

Effect of exotic mammalian predators on parasites of Cory's shearwater: ecological effect on population health and breeding success

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Received: 20 September 2012 / Accepted: 26 April 2013 / Published online: 25 May 2013
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Abstract Predator activity around the nests induces stress in breeding birds, which may have weaker immunity and are therefore more susceptible to parasite infections. The influence of predators on parasites has only been observed in land birds, and most studies are experimental. As seabird colonies offer excellent conditions for parasites, here we assess the influence of mouse, rat, and cat activity on parasites in Cory's shearwater (*Calonectris diomedea borealis*). Adults were examined for blood parasites and one adult and the juvenile from 53 nests were inspected for ectoparasites over two consecutive years (2010 and 2011). Nests differed in their physical characteristics and indices of mammal predator activity and were checked weekly to assess breeding success. Our results showed absence of blood parasites. Among the environmental factors, predator pressure received the most support (89 %) from the data as influencing nest ectoparasite intensity. Birds most infected had worse body condition, and breeding success was negatively influenced by predator activity and ectoparasite intensity. To our knowledge, this is the first analysis of the interaction between mammal predators and ectoparasites in seabird species and supports greater protection through eradication

efforts. In addition, we provide the first data on the endoparasite fauna of Cory's shearwater.

Introduction

Breeding individuals are especially vulnerable to parasites (Festa-Bianchet 1989; Oppliger et al. 1996) because physiological and environmental stress factors occurring during the breeding period weaken the immune system and contribute to an increase in parasitism (Bell 1980; Clayton 1991; Gustafsson et al. 1994). Weaker individuals more intensely infected by parasites are especially vulnerable to predation (Anderson 1979; Holmes and Bethel 1972; Packer et al. 2003; Temple 1987).

The effects of parasites on vulnerability to predation has been previously observed in small and medium-sized land birds (Møller and Nielsen 2007; Temple 1987), and most interpretations come from experimental studies. Under natural conditions, Hudson et al. (1992) observed that severely infected red grouse (*Lagopus lagopus scoticus*) were rapidly predated, resulting in low values of parasites.

Seabirds have a long breeding period and form dense colonies with excellent conditions to harbor large numbers of parasites (Clifford 1979). The Cory's shearwater (*Calonectris diomedea borealis*) (Procellariiformes) coexists with exotic mammalian predators on all islands of the Azores archipelago (Portugal). A recent study there confirmed that predation of chicks and eggs by introduced black rats (*Rattus rattus*) and cats (*Felis catus*) is the main cause of nest failure ($n=287$; Hervías et al. 2013). Yet, in this seabird species, despite direct predation on chicks and eggs, predators may have an indirect effect on adult birds, since predator activity around the nests (hereafter predator pressure) could stress individuals and therefore increase their probability of bearing parasites. High parasite intensities

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infecting birds have been widely recognized as an important potential factor for body condition (Møller 1997) and can have a negative influence at individual and population levels (Atkinson and Van Riper 1991). Most studies on breeding seabirds have focused on predation by introduced mammals threatening seabird survival (Bonnaud et al. 2009; Jones et al. 2008; Towns 2009). However, the interaction between predators and parasites is a key factor to understand the population dynamics and life-history traits of these species and, as far as we know, their effect on the health of seabirds is unknown.

The main goal of this study was to assess the effects of predators and ectoparasites on the health of Cory's shearwaters. For this purpose, we determined the ectoparasites of adults and juveniles and blood parasites of adults in nests with different physical characteristics and indices of mammalian predator activity. Specifically, we tested the hypothesis that the stress associated with nest predator pressure could increase the risk in adult birds and adult-sized juveniles of harboring a high ectoparasite intensity that would affect bird body condition and reduce breeding success (Bosch et al. 2000; Brown et al. 1995; Chapman and George 1991; Hurtrez-Boussès et al. 1997; Loye and Carroll 1998). As ectoparasite intensity could also be influenced by several other factors such as bird and ambient conditions, these factors were also evaluated to see how they may act synergistically to explain parasite levels. Additionally, we studied the endoparasites in Cory's shearwaters for the first time, thus improving knowledge of their parasite fauna.

