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Demographic consequences of native fox predation on Socotra cormorants on Siniya Island, United Arab Emirates

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Predation by both native and introduced terrestrial predators is a major threat to colonially breeding seabirds leading to low breeding success and negative demographic effects. The Socotra cormorant *Phalacrocorax nigrogularis* is a regionally endemic seabird categorized as Vulnerable by the IUCN. It breeds on islands in the southern Arabian Gulf and in the Gulf of Oman. One colony, Siniya Island, on the northern United Arab Emirates hosts about 40% of the global breeding population. Socotra cormorants are ground nesters and are vulnerable to predation by native Arabian red foxes *Vulpes vulpes arabica*, occurring naturally on Siniya island. We used camera trapping to estimate the population size and diet composition of foxes on the island. A total of 24 foxes were identified including adults and cubs, and cormorants and their eggs dominated the fox's diet (80%) during the breeding season. We estimated that the foxes killed >3500 cormorants during the season. The cormorant population was modelled using Vortex. The simulated population increased from 46 500 individuals (corresponding to the known population in 1995) to stabilize between 154 000 and 188 000 birds after 2010 in the absence of mortality from predation. Simulated mortality showed various degrees of population suppression and increasing extinction probabilities at higher degrees of predation. The model was more sensitive to predation of adult birds. Predation rates causing up to 35% juvenile mortality stabilized at <250 000 birds. Contrastingly, adult mortality of >25% caused the population to stabilize at <80 000 birds. Actual population estimates from 2011–2015 ranged from 79 000–124 000 birds. Thus, our model suggested that the cormorant population was suppressed due to predation at levels consistent with 20–25% adult mortality in the simulated population. Continual monitoring of the impact of foxes is essential and management of foxes may be recommended as a conservation measure if predation pressure increased.

Keywords: camera trapping, fox predation, island breeding colony, *Phalacrocorax nigrogularis*, Socotra cormorant, United Arab Emirates

Worldwide, seabirds are undergoing large-scale and long-term substantial population declines due to anthropogenic activities such as disturbance, development, habitat loss, pollution and fishing gear entanglement (Palczyński et al. 2015). Typically, seabirds are cliff or ground-nesters preferring to nest on islands, with few defences against avian or mammalian predators (Patton and Southern 1978, Millus et al. 2007), making them especially vulnerable to both native and non-native terrestrial predators, including feral cats *Felis catus*, foxes (*Vulpes* spp., *Alopex lagopus*) and rats *Rattus* spp. (Burger and Gochfeld 1994, Lavers et al. 2010, Towns et al. 2011). Globally, predators have been introduced,

sometimes purposefully, to seabird islands, with catastrophic consequences on breeding success of many seabird species (Towns et al. 2011). For example, Arctic foxes *Alopex lagopus* and red foxes *V. vulpes* were introduced to 455 Alaskan islands in the North Pacific to enhance the production of fur in the 1800s (Bailey 1993). Foxes caused major impacts on a variety of terrestrial and marine species including waterfowl, shorebirds and seabirds, with significant declines in productivity (Bailey 1993). Furthermore, long term studies have indicated foxes had cascading effects on these fragile island ecosystems, transforming the plant communities from grasslands to dwarf-shrub complexes (Croll et al. 2005).

The impact of native predators on birds has received less attention and presents a gap in worldwide studies (Birkhead and Nettleship 1995, Millus et al. 2007, Lavers et al. 2010, Towns et al. 2011). Foxes that have arrived on islands without human assistance may have substantial impacts on breeding seabirds and other species. For example, pack ice in the

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North Atlantic often connects islands facilitating the arrival of Arctic foxes on otherwise inaccessible, remote islands. Arctic foxes that arrived on the Gannet Islands, Labrador, had deleterious demographic impacts on breeding seabirds (Birkhead and Nettleship 1995, Lavers et al. 2009). Islands with resident fox populations caused breeding failures and resulted in a total cessation of breeding in razorbills *Alca torda* and murres *Uria* spp. and substantially lower breeding success in Atlantic puffins *Fratercula arctica* (Birkhead and Nettleship 1995). In contrast, among the Gannet Island group, the islands that are inaccessible to foxes maintain high seabird reproductive success, suggesting that elsewhere, this native predator may have major negative demographic effects on seabird populations. Further population modelling using survival data from the Gannet Islands focusing on razorbills indicated that intermittent arrival of non-resident Arctic foxes (estimated from fox presence from 1980–2000) could reduce the stochastic growth rate by 0.017% with projected future declines in razorbill populations (Lavers et al. 2009).

Semi-enclosed gulfs and seas often host substantial seabird colonies that could be vulnerable to native predators due to their relative proximity to the mainland (Schreiber and Burger 2002, Towns et al. 2011). The Arabian Gulf is a shallow, semi-enclosed basin with rapid turnover, characterized by high salinity and high average temperatures (John et al. 1990). The region has been undergoing rapid degradation due to oil exploitation and rapid coastal and urban development (Gardner and Howarth 2009). Furthermore, the Arabian Gulf is situated in a region characterized by a harsh environment. Temperatures soar to over 50°C and terrestrial environments are typically dry due to low precipitation (<100 mm year⁻¹). Nevertheless, the Arabian Gulf harbours a relatively rich variety of breeding or wintering seabirds (about 26 species; Jennings 2010). Many of the seabird colonies have been vulnerable to not only disturbance due to development, but also due to the introduction of native or feral predators (Jennings 2010, Muzaffar et al. 2013).

The Socotra cormorant *Phalacrocorax nigrogularis* is a prominent, locally abundant, regionally endemic species that has two disjunct populations, one limited to the Arabian Gulf and adjacent Gulf of Oman regions, and a second population spanning from coastal regions of southern Oman to the Gulf of Aden adjacent to the Red Sea (Jennings 2010). The species is currently categorized as Vulnerable by the IUCN (BirdLife International 2017). The global population of this species is estimated to be 750 000 individuals, with about 110 000 breeding pairs mostly living and breeding within the Arabian Gulf (about 90%; Jennings 2010, BirdLife International 2017). Fourteen colonies are currently known in the Arabian Gulf and at least seven colonies are extinct due to oil exploitation activities and concomitant disturbances of islands that seabirds used to breed on (Jennings 2010, BirdLife International 2017). Two major breeding concentrations are known; 1) the Gulf of Salwa region west of Qatar hosts about 20 000–50 000 pairs on three islands belonging to Saudi Arabia and one island belonging to Bahrain; and 2) Siniya Island, in the south-eastern portion of the Arabian Gulf, within the United Arab Emirates (UAE), hosting 28 000–41 000 pairs (representing about 30–40% of the global breeding population) (Jennings 2010, Muzaffar et al. 2017a, Fig. 1A). In addition to these major concentrations, there are

another eight colonies off the coast of Abu Dhabi, UAE and one colony near Qatar (Jennings 2010), each hosting from a few hundred to fewer than 3000 pairs. The small number of breeding colonies makes this species especially vulnerable to decline and earlier estimates suggest that the population of the Arabian Gulf has declined by 60–80% since the 1980s possibly due to habitat loss, pollution or introduced predators (Jennings 2010).

