Pessimistic scenario		
Extinction threshold: 5 pairs	18±0.03 yr	43±0.09 yr
Extinction threshold: 10 pairs	14±0.03 yr	37±0.07 yr
Extinction threshold: 20 pairs	11±0.03 yr	32±0.07 yr

Option 2: Rat Eradication

With complete rat removal, the RTTR annual population growth rate was between 1.01 ± 0.001 and 1.07 ± 0.001 (Fig. 7a). The WTTR annual population growth would be between 1.048 ± 0.002 and 1.052 ± 0.0007 (Fig. 7b). The probabilities of extinction before 200 yr were equal to zero for both populations (Table 7, Fig. 7).

Option 3: Rat Control at Nests: Proportion of Nests to Be Targeted

According to the PVA, we estimated BS_t equal to 0.51 and 0.53 for WTTR and RTTR respectively. According to Eq. 2, 74% of WTTR nests (i.e., 74 nests based on the current population size) and 63% of RTTR nests (647 nests) must be successfully targeted for rat control each year to avoid any further population decline.

DISCUSSION

Effect of Rats, Barn Owls, and Pied-crows on Tropicbird Breeding Success

We did not find any evidence of predation on adult tropicbirds. This suggests that the main demographic parameter impacted by predators is the breeding success, which was very low on the main island. To our knowledge, such a prolonged low breeding success has rarely been observed for tropicbird populations (but see Boeken 2016; Append. 7). Our data suggest no correlation between the fate of nests and the number of rats observed visiting. Few predations by rats have been observed during our camera trap survey, probably because our monitoring occurred predominantly during the incubation period, and predation mainly occurred when adults were away from the nests, often just after hatching, as shown by the drop in daily nest survival just after hatching. During the incubation stage, adults rarely left their eggs unattended and success remained relatively high. However, as soon as young chicks were left alone, they were rapidly depredated by rats and to a lesser extent by barn owls and pied-

crows, (Russell and Le Corre 2009, Russell et al. 2011, Ringler et al. 2015; *personal communication*, TAAF). These behaviors of brood neglect, combined with egg predation while adults were in the nest, confirm that tropicbirds have very limited anti-predator behaviors against novel predators. Indeed, the species' natural behaviors are insufficient to repel such predators, and they have limited ability to develop anti-predator behaviors when confronted with introduced predators and imminent extinction. This is particularly dramatic when tropicbirds coexist with rats and corvids because these predators are known to be opportunistic and very efficient predators of many seabird species (Schaefer 2004, Gabriel and Golightly 2014, Rees et al. 2015). They disturb adults until eggs and chicks are accessible to attempt predation, as observed in three of our monitored nests. Although predation by barn owls was recorded once and presumed elsewhere (Ringler et al. 2015), it currently seems to be rare and anecdotal compared with rat predation.

Tropicbird Population Viability

Although population growth rate of seabirds is generally more sensitive to changes in adult survival than to changes in breeding parameters (Le Corre 2008), our viability analysis showed that an extremely low breeding success such as the one observed on Europa, will lead to population decline and extinction, as previously demonstrated for other seabird populations (e.g., Jenouvrier et al. 2005, Rolland et al. 2009). A very low breeding success is particularly harmful for these populations because tropicbirds are highly philopatric (Schreiber and Schreiber 1993), so immigration may not compensate for a lack of local recruitment due to low breeding success. On Europa, the RTTR population has declined by more than 70% during the last 25 yr and this trend will continue until extinction in 32–85 yr if no conservation action is undertaken. The situation is even worse for the endemic WTTR, which is totally isolated from other populations, as genetic studies suggest that there is no immigration from other populations (Humeau et al. 2020). Our PVA suggests extinction in 11–50 yr. The WTTR population meets the "E criteria" of the Critically Endangered status defined by International Union for the Conservation of Nature (IUCN 2022): over 100 yr, the probability of extinction in the wild is more than 50% (equal to 100% in our case). Thus, based on our results and in accordance with Humeau et al (2020), we confirm that this endemic is currently critically endangered.