Methods

Study area

The present study took place in 2010 and 2011 on Corvo (39° 40' N, 31° 7' W), the smallest (17 km²) and least populated island of the Azores archipelago. It has only been inhabited since the end of the 15th century. Its natural laurel forest has almost completely disappeared, having been converted to farmland intensively grazed by domestic cows (*Bos taurus*) which occupy the interior area of the island. The climate is rainy (mean annual rainfall: 915.7 mm, relative humidity between 74 % in October to 85 % in June, when fog is more frequent), generally windy (mean 19 km/h), and the temperature varies between 14 °C in February and 20 °C in July (mean 17.6 °C). Regarding exotic mammals, black rat and house mouse (*Mus domesticus*) appeared after 1717, and cats were intentionally introduced later to control them (Cordeiro 1717). There are also wild goats (*Capra aegagrus hircus*) and sheep (*Ovis aries*), but they are mainly restricted to the cliffs of Corvo, away from our study area (Hervías et al. 2012).

Cory's shearwater has a long breeding period, from late February to early November (Monteiro et al. 1996). A total of 53 Cory's shearwater nests were selected along the interior southern and eastern part of the island taking into account its accessibility and presence of breeding birds. Nests were checked every week, from 15th May (some days prior to laying) to 31st October (when juveniles leave the colonies), using a torch and a burrow-scope (elongated remote camera). On each visit, we recorded the presence of adult, egg, or chick, and breeding success was estimated as: n chicks fledged/ n breeding pairs.

Collection of parasites

Because ectoparasite intensity varies during the breeding season (Gómez-Díaz et al. 2008), the sampling period was restricted to one visit on 25–30 July to examine adults and one visit on 25–30 October for juveniles, over two consecutive years (2010 and 2011). We selected the end of July to assess ectoparasites in adults because we were interested in the intensity during the peak in nest predation (the first 2 weeks after hatching; mean hatching date 24th July, $n=287\pm 22.0$ SE; Hervías et al. 2013). For each nest, one adult and the juvenile if still alive were captured under license and carefully inspected for ectoparasites each year (in total 106 adults: 51 males and 55 females; 53 juveniles: 26 males and 27 females).

Ectoparasites from each bird were quantified by a 2-min visual examination of each body region: (1) head and mantle, (2) wings, rump and tail, and (3) belly and breast (Gómez-Díaz et al. 2008). Ectoparasites were collected and preserved in 70 % ethanol until identification in the laboratory. Arthropods were mounted in Hoyer's medium (Krants 1978) and identified according to Vermeil and Marguet (1967), Jones et al. (1972), Price and Clay (1972), and Estrada-Peña et al. (2004).

In July 2010, we also collected blood samples from the foot vein of adult individuals. Immediately after, blood smears were prepared using the classical two-slide wedge technique, they were fixed in ethanol 96 % for 3 min, air-dried, and stored in a cool dry place until analyses. Smears were stained using Hemoquick® (Labo-moderne; methyl alcohol 89 %, Giemsa–Wright stain 0.46 %) and examined for parasites under a 40× microscope.

A total of 13 (8 juvenile and 5 adult) Cory's shearwaters were found dead outside the studied area, from March 2010 to October 2011. The cause of death was determined by necropsies and ranged from fractured bones to superficial and internal bleeding and always excluded parasitic diseases. Dead birds were only examined for gastrointestinal parasites and were not included in any of the statistical analyses. They were individually stored in sealed plastic bags and preserved at –20 °C until necropsy. In the laboratory (University of Murcia, Spain), sections of the

alimentary tract (divided into esophagus, crop, proventriculus, ventriculus, small, and large intestine) were scraped, and the contents washed in a sieve (mesh size 0.3 mm diameter). Both contents and mucosa were observed under the stereomicroscope for helminths. Nematodes were collected, fixed, and cleared with lactophenol for examination. Platyhelminths were stained with Semichon's acetic carmine (Pritchard and Kruse 1982). Helminths were identified using morphometric characteristics according to Skrjabin et al. (1951), Baer (1954), Yamaguti (1971), and Anderson et al. (1974).