Both Arabian red foxes *V. v. arabica* and feral cats *Felis catus* prey on Socotra cormorants (Muzaffar et al. 2013). Arabian red foxes arrived on Siniya Island in the 1980s when land bridges formed at low tide (Muzaffar et al. 2013). It is unlikely that foxes regularly move to and from the island since the deep channels separate the island from the mainland. Thus, the fox population on Siniya Island is assumed to be a closed population. The presence of foxes is known to have adverse impacts on survival and long-term reproductive success of seabirds (Birkhead and Nettleship 1995, Towns et al. 2011) due to their generalist feeding strategies and their tendency to overkill and hoard eggs and carcasses (Patton and Southern 1978, Drake et al. 2011, Towns et al. 2011). Additionally, feral cats were also introduced to Siniya Island more recently (date unknown, but perhaps in the late 2000s, Ministry of Climate Change and Environment, pers. comm.). Foxes on Siniya Island appear to eat selectively around the neck and breast of cormorants, leaving most of the carcass partly uneaten (~70% is wasted; Muzaffar et al. 2013). Foxes on Siniya Island are known to hoard food to help survive the harsh summer months when food is scarce (Muzaffar et al. 2012, 2013). Both foxes and feral cats ate large numbers of eggs, chicks and adults of Socotra cormorants, with an estimated mortality of about 2000 Socotra cormorants per breeding season (approximately between August to January, but rarely extending into April) (Muzaffar et al. 2013). However, this number was probably an underestimate since the population size of foxes or cats, hoarding behaviour of foxes, detection probability of carcasses, and the diet of foxes were not adequately characterized (Muzaffar et al. 2013). Nevertheless, population modelling suggested significant detrimental effects on breeding Socotra cormorants, with major population crashes predicted within 50 years under the assumption of an annual total mortality of 2000 individuals (Muzaffar et al. 2013). Feral cats have not been sighted on the island since 2012, possibly because the few individuals were unable to persist. In contrast, red foxes continue to persist on the island.

We conducted this study to better quantify the fox population and their potential impact of breeding Socotra cormorants on Siniya Island. The objectives of our study were; 1) to estimate fox population size and diet using remote camera trapping techniques; and 2) to determine the potential demographic consequences of this fox predation on cormorants breeding on Siniya Island using population modelling.

Study area

Siniya Island is 26 km² located around 2-km north-east of Umm Al Quwain emirate, UAE (25°36'20.63"N,

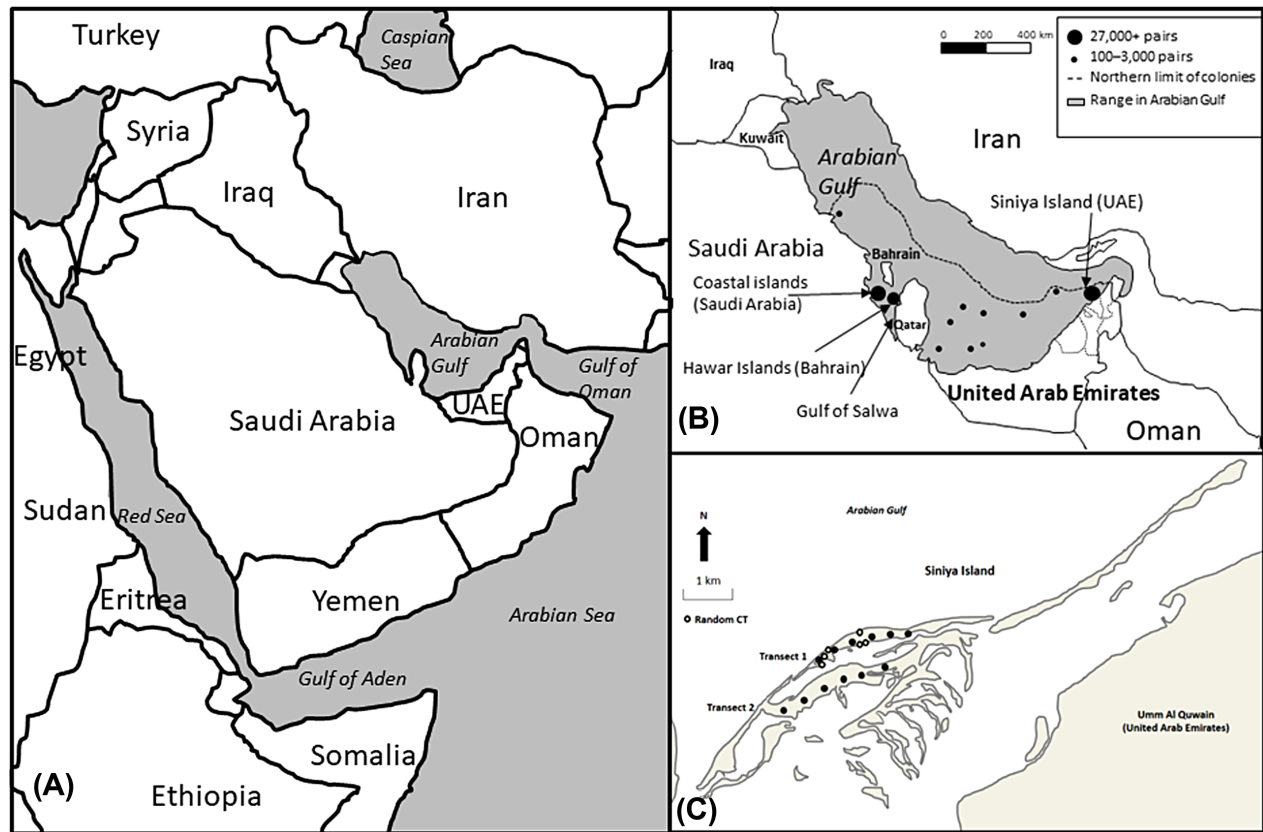


Figure 1. (A) Map showing the Middle East region; (B) Map showing the location of Siniya Island, United Arab Emirates and other Socotra cormorant breeding colonies within the Arabian Gulf. (C) Layout of camera traps located on two transects namely Transect 1 (T1) and Transect 2 (T2) (closed circles) and near den sites (Random transect, open circles).

55°36'28.85"E), southeast of the Arabian Gulf (Fig. 1A). Many shallow, muddy lagoons and tidal inlets shape the island, mangroves *Avicennia marina* occur in patches around the lagoons. Coastal vegetation consists mainly of *Haloxylon–Arthrocnemum macrostachyum* scrub complex which surround cormorant breeding areas and fox den sites on the north of the island, and a plantation of *Prosopis juliflora* and *Acacia* spp. close to abandoned dwellings. There are no full-time inhabitants on the island although there are large palaces on the eastern side used as holiday homes during the winter months. Winter in the UAE is from October to April with cool average day temperatures on average 25°C and summer months from May to September with high humidity (up to 90%) and day temperatures reaching up to 50°C. The total area of the island is 27 km².