Effect of Rat Eradication on Tropicbirds of Europa

Both camera trap surveys and estimates of the breeding success on the rat-free islet confirmed that rats are the main predators of eggs and chicks of both species of tropicbirds. Our modeling analyses predicted an increase of the populations if breeding success reached 0.66 for WTTR and 0.79 for RTTR, which can be achieved only by eradicating rats.

The RTTR also breeds at Nosy Vé (360 km from Europa), southeast of Madagascar (Cooke and Randriamanindry 1996). Nosy Vé was infested by rats until 2000, and the population size of RTTR was about only 100 pairs at this time (Le Corre et al. in press). Since rat eradication in 2000, the population has increased exponentially (>800 pairs in 2019) and is still increasing (Le Corre et al. in press). Thus, we predict a similar trend for the two species after the eradication of rats at Europa Island.

Recommendations

Management recommendations

Our results indicate that if no management action is undertaken, predation by rats will lead to the local extinction of the RTTR population of Europa (which was once the largest population of the WIO) and of the endemic and critically endangered WTTR population of Europa (Humeau et al. 2020). Rat eradication will improve breeding success and will save both populations from extinction. We consider rat eradication as the only guaranteed way to reverse this trend, as this will lead to a substantial increase in breeding success, which will also buffer against other threats. Thus, we urge the eradication of rats from the entire island as soon as possible. Although our results suggest that predation by pied-crows is relatively uncommon, we recommend control of the pied-crow population to reduce nest disturbance, knowing that pied-crows are likely subsidized by human presence. Rat eradication on Europa would also be beneficial for other seabird species (Brooke et al. 2018), such as the tropical shearwater (*Puffinus bailloni*), for vegetation (as in Wolf et al. 2018) and for other species that are currently potential prey of rats, such as the Madagascar white-eye (*Zosterops maderaspatana*) (Berry and Taisacan 2008) and skinks, including the threatened endemics *Trachylepis maculilabris infralineata* and *Cryptblepharus bitineatus* (Probst 1998, Sanchez and Probst 2015). The positive impact of rat eradication on terrestrial ecosystems has been rapidly observed on nearby Tromelin Island where seabird and vegetation recovery has been spectacular since rat eradication (Le Corre et al. 2015). Rat eradication also has cascading positive effects on marine coastal habitats by reactivating the nutrient inputs originating from seabird colonies (Benkwitt et al. 2021). An effective biosecurity plan, including early detection and incursion response protocols, should be rapidly implemented to avoid any other new species introduction, including potential tropicbird predators and a re-invasion by rats (if rats are eradicated) (Clout and Russell 2008, Russell et al. 2008).

Rat eradication is now conducted routinely on temperate islands with a very low failure rate (8.5%). On tropical islands, failure rate is higher (18.8%) (Russell and Holmes 2015) for various reasons including higher non-target species interaction with bait (e.g., land crabs) (Griffiths et al. 2011), and higher and more uncertain natural food availability, which increases rat productivity and decreases bait attractiveness (Wegmann et al. 2011, Griffiths et al. 2019). However, the success rate can be improved in tropical areas by considering rainfall and natural food availability and by using bait appropriate to the environment (Ringler et al. 2014, 2021, Keitt et al. 2015). Some tropical islands, such as Europa, have large mangroves that are favorable habitats for rats (Harper et al. 2015), but where rats might be more difficult to eradicate. Indeed, mangroves are subject to tidal inundation, which may wash away the baits when disposed on the ground (Harper et al. 2015). Ringler et al. (2021) conducted a feasibility study of rat eradication in the mangrove of Europa. This study suggests that eradication of rats from Europa could be successful using appropriate alternative approaches such as "bait bolas" or bait blocks dispersed into mangrove with aerial technology such as drones (Wegmann et al. 2008, Harper et al. 2015, Samaniego-Herrera et al. 2018, Marris 2019, Ringler et al. 2021). Rat eradication could also be facilitated using elevated baiting platforms fixed on mangrove trees or floating structures (Siers et al. 2018).