Bird body size and body condition index

All sampled birds were weighed using a Pesola balance (to the nearest 5 g) and measured (right wing length in adults and juveniles using a stopped ruler, and right tarsus and culmen length only in adults using a vernier calliper) always by the same person. Age was assessed in two categories: juveniles when <3 months and breeders or adult sexually mature (see Brooke 2004). Sex of juveniles and adults were determined from their sexually dimorphic vocalizations (Bretagnolle and Lequette 1990). After handling, all birds were immediately released into their burrows.

Wing, tarsus, and culmen length of each individual were entered in a Principal Component Analysis to calculate its body size index. Because Cory's shearwaters are sexually dimorphic (Granadeiro 1993; Monteiro et al. 1996), we performed separate PCAs for males and females. PC1 had the highest degree of correlation with body measurements and accounted for 74 % and 75 % of the total variance in size of adult males and females, respectively. The body condition index was calculated as the residuals from the linear regression of body mass of males and females on PC1 factor scores (males: $r=0.87$, $F=53.2$, $p<0.001$; females: $r=0.84$, $F=79.6$, $p<0.001$).

Previous studies showed that underfed fledglings of sooty shearwaters *Puffinus griseus* present a lower body mass (Sagar and Horning 1998) and underfed fledglings of Cory's shearwaters had shorter wing length than chicks fed normally (Ramos et al. 2003). Therefore, we used chick body mass and wing length at 15 weeks of age (prior to fledging) as an indirect surrogate of food condition for chicks. We selected this period to reduce mass variance between juveniles due to temporal and spatial differences in food provisioning by adults during the chick-rearing stage (McCoy et al. 2002) and weighed juveniles on two consecutive days to obtain the mean body mass.

Environmental determinants of parasite intensity

We first identified the most important factors that could influence nest ectoparasite intensity, selecting physical variables associated with the suitability of habitat to

ectoparasites. For each nest, we measured: distance to nearest neighbour nest (meter), altitude above sea level (meter), substrate (either soil or rock), and vegetation cover (proportion of ground vegetation cover within 1 m of the nest cavity entrance) (Table 1).

Lice and fleas have different phases during their lifecycle—lice complete their entire life cycle on the host (Lee and Clayton 1995; Clayton and Tompkins 1995), whereas in most fleas, only adults feed on the host (Marshall 1981). They are therefore associated with their host's plumage and breeding environment (nest), respectively. As the humidity under the plumage correlates with ambient humidity, this latter may be an important environmental factor determining the distribution of lice. Moyer et al. (2002) observed a dramatic reduction in louse abundance at 25 % relative ambient humidity, whereas the abundance of lice was higher when humidity averaged 50 %. Fleas could also be affected by ambient humidity. Larval survival of two *Xenopsylla* species was significantly lower at 55 % humidity than at higher humidities (Krasnov et al. 2001). However, the mean relative humidity on Corvo (80 %) is higher than the values used in experimental studies to detect variation in the number of lice or fleas. This high ambient humidity would thus not cause much variation in ectoparasite intensity among nests. The weather of Corvo is characterized by two marked

Table 1 Mean values, standard deviation (SD) and ranges of nest physical characteristics, house mouse, black rat and cat activity indices (predator variables) and breeding success (chicks/pair), measured in 53 nests. Mean ectoparasite intensities, as specimens per infected animal, SD and range of two species of lice (*Halipeurus abnormis* and *Austromenopon echinatum*) and one of flea (*Xenopsylla gratioiosa*) found in adult ($n=106$ ad) and juvenile ($n=53$ ju) Cory's shearwaters on the island of Corvo (Azores) in 2010 and 2011 (see “Methods” for details on how burrow-level and predator variables were measured)

Nest-level variables		Mean	SD	Range
Distance to nearest neighboring nest (m)		2.48	1.15	0.5–16.3
Elevation (m a.s.l.)		153.67	57.9	7–257
Dominant substrate		Soil		Soil–rock
Vegetation cover (%)		44.3	23.4	0–100
Predator-level variables				
Mouse abundance index		0.33	0.21	0.4–0.2
Rat abundance index		0.28	0.17	0.5–0.1
Cat/trap/day		0.10	0.07	0–5
Breeding success		0.41	0.29	0–1
Ectoparasite intensity				
	Age			
<i>Halipeurus abnormis</i>	Ju	5.00	2.80	10–2
	Ad	4.11	1.95	8–2
<i>Austromenopon echinatum</i>	Ju	1.26	0.83	2–0
	Ad	1.11	1.07	3–0
<i>Xenopsylla gratioiosa</i>	Ju	2.03	1.89	5–0
	Ad	0.69	0.22	2–0