Socotra cormorants breed between August and December on Siniya Island (Jennings 2010, Muzaffar et al. 2012, 2015, 2017a). Birds typically depart from Siniya Island by January after breeding activities have concluded (Muzaffar et al. 2017b). Socotra cormorants are large ground nesting birds, building scrape nests with sand and gravel (Jennings 2010, Muzaffar et al. 2012, 2015). The adults show limited aggression towards non-avian threats and are prone to abandoning nests when threatened (Muzaffar et al. 2013). Socotra cormorants on Siniya Island typically lay between 3–4 eggs, incubating them for 20–25 days (Muzaffar et al. 2017a). About 51–81% hatching success has been reported (Muzaffar et al. 2012, 2015, 2017a).

Methods

Camera trapping

We deployed a total of eighteen compact Bushnell X-8 Trail cameras to determine fox dietary choices. Each camera was 120 × 94 × 46 mm in dimension, with a focal length of 17.6 mm and maximum distance of detection of 45 m. To identify individual foxes and estimate fox population size, 12 cameras were deployed on two transects, which were in operation between 7 April and 6 June 2014. Each transect consisted of six camera traps separated by 500 m (total transect length = 2.5-km). Transect 1 (T1) ran through areas where the cormorants bred close to the shoreline in previous years (Muzaffar et al. 2015, 2017a, Fig. 1B). Transect (T2) ran through the plantation area of *Prosopis juliflora* where the cormorants bred in 2011 (Muzaffar et al. 2012, 2015, 2017a, Fig. 1B). Both transects were orientated in an easterly direction and were never moved once deployed. To examine the diet of the fox on Siniya Island, we deployed an additional six cameras in cormorant nesting areas in locations recognized for high fox activity, such as at den sites (Fig. 1B). These cameras were designated as 'Random' and run from 10 February 2014 to 10 June 2014 and again from 01 October 2014 to 04 June 2015. We also calculated the individual areas surrounding the two transects to estimate density of the foxes.

All cameras were set to take ten second videos after a one second delay, and initially the passive infrared (PIR)

sensor (of 15 m range) was set to medium (later changed to high when temperatures increased to $>30^{\circ}\text{C}$ in April). The cameras were mounted 30–40 cm above the ground on trees or using driftwood posts. The location of each camera trap was recorded using a global positioning system (GPS) and entered into QGIS software (QGIS Development Team, <http://qgis.osgeo.org>). Cameras were checked and SD card data downloaded every two weeks to ensure enough storage space and battery life.

Individual identification and fox population size

We estimated the fox population on the island using camera-trapped individuals, identifying them individually based on observable anatomical differences. We used the total number of identifiable individuals as the minimum population of foxes on the island. We assumed that the Siniya Island fox population was closed without immigration or emigration, given that potential land bridges during low tide were flooded and did not provide suitable crossing points for individual foxes during the period of our study (Whelan et al. unpubl.). Although G uthlin et al. (2014) cautions against the reliability of identifying mammals with few distinct natural markings, the use of short videos and distinctive characteristics such as the tail shape and repeat sightings make identification relatively easy (Sarmiento et al. 2009). Features used to identify foxes captured on images included unique tail shapes and injuries (examples in Fig. 2).

We summarized the total number of images taken (approximately 5000), identifiable foxes and trap nights of effort after subtracting days where cameras malfunctioned, were stolen or ran out of data storage. Foxes that were captured within 10 min of each other at the

same station were counted as one capture. Cameras were deployed for a total of 341 consecutive camera trap days in Transect 1 (T1) and 275 consecutive camera trap days in Transect 2 (T2). Camera trap days were defined as the number of days from the first day that the camera was deployed until last picture was taken following Ancrenaz et al. (2012).

We estimated the total potential area of occupancy of foxes on the entire island using Earth Point (2015). We excluded areas consisting of mudflats, mangroves, small islets or areas with dense shrub, that are unlikely to be used by foxes due to limited accessibility or absence of hard ground. Total useable habitat was estimated at 11.10 km² or approximately 41% of the total area of the island.

Fox diet

The diet of foxes living on Siniya Island was quantified based on observed dietary items seen in camera trap footage from the ‘random’ cameras. All dietary items were tabulated and categorized into broad types. The biomass of individual items was calculated (based on published values of mean mass for given taxa of food items) to determine relative portions of each of these items in the diet.

The mass of Socotra cormorants was set at 1.548 kg (Muzaffar unpubl.); ‘gulls’ set at 0.224 kg (based on medium-sized or small gulls that remain near the island throughout the year, including black-headed gulls *Chroicocephalus ridibundus*, common gulls *Larus canus*, slender billed gulls *C. genei*; masses estimated from del Hoyo et al. 1993); ‘passerines’ set at 0.027 kg (based on observed wheatear-sized passerine birds; mass estimated from del Hoyo et al. 2006); ‘waders’ set at 0.150 kg (shorebirds such as sanderlings *Calidris alba*, ruddy turnstones *C. leschenaultia* or dunlins *C. alpina*, that are commonly

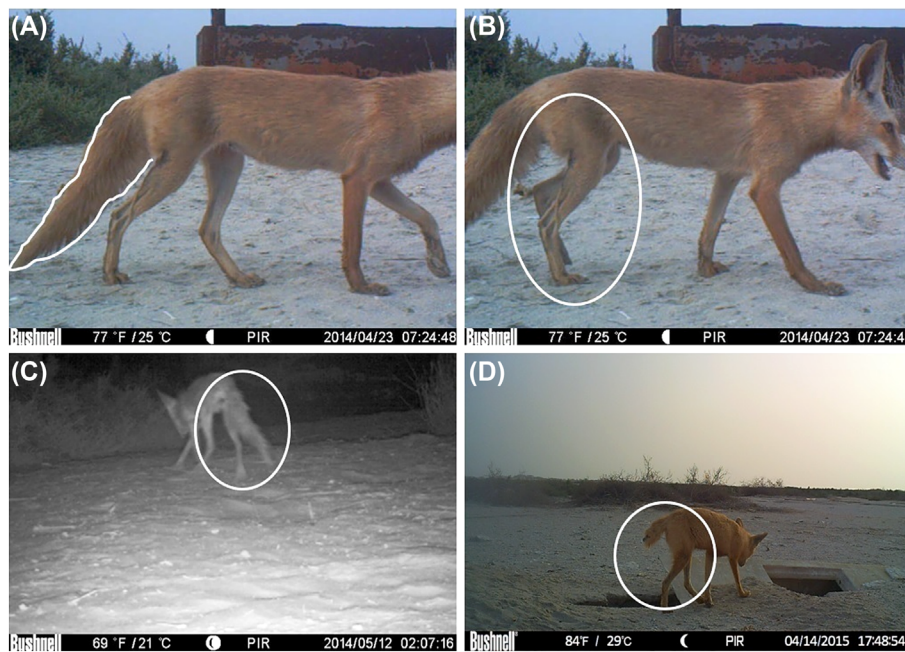


Figure 2. Examples of distinct characteristics used in the identification of individual foxes on Siniya Island: (A) adult female showing slightly curved tail; (B) same adult female showing area of injury on right leg; (C) adult male with distinct tail; (D) adult female with part of tail missing.