We are aware that entire eradication of rats from Europa will be an expensive process that takes time to plan, fund, and implement. This is why we tested the effect of targeted rat control on RTTR and WTTR populations as an interim measure. However, we note it would be extremely difficult to successfully control all rats around 697 RTTR nests and 74 WTTR nests each year. Therefore, targeted rat control is not a sustainable long-term solution in our opinion. However, it provides a temporary solution to avoid any further population decline until an entire rat eradication program on Europa is undertaken.

Monitoring recommendations

Maintaining the monitoring effort of the ecosystem over time will be necessary to measure the effect of rat eradication (if eradication is undertaken), particularly on seabirds, landbirds, vegetation, and skinks, which are all highly impacted by rats. As explained previously, the high abundance of rats benefits the barn owl population. Owls mainly eat rats, but to a lesser extent, chicks of sooty terns, frigatebirds, RTTR, and occasionally WTTR (Ringler et al. 2015; Append. 5). The biogeographic status of the barn owl population of Europa is still unknown. However, many endemic subspecies of barn owls are known around the globe, as in Madagascar, for example (Uva et al. 2018). Therefore, it is important to conduct studies in order to determine the biogeographic status of the barn owl of Europa and, if required, implement appropriate management to avoid secondary poisoning (temporary captive rearing of the owls). A second important step is to study the diet of barn owls after rat eradication to quantify the potential long-term impact of barn owls on seabirds.

Methodological Limitations

Our study has some limitations, but we are confident that they have little impact on our main results and conclusions. First, we used published estimates of survival and recruitment rates from other tropicbird populations because we did not have the information from our populations, which may reduce the accuracy of the demographic projections. However, by designing two scenarios (optimistic and pessimistic) that included all the known range of survival rates for the two species, we have tried to compensate for this lack of knowledge by simulating a range of possible trajectories. The two populations showed the same general patterns regardless of the survival values: a probability of extinction of 100% without rat control or eradication, and a population recovery after rat eradication. Furthermore, the stochastic population growth rates estimated for the two populations were very close to the observed population growth since 1997, which suggests that our models had congruence with the empirical data.

Second, WTTR breed asynchronously at Europa as in most parts of its range (Prys-Jones and Peet 1980; e.g., Phillips 1987, Ramos et al. 2005). Thus, a fraction of the population (those that were not breeding during our field sessions) was not included in our study. However, there is no reason to believe that this fraction would have a different breeding success and demographic rates,

as nest predators are active all year round. Ultimately, the population growth should remain the same, and only time to extinction might be a little longer.

Third, we may have slightly overestimated the breeding success and the daily survival rate of the nests because the nests included in the study were not monitored entirely from first egg-laying to fledging or failure, but only from the date of discovery of the nest (the laying date was unknown). This is a very common bias in nest survival studies, which leads to an overestimation of the breeding success because nests that have failed early are overlooked (the so-called "apparent breeding success;" Mayfield 1961, 1975). However, this overestimation of breeding success should be very low because failure mainly occurs after hatching and not at the beginning of the incubation period. In our context, the real breeding success may be very slightly lower than the one estimated, but this would not modify the population dynamics.

CONCLUSION

Since 1997, tropicbird populations breeding on Europa drastically decreased as a consequence of an extremely low breeding success due to rat predation. Pied-crows and barn owls played a role in this decline, but the main predators are rats. This low breeding success will undoubtedly lead to local extinction of both the tropicbirds, including the endemic WTTR, within the next decades. In order to preserve these populations from extinction, we urgently recommend interim control of rats around tropicbird nests until such time as eradication of rats from the whole island is undertaken.