seasons, cooler winters and hotter summers but the hottest and coldest temperatures are much milder than in other locations at the same latitude. The highest variability in weather occurs during the months of November to April (outside the Cory's shearwater breeding period). Therefore, as weather changes throughout the year are small and gradual on Corvo, our nest characteristic variables should reflect the overall conditions of the nest for parasites.

On Corvo, rats and cats predated upon Cory's shearwater eggs and small chicks Hervías et al. (2013), but adults and adult-sized juveniles may be large enough to deter nest intruders such as rodents. However, rats and even mice feed on eggs and chicks, probably scavenging rather than predating (Hervías et al. submitted), and therefore, rodents would visit shearwaters' nests throughout the reproduction period and could cause stress in breeding birds. We evaluated monthly fluctuations in the abundance of rodents around the Cory's shearwater nests (from May to October 2010 and 2011) with 5 wax-blocks spaced 50 m apart around each nest (Thomas 1999) to estimate the relative abundance index of black rat and house mouse affecting each nest, as the number of wax-blocks with bite-marks divided by the total number of wax blocks used per nest. Because bite-marks from different rodent species differed in size (house-mouse has shorter and narrower incisors), we were able to estimate a single abundance index for each species. The activity of feral cats around each nest was studied using one passive infra-red motion sensor cameras (Bushnell TrophyCam 8MP), deployed for three consecutive nights in the incubation and chick-rearing period. Cats recorded by camera traps were individually identified based on habits and coat color pattern (Sarmiento et al. 2010). For each nest, the relative index of cat activity was measured as the number of cats per active camera trap day (Table 1).

Because nest characteristics and predator activity variables could covary, three categorical principal component analyses were applied. The two first incorporated the mean values of mouse and rat abundance index and cat/trap/day during the incubation and chick-rearing periods of Cory's shearwater to obtain an index of predator activity during the incubation and chick-rearing periods, respectively, and the third a combination of the four nest characteristic variables as an index of physical characteristics of nests. PC1 had the highest degree of correlation with rat and mouse abundance and distance to nearest neighboring nest, and accounted for 79 % of the total variance in predator activity during incubation and 81 % chick-rearing periods and 76 % in nest physical characteristics.

Finally, we assumed that human disturbance and diseases did not account for ectoparasite intensity values, since there has been no evidence of human exploitation of Cory's shearwater there since the late 1990s, and to our knowledge, the birds were not affected by diseases (only three 4-week

old chicks showed avian poxvirus, but the nodules were completely gone before fledging).

Data analysis

Our definitions of prevalence (P) and mean intensity (MI) were determined according to Bush et al. (1997). Specifically, P is the percentage of individuals examined who were infected, and MI is the estimated number of parasites per infected individual, measured in specimens per infected animal (spia).

The Mann–Whitney test was used to assess differences in ectoparasite intensity between males and females and between adults and juveniles. To evaluate annual differences in food conditions for juveniles, we compared wing length and body mass between 2010 and 2011 using separate Student tests for males and females. All these tests were two-tailed, with significance level set at $\alpha=0.05$ and performed with Systat 13. Descriptive statistics are expressed as mean \pm SD.

Since factors affecting the ectoparasite intensity in chicks and adults could be different, and explanatory variables tested such as environmental factors during incubation and chick-rearing periods could differ slightly, we performed separate analyses for each age class.

Seven candidate models (GLMs) were generated representing different biological hypotheses to explain variation in nest ectoparasite intensity. Specifically, we tested whether ectoparasite intensity varied with (1) predator activity index during the incubation for adults and during the chick-rearing period for juveniles (predator model), (2) with physical characteristics of the burrow (nest model), (3) with body condition index for adults (body-condition model) and food condition for juveniles (food model) or (4) combinations of these three variables: three pair-wise (1+2, 1+3, and 2+3) and one trio-wise (1+2+3). We used a model with a Poisson error distribution and log link function and fitted a different model for each ectoparasite species.