seen on the colony during spring and fall migration; masses estimated from Chandler 2009); ‘fish’ set at 0.007 kg (based on the mean sizes of abundant small, forage fish such as anchovies *Engrasicholina* spp., or flying fish *Parexocoetus* spp., noted in the diet of cormorants that are abundant on the nesting areas where they are regurgitated for young, masses from Froese and Pauly 2014); ‘rats’ set at 0.034 kg (based on mass of brown rats *Ratus norvegicus*, from Leslie et al. 1946); ‘eggs’ set at 0.05 kg (recognized as cormorant eggs and biomass estimated from egg volumes from Muzaffar et al. 2012); and ‘unknown’ items set at 0.082 kg, estimated from the mean biomass of all small items excluding cormorants.

Impact of fox predation

We estimated fox food requirements following Muzaffar et al. (2013). We used the following allometric equation to calculate the daily biomass required by red foxes (Nagy 1987):

$$b = 3.35 (2.86/18) (\text{weight})^{0.813}$$

where b = biomass in kilograms.

We used a mean weight of 3.1 kg for red foxes in the Middle East, following MacDonald et al. (1999). We estimated the portion of the fox diet that consisted of cormorants based on our diet data. We calculated the number of days that cormorants were present on the island and estimated relative proportions of the diet by month. Number of cormorants captured (N_c) was then estimated using the following formula (Nagy 1987):

$$N_c = b(\text{number of days}) / (\text{proportion eaten})(\text{weight})$$

Cormorant population model

We modelled the population of Socotra cormorants using Vortex (ver. 10.1; Lacy and Pollock 2018). We parameterized the model using partly published data on Socotra cormorants (Muzaffar et al. 2012, 2013) and estimates from other cormorant species (Nelson 2005) (Table 1). Vortex uses a stage-structured model to determine population persistence (Lacy and Pollock 2018). The age class was divided

into 0–1, 1–2, more than 2 years. Age at first breeding was set at one year, based on the finding that Socotra cormorants start breeding on their second year (Muzaffar et al. 2017a). Mortality of 0–1 year-old birds was set at 45% (with 8% environmental variability), more than 1 year-old birds at 12% (with 5% environmental variability), based on great cormorants *Phalacrocorax carbo* (Nelson 2005). Clutch size was set at 1–3 and fledging success was set at 1.34 nest⁻¹ (from Muzaffar et al. 2012). Proportion of nests with one, two or three eggs was set to be 16, 33 and 51% respectively (Muzaffar et al. 2012). The initial population size was set at 46 500 individuals (from Jennings 2010, estimated in 1995). The carrying capacity of the island was set at 300 000 individuals based on the observation that additional habitat was present on Siniya Island that could support a significant increase in the population (Ksiksi et al. 2015). We modelled the population for 50 years using 1000 simulations.

We used the percentage abundance of cormorants in the diet of foxes to estimate the daily consumption of cormorants during the months of September–March. We created different scenarios of higher or lower mortality rates (sensitivity analysis) to illustrate how fox predation could influence the baseline population model.

Sensitivity analysis

We tested the sensitivity of population persistence to varying levels of juvenile mortality due to predation by varying juvenile mortality rates from 25% to 60% (using 5% increments) (Table 2). We tested sensitivity to adult mortality by varying adult mortality rates from 8% to 30%. We also compared these projections to the total (actual) population of cormorants on Siniya Island from 2011 through to 2016 (Muzaffar et al. 2017a). We altered the proportion of birds with no broods from 0% (all breeding pairs had broods) to 50% (half of the breeding pairs had broods). We altered the maximum number of eggs per brood from two to four. We tested for sensitivity to age at first breeding by varying this parameter between 1–3 years. Life span was varied from 10–20 years and maximum age of breeding was altered from 10–20 years. This was based on the observation that Socotra cormorants could live for up to 20 years in captivity (R. Khan pers comm.).

We separately modelled the impact of catastrophes on the baseline population model by imposing a 10% frequency of

Table 1. Key parameters used to model population change in Socotra cormorants on Siniya Island, UAE.

Parameter	Estimate for baseline model	Source
Initial population size (individuals)	46 500	Jennings 2010, Muzaffar et al. 2013
Sex ratio (assumed)	1:1	Nelson 2005 [†]
Number of broods	1	Muzaffar et al. 2012
Clutch size	1 to 3	Muzaffar et al. 2012
Proportion of clutches with 1, 2, 3 eggs	16, 33, 51	Muzaffar et al. 2012
Fledging success (per nest)	1.34	Muzaffar et al. 2012
Age at first breeding	1	Muzaffar et al. 2017a
Maximum age of breeding (estimated)	10	Nelson 2005 [†]
Carrying capacity (estimated individuals)	300 000	Muzaffar et al. 2013
Mortality rates		
nile mortality	45%	Muzaffar et al. 2013
adult mortality	12%	Muzaffar et al. 2013

[†]Source includes another cormorant species.

Table 2. Range of parameter values used in sensitivity analysis for the modelled Socotra cormorant population. See text for details.

Parameter	Range	Source
Mortality: juveniles	25–60%	Muzaffar et al. 2012
Mortality: adults	8–30%	Muzaffar et al. 2012
Maximum brood size (numbers)	2–4	Jennings 2010, Muzaffar et al. 2017a
Age at first breeding (years)	1–3	Nelson 2005, Muzaffar et al. 2017a
Life span (years)	10–20	Nelson 2005, R. Khan pers. comm.
Maximum reproductive age (years)	14–20	assumed
Catastrophe Frequency	10%	Lacy and Pollock 2018
severity: reproduction	25–50	Jennings 2010
Disturbance severity: reproduction	50–100%	Jennings 2010

catastrophes. We varied the severity of catastrophes by imposing an additional 10% mortality on breeding adults during these catastrophes and varying reproduction rates from 1.0 (in the baseline); to 0.75 (75% of breeding birds are able to breed: Catastrophe 1); to 0.5 (50% of breeding birds are able to breed: Catastrophe 2). These variations were estimated based on our own observations of 2–3 storms of varying severity in each field season and corresponding reduction in successful breeding success between 2011 and 2016 (Muzaffar et al. 2017a). Similarly, we tested the sensitivity of the model to other disturbances (like presence of humans on the colony, Muzaffar et al. 2017a) by varying severity of disturbance on reproduction from 0.5 (50% of breeding birds are able to breed) to 0 (total breeding failure) and imposing an additional mortality of 20%. We characterized these disturbances as Disturbance1–4, with successively higher levels of reproductive declines. Although these levels of disturbance have not been observed at Siniya Island, they have been widespread in other parts of their range (Jennings 2010).