Responses to this article can be read online at:
https://www.ace-eco.org/issues/responses.php/2174

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Appendix 1: Seabird populations of Europa island at the end of XXth century. According to Le Corre & Jouventin (1997)

| Species	Populations size (pairs)
Sooty tern (*Onychopryon fuscatus*)	500000 – 1000000
Red-footed boobies (*Sula sula*)	2800 – 3800
Lesser fregatebird (*Fregata ariel*)	1000 – 1200
Great frigatebird (*Fregata minor*)	700 – 1100
Red-tailed tropicbird (*Phaethon rubricauda*)	3000 – 4000
White-tailed tropicbird (*Phaethon lepturus europae*)	500 – 1000
Tropical shearwater (*Puffinus bailloni*)	< 100
Caspian tern (*Hydropogne caspia*)	12

Appendix 2: Demographic parameters for scenarios considered to model population growth for the red-tailed and white- tailed tropicbird populations at Europa Island. β_i is the age-specific breeding probability for age i. ΦAD is the mean adult survival rate (± standard error) and ΦPB the mean pre-breeding survival rate (± standard error) and. α is the sex ratio at birth and IBF is the Individual Breeding Frequency.

Scenarios	Survival rate	Constants parameters within the population
Optimistic	ϕAD_{max}=0.92 (Doherty et al, 2004)	β_1=0.004, β_2=0.025,
	ϕPB_{max}=0.80±0.04 (Doherty et al, 2004)	β_3=0.252, β_4=0.457,
Pessimistic	ϕAD_{min}=0.86±0.04 (Schreiber et al. 2004)	β_5=0.438, α=0.5
	ϕPB_{min}=0.77±0.09 (Schreiber et al. 2004)	IBF_{RTT}=1, IBF_{WTT}=1.61
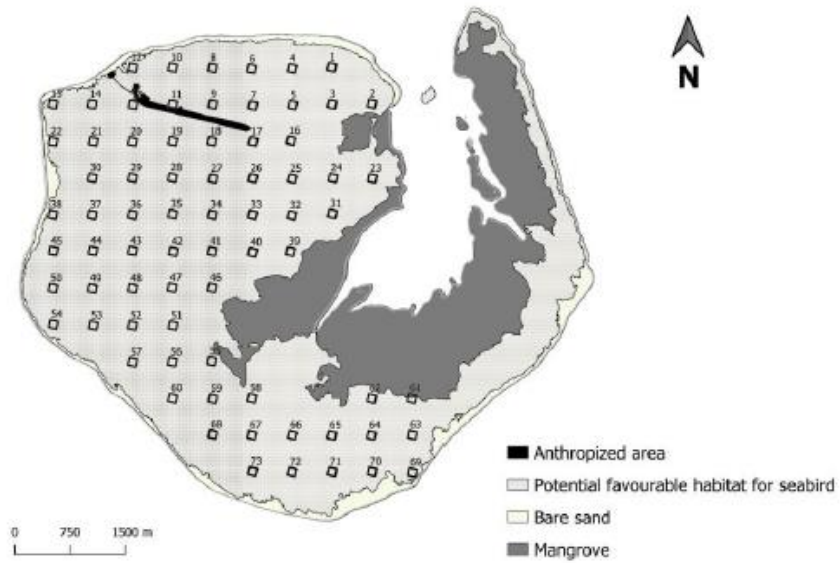
Appendix 3 : Distribution of prospected quadrats to estimate population size of tropicbirds on Europa.