To assess the influence of predators, ectoparasites, adult body condition index, and nest characteristics on the breeding success of Cory's shearwater (1=chick fledged, 0=chick not fledged), we constructed ten GLMs with a binomial error distribution and logit link function: (1) predator activity index during the incubation period (predator model), (2) total parasite intensity of fleas and lice (ectoparasite model), (3) body condition index (body-condition model), (4) nest characteristics index (nest model), and (5) a combination of these variables.

The Akaike Information Criterion (AIC) was used to rank the models according to their capacity to describe the data parsimoniously (Burnham and Anderson 2002). We report the support for each of those models in terms of evidence ratio and the Akaike weight ω AIC, using the R-package “*secr*” in R 2.12.1 (R Development Core Team 2010).

Results

Cory's shearwater nests: general data

The mean distance to the nearest neighboring nest was 2.5 m and the mean elevation was 153.7 m a.s.l. (Table 1). The highest percentages of vegetation cover were measured over nests at higher elevations. Predominant substrate was soil, a few nests were in rock substrate and showed the lowest values of vegetation cover and mean elevation. The mean abundance index of house mouse during the incubation period was 0.30 ± 0.21 and of black rat 0.24 ± 0.17 , whereas over the chick-rearing period, they were 0.35 ± 0.23 and 0.34 ± 0.12 , respectively. We identified 11 individual cats in 36 single detections over the incubation period and 13 individual cats in 89 single detections during the chick-rearing period. In total, 82 % of nests were visited by at least one individual cat. The mean value of breeding success was 0.41 ± 0.29 chicks fledged/breeding pair.

The parasites

All birds harbored ectoparasites. We identified two species of lice (*Austromenopon echinatum* and *Halipeurus abnormis*), one of flea (*Xenopsylla gratioiosa*), and two individual ticks (*Ixodes ricinus* and *Haemaphysalis punctata*) (Table 1). *H. abnormis* was the most common ectoparasite ($n=366$; $P=100\%$). Ticks were not considered for statistical analyses because of their low prevalence.

We did not find any blood parasites in the 53 smears analyzed in our study.

Eleven of the 13 dead Cory's shearwaters harbored 59 helminths belonging to three nematode and two platyhelminth species ($P=84.6\%$, $MI=5.4$ spia ± 2.9 SD). Within Nematoda ($n=40$ specimens), two species, *Seuratia shipleyi* ($P=38.5\%$, $MI=6.2$ spia ± 9.6) and *Contracaecum rudolphii* ($P=7.7\%$, $MI=1.0$ spia ± 2.8), were identified in crop, proventriculus, and ventriculus and one species in small intestine, *Thominx contorta* ($P=30.8\%$, $MI=2.0$ spia ± 9.2). One species of cestodes, *Tetrabothrius minor* ($n=17$; $P=30.8\%$, $MI=4.3$ spia ± 10.0) and one trematode, *Cardiocephalus physalis* ($n=2$; $P=15.4\%$, $MI=1.0$ spia ± 7.2), were found in the small intestine.

Cory's shearwater juveniles had higher parasite intensities than adults (Mann–Whitney test $z=1.97$, $p=0.01$) for both lice and fleas, but we did not find a significant influence of host sex on ectoparasite intensity (Mann–Whitney test $z=0.9$, $p=0.42$).

Body condition and breeding success of Cory's in relation to ectoparasite intensity and predator activity

Juvenile body mass (BM, grams) and wing length (WL, millimeter) for 2010 (males, $BM=930.1 \pm 55.4$, $WL=$

35.9 ± 8.2 ; females, $BM=810.2 \pm 57.4$, $WL=35.1 \pm 4.2$) and 2011 (males, $BM=870.5 \pm 57.1$, $WL=35.3 \pm 7.4$; females, $BM=750.4 \pm 46.9$, $WL=34.2 \pm 4.7$), as an indirect surrogate of food conditions for juveniles, did not show significant differences between years for males (t test, $WL: t=1.56$, $p=0.24$; $BM: t=0.87$, $p=0.14$, both with $d.f.=1$) or females ($WL: t=1.23$, $p=0.16$; $BM: t=0.68$, $p=0.13$, both with $d.f.=1$).