Results

Over a total period of 63 days, a total of 2331 captures were recorded in Transect 1, of which 140 videos were of foxes

Table 3. Camera trapping summary for Transect 1 and 2. False captures = videos of a trigger with no apparent subject, double counts = individual foxes captured within 10 min considered one 'event', % fox activity = proportion of foxes captured compared to all other animals. Each transect is coded (T1 or T2). The alphabet following the code represents individual cameras.

Camera	Date started	Total camera days	Total captures	Total captures excl. false captures	Total captures of foxes	Total captures (–) double counts	% fox activity
T1A	07/04/2014	61	57	32	23	23	72
T1B	07/04/2014	61	65	49	34	33	67
T1C	07/04/2014	61	47	25	23	22	88
T1D	09/04/2014	63	69	33	15	15	45
T1E	09/04/2014	32	21	6	5	5	83
T1F	09/04/2014	63	2072	52	47	42	81
					Total	140	
T2A	16/04/2014	55	110	71	15	15	21
T2B	16/04/2014	55	62	26	0	0	0
T2C	16/04/2014	55	75	42	3	3	7
T2D	16/04/2014	55	221	196	5	5	3
T2E	16/04/2014	55	334	101	9	9	9
T2F	16/04/2014	N/A	N/A	N/A	N/A	N/A	N/A
					Total	32	

(Table 3). In comparison, over a total period of 55 days, 802 captures were recorded in Transect 2, with only 32 videos taken of foxes (Table 3). All remaining videos were false triggers from vegetation, wind or birds.

A total of 15 foxes were individually identified in Transect 1 consisting of 5 males, 3 females, one adult of unknown sex and 6 cubs (Table 4). One male was captured at either end of Transect 1 and also across a small tidal inlet, indicating a minimum range width of 4 km. The majority of foxes were caught in one of the cameras in Transect 1 (T1B).

A total of four foxes were individually identified on Transect 2, namely two males and two adults of unknown sex (Table 4). The two adult males were captured at either end of this transect, suggesting that they had a minimum foraging range width of 2 km. Camera T2F was stolen before any data could be retrieved.

Thus, the minimum population size of foxes was 24 (including all camera traps), composed of 8 males, 7 females, 3 adults of unknown sex and 6 cubs (Table 4). Foxes from Transect 1 and Random cameras overlapped because they were within the same general area (Fig. 1B). Table 4 only shows those exclusively captured in Random and not in Transect 1. We did not see any evidence of mixing between individuals captured on Transect 2 and those from either Transect 1 and Random cameras. Thus, we suggest that there was a difference in the density between the two areas. Transect 1 had a density of 15.41 foxes km⁻² which is due largely to the presence of cormorants breeding repeatedly in the area and due to the complete separation of this sand bank from the rest of the island by two shallow lagoons (1–2 m deep and 50 m wide at low tide). The density of foxes from T2 where cormorants last nested in 2011 was much lower at 2.66 foxes km⁻².

Fox diet

Foxes were observed carrying various food items including cormorant carcasses, cormorant eggs, small rodents, passerine birds and gulls (Fig. 3, 5). Most foraging activities were nocturnal (Fig. 3, 4). Estimates of the biomass of dietary items indicated that cormorants dominated the diet (almost 90% of the total biomass) in March 2014, followed by no

Table 4. Number of individual foxes captured on camera traps on Transects 1, 2 and Random camera traps (see text for details), including age and sex if known. Numbers in Random camera traps represent foxes that were exclusively captured on these cameras.

Location	Adult			Cub			Total
	Male	Female	Unknown	Male	Female	Unknown	
Transect 1	5	3	1	1	1	4	15
Transect 2	2		2				4
Random	2	2				1	5

cormorants in April and May 2014 (Fig. 5). Similarly, in 2015, cormorants dominated the diet representing almost 80% of the total biomass in January, followed by between 60 and 70% of the biomass in February and March, before disappearing from the diet in the remaining months (April, May and June). Smaller items, that were often difficult to identify, became more abundant in the diet after the cormorants had left the island (from April onwards, Fig. 5). Foxes were not captured with food from October to December 2014 (Fig. 5) probably because the fox pups of the previous year were already large and were feeding away from these cameras (near dens). New pups were first observed in late December, 2014 after which foxes were seen bringing back food to the dens (Fig. 5). Thus, we assumed that consumption of cormorants was at least as high as 80% during these periods, as birds are actively breeding during these months in the colony and carcasses left by foxes were found in many locations around the island. The number of days when cormorants were present in the diet was 212 (based on observed cormorants in the diet January, February and March, and assumed cormorants in the diet in September, October, November and December). Since the observed proportion of cormorants in the diet during January, February and March was 79%, we assumed that

the proportion of cormorants in the diet during September to December was at least 79% since this is the peak of the nesting period (Muzaffar et al. 2017a). Thus, we estimated the biomass of consumed Socotra cormorants during that period to be 5367 kg corresponding to 3578 individual cormorants year⁻¹.

Impact on cormorant population

The baseline population model rose from 46 500 birds in 1995 and plateaued around 265 000 bird from the year 2020 onward (Fig. 7). The stochastic-r (intrinsic growth rate) for the baseline scenario was 0.113 with zero probability of extinction (PE) (Table 5). It is evident in the different scenarios for juvenile predation that all population curves showed an increasing trend until stabilization (Fig. 6). Stochastic-r values kept declining as the predation rate increased, while the PE remained zero for all scenarios. Population at juvenile predation rate of 25% and 30% kept increasing sharply until 2010 reaching around 270 000 individuals at which it stabilized for the rest of the projected years. Stochastic-r values were 0.196 and 0.174 respectively. At 35% juvenile predation rate, the simulated population increased significantly between 1995 and 2011. In the following years, it stabilized