Appendix 4: Life cycle graph and transition matrix for red-tailed (*Phaethon rubricauda*) and white-tailed tropicbird (*Phaethon lepturus europae*). PB_i is pre-breeding stage at age i and AD adult (or breeder) stage. ΦAD is the adult survival rate and ΦPB the juvenile survival rate. F_i is the fecundity at age i+1 and equals $\Phi PB \times \beta_{i+1} \times BS \times \alpha$ and F_A is the adult fecundity and equals $\varphi Ad \times \alpha \times BS$. G_i is the probability of surviving and stay non breeder from age i-1 to i and equald $\Phi juv \times (1-\beta_{i+1})$. M_i is the probability of surviving and maturing from age i-1 to i and was $\Phi PB \times \beta_{i+1}$. β_i is the age-specific breeding probability for age i ($\beta_1=0.004$, $\beta_2=0.025$, $\beta_3=0.252$, $\beta_4=0.457$, $\beta_5=0.438$) and α is the sex ratio ($\alpha=0.5$). According to Doherty et al, 2004.
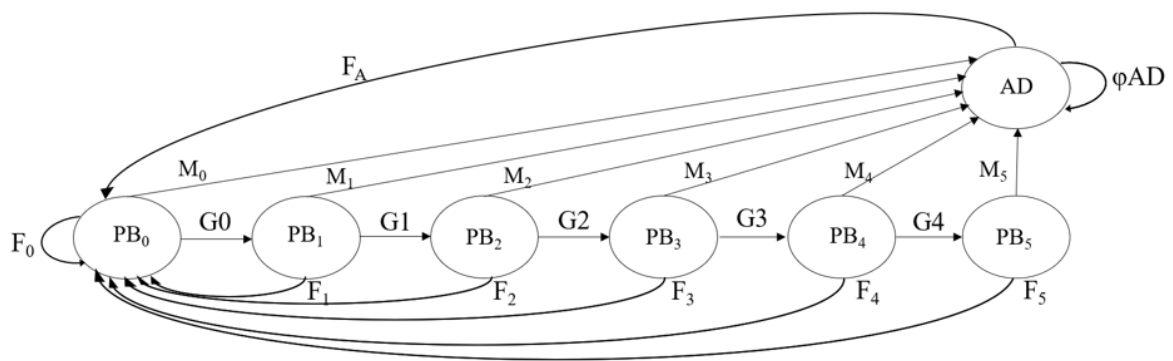
F0	F1	F2	F3	F4	F5	FA
G0	0	0	0	0	0	0
0	G1	0	0	0	0	0
0	0	G2	0	0	0	0
0	0	0	G3	0	0	0
0	0	0	0	G4	0	0
M0	M1	M2	M3	M4	M5	φAD

Predation of a chick of white tailed tropicbirds (*Phaethon lepturus europae*) in nest by a Barn owl (*Tyto alba*)

Predation of a unattended egg of red-tailed tropicbirds (*Phaethon rubricauda*),by rats (*Rattus rattus*)

Disturbance of an adult of white tailed tropicbirds (*Phaethon lepturus europae*) by a pied crow (*Corvus albus*) (picture 1 and 2) in order to try to enter in the nest (last picture)

Appendix 6 : Daily Survival Rate (DSR) analysis for 128 nests of red-tailed tropicbirds

Model	AIC	ΔAIC	Weight	Deviance
DSR (age)	544.23	0	1	540.23
DSR (constant)	623.51	79.28	0	621.51

Appendix 7: Breeding success of tropicbird populations on different sites with different status of conservation.

Site	Species	Alien predators	Breeding success	Authors
Peña Bianca Island, Mexico	*Ph.aethereus*	None	0.77 to 0.57	Hernandez et al, 2018
South and south-west Caribbean Netherland	*Ph.aethereus*	Feral cats	0	Boeken, 2018
Old Booby Hill, Caribbean Netherland	*Ph.aethereus*	None	0.65	Boeken, 2018
O'ahu, Hawai'i	*Ph.rubricauda*	Mangoose and rats (but control)	0.59 ± 0.04	Vanderwerf & Young, 2014
Bermuda (2013-2015)	*Ph. lepturus catesbiy*	Rats	0.39±0.13	Mejias, 2017
Aride	*Ph. lepturus*	None	0.33±0.08	Ramos et al 2005
Cousin	*Ph.lepturus*	None	0.36	Phillips, 1985
Ascension	*Ph. lepturus*	Cats and rats	0.30	Stonehouse, 1962