The most parsimonious model to explain variation in ectoparasite intensity between nests included “predator activity” as an explanatory variable, independently of the host age. The model indicated that ectoparasite intensity of adults increased with higher predator activity for both lice ($b=3.86 \pm 2.10$; explaining 88.6 % of the variation in parasite intensity) and *X. gratioiosa* ($b=1.83 \pm 0.12$; 89.4 % of the variation) in adults and, in juveniles, for both lice ($b=2.16 \pm 3.11$; explaining 74.5 % of the variation) and *X. gratioiosa* ($b=0.97 \pm 1.14$; 80.3 % of the variation) (Table 2). Body condition index of adults also received some support from the data and indicated that parasite intensity of lice and fleas increased with lower body-condition index ($b=-0.05 \pm 0.02$).

The GLMs constructed to explain breeding success or failure in Cory's shearwater nests revealed that the combination of “predators and ectoparasites” received the most support from the data (Table 3) and explained 89.7 % of the variation. This model indicated that breeding success decrease with high predator activity ($b=-0.43 \pm 0.22$) and ectoparasite intensity ($b=-1.25 \pm 0.38$).

Discussion

Ectoparasite intensities and predatory activity: ecological effects on Cory's shearwaters

Our study of predator and parasite effects on seabirds, such as the Cory's shearwater, demonstrates that mammalian predators can influence the risk of harboring ectoparasites. Ectoparasites were more abundant in birds affected by greater predator activity around nests. The effects of exotic mammalian predators on ectoparasite intensity negatively influenced bird body condition, which in turn reduced breeding success.

Few studies have previously studied the interaction between predators and parasites in small and medium-sized birds, and their effects were not clear. Clinchy et al. (2004) observed more parasites in breeding song sparrows (*Melospiza melodia*) already stressed by high predator activity. Nevertheless, high predator activity did not increase the parasite intensity in hen red grouse (Moss et al. 1990). Moreover, virtually every relationship between predators and parasites has been observed experimentally, probably

Table 2 Summary of the three best candidate and null models (GLMs) explaining variation in parasite intensity for Cory's shearwater adults ($n=106$) and juveniles ($n=53$) of lice (*Austromenopon echinatum* and *Halipeurus abnormis*) and flea (*Xenopsylla gratioiosa*), in 53 nests monitored on Corvo Island in July and October of 2010 and 2011 (see text for definition of variables)

		Model	K	AIC_c	ΔAIC_c	ωAIC_c	Deviance
Adult birds	Lice	Predator model	24	559.26	0.0	0.14	532.17
		Body-condition model	25	561.00	0.7	0.11	533.23
		Nest model	24	565.73	2.6	0.08	534.61
		Null model	21	571.51	4.5	0.01	541.25
	Fleas	Predator model	25	301.41	0.0	0.21	295.12
		Body-condition model	24	303.68	1.1	0.18	296.33
		Nest model	25	306.14	2.5	0.07	297.40
		Null model	21	310.23	5.6	0.01	302.51
Juvenile birds	Lice	Predator model	24	420.52	0.0	0.19	402.32
		Predator+nest model	25	424.11	1.9	0.10	403.56
		Nest model	24	425.37	2.3	0.07	405.25
		Null model	21	406.16	4.1	0.01	411.55
	Fleas	Predator model	24	254.62	0.0	0.11	225.13
		Nest model	24	258.05	0.9	0.08	226.29
		Predator+food model	25	259.79	1.8	0.05	228.36
		Null model	21	266.33	4.6	0.01	233.51

because the incorporation of interacting factors may be difficult in field situations (Hudson et al. 1992 and references cited therein). We are not aware of any prior field study on the effects of nest predator pressure on ectoparasite intensity in seabird species. Factors influencing parasite populations such as environmental factors and food condition may have had little interaction with parasite intensity during our study on Corvo. Behavioral studies suggest that vertebrates are afflicted by the constant tension between finding food and avoiding predators (Daoust et al. 1998; Forrester and Lankester 1997). In the present study, birds may have been under some food stress in 2011 (see BM and WL values); however, food conditions for juveniles did not differ between 2010 and 2011. Thus, food stress could occasionally be interacting synergistically with predators, making birds more susceptible to parasitism. However, as we only consider the pattern of food conditions over two consecutive years, this hypothesis merits further testing. Although other factors that were not possible to measure

here could also influence ectoparasites, variation in ectoparasite intensity among nests is most likely due to differences in abundance of mammal predators. This suggests that birds facing higher predator activity were more stressed (Clinchy et al. 2004) and therefore more easily affected by a large number of parasites (Raouf et al. 2006).