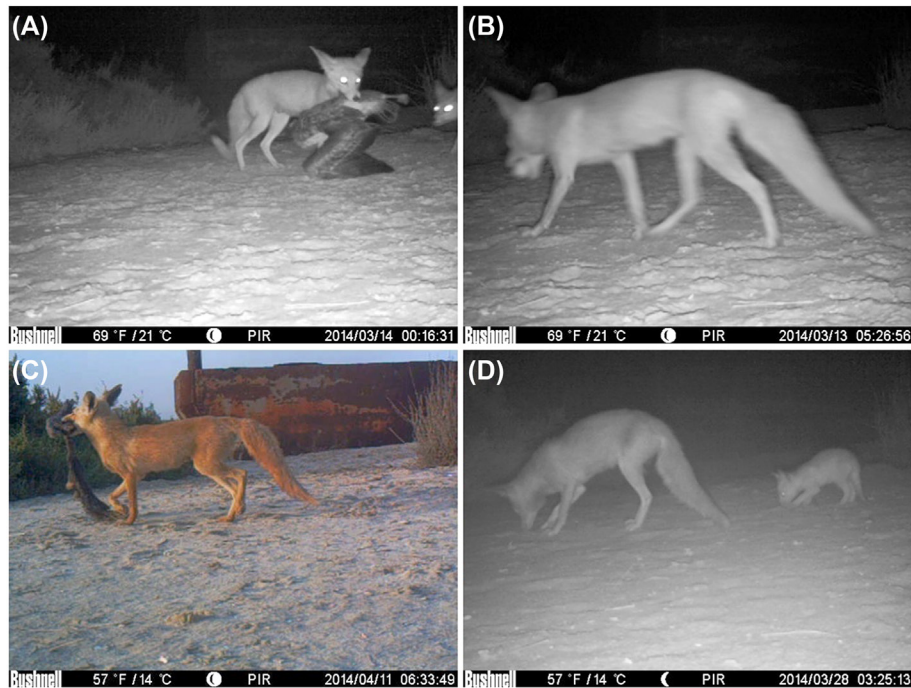


Figure 3. Examples of food items brought back to one of the den sites by the same adult female. (A) Juvenile Socotra cormorant; (B) Socotra cormorant egg possibly excavated from hoard seen in other cameras; (C) adult Socotra cormorant; and (D) female and pup digging in front of den site to excavate or bury eggs or other food items.



Figure 4. Fox foraging near a group of creching chicks (shown in white) with a few adults in attendance (large, black individuals).

after reaching about 276 000 individuals with 0.155 as intrinsic growth rate. At 40% juvenile predation rate, the cormorant population settled at nearly 273 000, with a corresponding stochastic- r of 0.136. Likewise, at 50% predation rate, the simulated population rose to 255 000 birds in 2038. The stochastic- r value declined noticeably to reach 0.09. The last two juvenile predation scenarios, 55% and 60%, showed a steadily increasing trend where they seemed to be stabilising around 230 000 and 180 000 respectively. Stochastic- r values dropped further to give 0.062 at 55% juvenile predation rate and 0.0365 at 60% juvenile predation rate.

Adult predation scenarios indicated more drastic changes in the simulated populations. The simulated population of 8% annual adult predation showed an increase in the population size from 46 500 birds in 1995 stabilizing at around 280 000 birds from 2020 onwards. The stochastic- r was 0.145 with zero PE. Similarly, increasing the adult mortality

to 10% showed an increase in the population which stabilized at around 270 000 birds in 2020. The corresponding stochastic- r value was 0.129 with zero PE. Depredation of adults with a mortality rate of 15% had an intrinsic growth rate of 0.0871 with zero PE. The population stabilized at around 240 000 birds by the end of the simulated 50 years. Adult mortality of 25% created a negative intrinsic growth rate (-0.0072) with zero PE. The modelled population plateaued at 75 000 individuals from the year 2010. As adult mortality rates increased further, the stochastic- r values became more negative, with corresponding declining trends in simulated population size. At adult mortality rate of 27%, the simulated population remained around 46 500 birds. The corresponding stochastic- r was -0.254. Further elevation of adult cormorant mortality rates to 30% projected a population lower in size than the initial one (46 500 birds). The population reached 15 000 by the end of the simulated years with stochastic- r of -0.055 and PE of 0.004.

Sensitivity to other parameters

Reduction of maximum brood size to two eggs reduced the stochastic- r to -0.0013, driving the population to much lower levels and stabilizing at around 49 000 individuals in 50 years (Table 6). Increasing the brood size to four eggs had the opposite effect of increasing stochastic- r and stabilizing the population at a higher level. Altering age at first breeding to two years had the effect of slowing population growth and stabilizing the population at around 72 000 individuals. Age at first breeding of three years had a more dramatic effect on population growth, stabilizing the population at around 16 000 individuals. Increasing

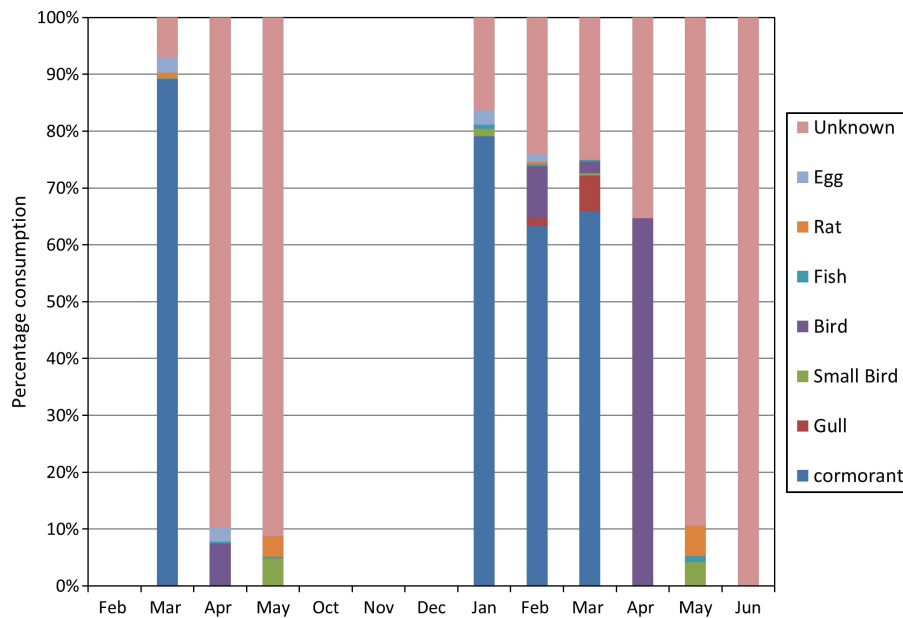


Figure 5. Relative abundance of dietary items based on estimated biomass of observed diet. Relative abundance of diet (measured as estimated biomass) categorized by type of food item (egg = cormorant egg; rat = small rodent possibly brown rat; fish = small forage fish usually anchovy, sardine or related fish abundant on nesting areas; wader = small to medium-sized shorebirds such as sanderlings, turnstones, dunlins, that are commonly seen on the colony during spring and fall migration; gull = any of the medium-sized or small gulls that remain near the island throughout the year, including black-headed gulls, common gulls, slender billed gulls; cormorant = Socotra cormorants, including juveniles and adults).

Table 5. Variation in the intrinsic rate of increase (r) of the population and probability of extinction (PE) under different scenarios.