Negative effects of ectoparasites on breeding success have previously been reported in other seabird species, e.g., the black-legged Kittiwake (*Rissa tridactyla*) (Boulinier and Danchin 1996) and the roseate tern (*Sterna dougallii*) (Ramos et al. 2001). In Cory's shearwaters, predation upon chicks and eggs was documented on Corvo (Hervías et al. 2013). Because adults can protect themselves against rat or cat predators, no effects of predators and parasites threatening breeding success were described on Cory's shearwater adults. This study suggests that predator activity around the nests must increase the stress of breeding seabirds, which become even more susceptible to parasite infections, and this may impair their ability to reproduce

Table 3 GLM model selection summary of ten candidate models explaining variation in breeding success of Cory's shearwater (1=chick fledged, 0=chick not fledged) on Corvo Island in 2010 and 2011 ($n=106$ adults; see text for definition of variables)

Model	K	AIC_c	ΔAIC_c	ωAIC_c	Deviance
Predator+ectoparasite model	22	223.01	0.00	0.24	197.13
Predator model	21	261.78	1.10	0.09	196.33
Ectoparasite+body-condition model	22	265.43	1.51	0.07	183.60
Predator+nest model	23	277.74	2.19	0.06	195.87
Ectoparasite+nest model	23	278.89	3.19	0.06	194.52
Body-condition model	22	279.57	3.89	0.05	192.01
Ectoparasite model	22	280.19	4.36	0.04	189.16
Nest model	21	283.09	5.38	0.01	194.11
Predators+body-condition model	21	289.25	7.93	0.00	193.92
Null model	20	297.42	9.21	0.00	195.15

successfully. Therefore, Cory's shearwater adults face an indirect threat associated with predators, suggesting that severely infected individuals have more breeding failures than mildly infected ones. The added impact of predators on seabird parasites should be considered with attention in future studies, since Cory's shearwater ectoparasites have potential effects on body condition, individual survival, and population health of the host (Atkinson and Van Riper 1991).

The parasitic fauna

The ectoparasitic fauna described in this study includes two lice species (*A. echinatum*, *H. abnormis*) and one flea species (*X. gratioiosa*), previously recorded from Cory's shearwater (Gómez-Díaz et al. 2008), and considered as specific parasites of this host (Beaucournu et al. 2005; Mifsud et al. 2008; Price et al. 2004). The feather damage caused by lice has energetic consequences (Booth et al. 1993), but it seems to have little effect on reproductive success (Clayton and Tompkins 1995). However, an abnormally high infestation of lice has proved to be unhealthy, as high numbers of *Austroripon* spp. killed a common gull in Northumberland (Ash 1960). Regarding fleas, *X. gratioiosa* may delay fledging or reduce survival of European storm-petrels (*Hydrobates pelagicus*) (Merino et al. 1999). Furthermore, ticks are generally associated with physical weakness of juveniles (Ramos et al. 2001; J. Bried, unpublished data). Although *I. ricinus* and *H. punctata* are frequently found in mammals, they can use birds as secondary hosts. Because these two tick species have never been described in seabirds, their presence in Cory's shearwaters could be considered as an occasional finding. A part of the life cycle of ticks occurs in the environment, in the soil or under vegetation, where they develop into the next phase, which remain quiescent around 1 year or move until the tick finds a suitable host to survive (Gray 2002). The occasional presence of small ruminants around the nests could explain why we found only two tick specimens in Cory's shearwater.