	Stochastic- r	SD(r)	PE
Baseline predation (45% juvenile, 12% adult predation)	0.1128	0.2237	0
25% juvenile predation	0.1964	0.2636	0
30% juvenile predation	0.1744	0.2552	0
35% juvenile predation	0.1545	0.2449	0
40% juvenile predation	0.1355	0.2333	0
50% juvenile predation	0.09	0.2141	0
55% juvenile predation	0.062	0.2031	0
60% juvenile predation	0.0365	0.1935	0
8% adult predation	0.1447	0.2151	0
10% adult predation	0.129	0.22	0
15% adult predation	0.0871	0.229	0
20% adult predation	0.0417	0.2401	0
25% adult predation	-0.0072	0.2519	0
27% adult predation	-0.0254	0.2571	0
30% adult predation	-0.0552	0.264	0.004

the life span to 20 years and varying the maximum age of reproduction from 12–18 years had the effect of increasing population growth rates and stabilizing the populations to more than 240 000 individuals. The scenario with Catastrophe 1 caused the population to stabilize at 150 000 individuals, whereas Catastrophe 2 caused the population to stabilize at around 130 000 individuals. Similarly, scenarios with disturbance (Disturbance 1–4), with added mortality and effects on reproduction caused populations to go into negative growth more rapidly, with all populations reaching between 15 000 to less than 40 000 individuals by 20 years.

Discussion

Native predators could exert demographic pressures on gregarious, colonial seabirds, often leading to rapid declines and local extinction (Burger and Gochfeld 1994, Birkhead and Nettleship 1995, Kirkwood et al. 2005, Millus et al.

2007, Goltsman et al. 2010, Lavers et al. 2009, 2010, Towns et al. 2011). Understanding demographic consequences of predation on such long-lived, K-selected species is crucial for the purposes of conservation planning (Lavers et al. 2010, Towns et al. 2011). Socotra cormorants have been declining throughout their range due to the cumulative effects of a variety of anthropogenic threats (Aspinall 2010, Jennings 2010). The population of cormorants in this study experienced increasing mortality rates due to fox predation. Fox predation could cause the population to stabilize at a smaller size than what would be theoretically possible given abundant food resources in the area (Muzaffar et al. 2015). Furthermore, effects on adult mortality, brood size, and reproductive rates (particularly breeding failure) could further exacerbate population growth rates and sometimes reduce population size to much lower levels. These parameters are also susceptible to further alterations at lower population size combined with greater predation rates as well as other types of disturbance at breeding colonies.

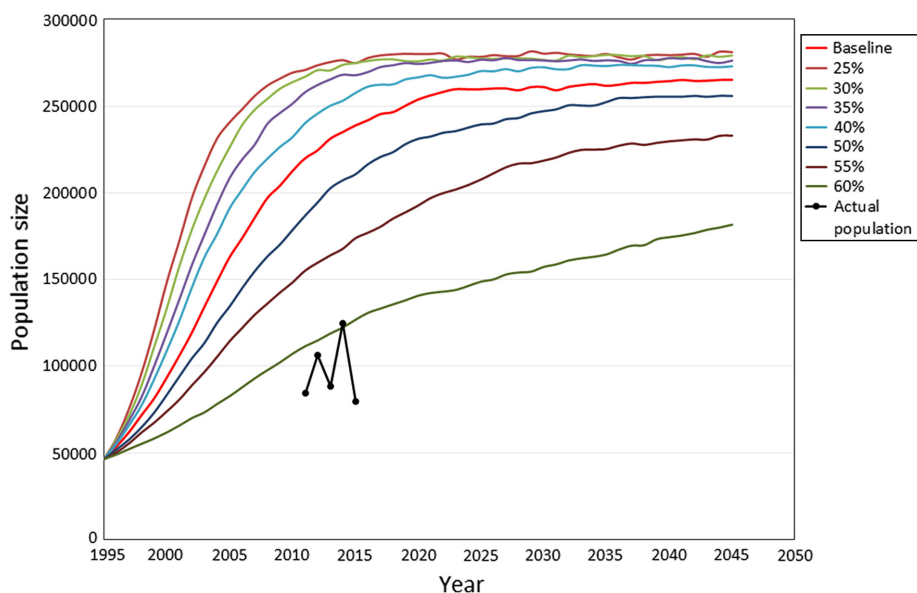


Figure 6. Socotra cormorant population trajectories of the baseline model (assuming no predation by red foxes) and varying levels of juvenile predation by red foxes (shown as percentage mortality relative to the total simulated population).

Table 6. Sensitivity to intrinsic rate of growth (r) and population size after 50 years (N Extant) of simulation in relation to key population parameters. SD=standard deviation. See text for details of parameters that were altered for catastrophe and disturbance scenarios.

	N Extant	SD	stoch-r	SD
Baseline scenario	183 837.99	41 597.98	0.0270	0.0888
Broodsize 2	49 234.83	24 410.96	-0.0013	0.0808
Broodsize 4	184 981.12	40 298.13	0.0272	0.0892
Age at first breeding (2 years)	72 504.81	31 223.16	0.0070	0.0853
Age at first breeding (3 years)	16 287.38	8923.91	-0.0236	0.0873
Life span (20 years)				
Reproductive age (16 years)	243 518.26	33 033.74	0.0342	0.0853
Reproductive age (18 years)	247 284.58	33 529.61	0.0349	0.0860
Reproductive age (20 years)	254 063.79	31 402.74	0.0360	0.0859
Catastrophe 1	147 425.86	47 373.45	0.0219	0.0981
Catastrophe 2	128 993.36	50 686.05	0.0187	0.1056
Disturbance1	16 977.62	18 472.81	-0.0297	0.1509
Disturbance2	8222.30	12 784.13	-0.0496	0.1716
Disturbance3	3478.06	6561.88	-0.0741	0.1972
Disturbance4	1554.08	4455.21	-0.1009	0.2308

The foxes in our study probably colonized Siniya Island by crossing temporary land-bridges at low tide possibly in the 1980s (Ministry of Environment and Climate Change 2011, pers. comm.). The population of foxes on Siniya Island was much larger than estimated earlier (Muzaffar et al. 2013), with a total population of at least 24 individuals with at least two breeding family groups per year. Allometric estimates of diet and observed dietary items captured in cameras suggested that foxes on Siniya Island were collectively eating more than 3500 individual cormorants per year. This estimate is significantly higher than earlier estimates of 2000 individuals per year (Muzaffar et al. 2013). Although we quantified some hoarding as part of our attempt to quantify diet, we did not estimate the size and abundance of hoards. For example, foxes that brought in eggs and were seen burying them but these were included in calculations of diet. However, Sklepkovych and Montevecchi (1996) showed that hoards of red foxes and Arctic foxes could have large number of items (in the hundreds) ranging from eggs through body parts to whole birds. The conditions on Siniya Island were hot and dry and we speculate that food items in hoards would dry out and become of limited dietary value over a relatively small amount of time (weeks). Thus, we suggest that the items in hoards were recovered relatively quickly and eaten when food became scarce. We still expect that a portion of the hoarded food would be lost (Sklepkovych and Montevecchi 1996) and our estimate of diet is therefore an underestimate.