We observed a reduction in ectoparasite intensity with host age. The lesser abundance of *A. equinatum* and *H. abnormis* in Cory's shearwater adults during the chick-rearing period than during prelaying and laying have been attributed to a probable vertical transmission of ectoparasites from parents to the chick (Gómez-Díaz et al. 2008). This hypothesis may apply to our data, as we examined one adult and the juvenile from 53 nests and found higher ectoparasite intensity in juveniles, but in our study, this could also be due to higher predator activity around the nests during the chick-rearing period. Forero et al. (2006) observed that incubating adults showed significantly higher levels of immunocompetence than nestlings. Therefore, the acquired immunity could reduce infection rates in the studied adults and facilitate the transmission of ectoparasites to juveniles inside the nests. No differences

between sexes in nest attendance during the incubation period of Cory's shearwaters (Granadeiro 1991) and, therefore, similar parasite exposure, could explain the lack of differences in ectoparasite prevalence between host sexes. However, the examination of both members of the same pair should be desirable in further studies.

No Cory's shearwaters showed blood parasites, which agrees with previous studies in seabirds (Esparza et al. 2004; Martínez-Abraín et al. 2004; Merino and Mínguez 1998). González-Solís and Abella (1997) also did not find blood parasites in Cory's shearwaters on the Chafarinas Islands. Like the Chafarinas, Corvo is an isolated island, more than 1,500 km from the European continent and, hence, probably difficult for parasite vectors to reach (e.g., Little and Earlé 1994).

This study also shows the first comprehensive reference to the gastrointestinal parasites of Cory's shearwater. *S. shipleyi* (Hoberg and Ryan 1989; Foster et al. 1996), *C. physalis* (Hoberg and Ryan 1989), and *T. minor* (Foster et al. 1996) have been previously recorded in greater shearwater (*Puffinus gravis*, Procellariiformes). *C. rudolphii* has been identified in Charadriiformes: razorbill (*Alca torda*), Brünnich's guillemot (*Uria lomvia*), common guillemot (*U. aalge*), ancient murrelet (*Synthliboramphus antiquus*), tufted puffin (*Fratercula cirrhata*) and horned puffin (*F. corniculata*) (Muzaffar and Jones 2004). Lastly, *T. contorta* has been observed in brown pelican (*Pelecanus occidentalis*) (Pelecaniformes) (Dyer et al. 2002) and gulls *Larus* spp. (Charadriiformes) (Pemberton 1963).

Conclusions and future directions

The causes of parasite infections and their real impact on wild bird populations are often difficult to identify and quantify. Our study provides direct support for the hypothesis that ectoparasite intensity varies with predator abundance. However, because Cory's shearwater breeding success was negatively influenced by both predator activity and ectoparasite intensity, differences between parasite and predator effects on breeding success are hard to find from our results. Therefore, bird stress should be quantified in future studies, to provide a mechanistic link between stress and fluctuations in bird parasite intensity and predator activity. In addition, more studies concerning endoparasites of seabird species are desirable, since the pathogenic effects of helminths on seabirds might lead to a population decrease (Galaktionov and Bustnes 1996).

Lastly, exotic mammal eradications are being considered necessary to safeguard many seabird populations on an increasing number of islands around the world (Aguirre-Muñoz et al. 2009; Brooke et al. 2007; Capizzi et al. 2010; Oppel et al. 2011; Veitch et al. 2011), and the negative impact of predators on Cory's shearwater parasitism gives

support to these measures. Apart from direct predation by exotic mammals, the indirect effect of predators on parasites and their negative effects on seabirds cannot be ignored, because they further impair seabird body condition and breeding success, and may have a negative impact on long-term population health (Marcogliese 2005).

Acknowledgments This study was made possible by LIFE07 NAT/P/000649 ‘Safe Islands for Seabirds’, coordinated by the Portuguese Society for the Study of Birds (SPEA) and co-financed by the European Union Commission. We thank P. Domingos, E. Díaz, F. Ceia, R. Ceia, S. Opiel, H. Cowen, T. Pipa, J. Benedicto, M. Goh and the Life Project team and volunteers for invaluable field help. We appreciate the input of J. Díaz, L. Chitimia and M. Kinsella who contributed to the identification of ticks and endoparasites. We are also grateful for the permission (no. 84; 2011) given by *Direcção Regional do Ambiente* (Horta, Portugal) for handling wildlife. The authors declare that all experiments described in this study complied with the current laws of Portugal.

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