The diet of foxes on Siniya Island was mostly made up of cormorants during the breeding season, when cormorants were readily available and presumably easy to catch. Foxes foraged at night and were successful in capturing young and adult cormorants. Once cormorants migrated after breeding, the foxes switched to a diverse assemblage of items, ranging from hoarded cormorant eggs, passerines, shorebirds and gulls. The months approaching the harsh summer were difficult as food items are hard to find. This is consistent with other studies of foxes on remote islands with breeding populations of seabirds. For example, foxes introduced in the Aleutian Islands resulted in declines in seabird populations as early as the 1800s (Bailey 1993). Foxes themselves diminished to low densities and eventually disappeared once

the seabird or other breeding bird populations were extirpated, as in the case of most islands of the Alexander Archipelago off the coast of Alaska (Bailey 1993). Similarly, Arctic foxes never persisted as resident populations on the Gannet Islands, as they moved out on ice floes at the onset of winter, when food became scarce (Birkhead and Nettleship 1995). In contrast, we suggest that the foxes of Siniya Island are probably able to survive the summers by scavenging, switching diets and feeding from fox hoards to persist through to the subsequent cormorant breeding season based on our observation that pups were born in early 2014 and survived to the following breeding season.

The population modelling exercise suggested foxes were suppressing the breeding population of cormorants by affecting egg, chick and adult survival. The model showed a gradual increase in the simulated population from about 46 500 birds to over 270 000 individual cormorants in the absence of predation (Fig. 6, 7). Fox predation rates with mortality of 50% juvenile individuals per year could still allow the population to grow to above 250 000 individuals and remain stable (Fig. 6). Further increase in mortality could reduce population growth rates and suppress the population to below 250 000 individuals. On the other hand, mortality in adults that was 12% or less could increase and stabilise the population above 250 000 individuals (Fig. 7). Any further increase in mortality rates could suppress the population to much lower levels. For example, mortality rates of 25% or more could drastically reduce the population to well below 80 000 individuals. Thus, the simulated population was more sensitive to mortality of adults compared to juveniles. This was expected since adult survival is a critical factor in the population dynamics of K-selected species whereby increasing adult mortality typically increases extinction probabilities and reduces population growth rates in long-lived animals, including seabirds (Schreiber and Burger 2002, Lavers et al. 2010, Muzaffar et al. 2013). The simulated baseline population tended to stabilize at levels higher than the observed populations estimated between 2011 and 2016 (Muzaffar et al. 2017a, Fig. 6, 7). Muzaffar et al. (2017a) estimated the breeding population ranging from 28 000–41 000 pairs, or 84 000–124 000 individual cormorants (including juveniles and adults) during the five-year

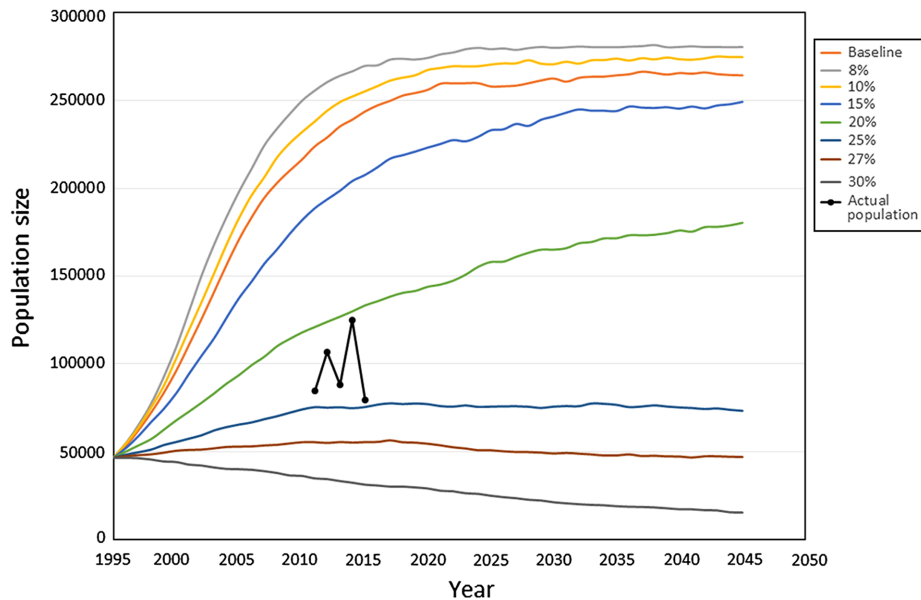


Figure 7. Socotra cormorant population trajectories of the baseline model (assuming no predation by red foxes) and varying levels of adult predation (represented as percentage mortality relative to the total simulated population).

study period. These estimates fell within population trajectories corresponding with 20–25% adult mortality rates (Fig. 7). Thus, we suggest that the current population of cormorants of Siniya Island are already suppressed with high levels of adult mortality. Since the observed estimates are aligned with a 20–25% mortality in the simulated population that has an increasing trend, we suggest that the population of cormorants is likely to continue to grow to stabilize between 150 000 and 200 000 individuals, in spite of high levels of fox predation (Fig. 7).

Additional detrimental effects imposed on the baseline population model (simulated as catastrophes or disturbances) could also impact the population negatively. Our simulated baseline population was especially sensitive to changes in brood size, age at first breeding and reproductive rates. The mortality at the egg stage (reduction of brood size) could be caused by predation by foxes or from other sources like bad weather (which we also observed for both cases). The frequency of these observations was difficult to estimate without more long-term studies. Similarly, age at first breeding observed for this species is one year (Muzaffar et al. 2017a). However, the percentage of individuals breeding at that age was low (1.62%, Muzaffar et al. 2017a). Species such as great cormorants or European shags *Phalacrocorax aristotelis* take longer time to recruit individuals (2–3 years) and experience (3–4 years) increases productivity (Horswill and Robinson 2015). We do not have this resolution of data, but suggest that Socotra cormorants may also be influenced by recruitment and experience. Our modelled populations suggested further reductions in population growth rates with delayed breeding in Socotra cormorants. Finally, changes in reproductive success modelled as catastrophes or disturbances also had further negative effects on the baseline population model. These were by far the most significant effects observed as populations could be reduced to less than 40 000 in 20 years and become nearly extinct in 50 years. Decrease in reproductive success or total reproduc-

tive failure has been observed in many colonies of Socotra cormorants either due to bad weather, human disturbance or fox predation (Jennings 2010, Muzaffar et al. 2013, 2017a).

Productivity and therefore breeding success could be reduced due to predation (Burger and Gochfeld 1994, Birkhead and Nettleship 1995, Kirkwood et al. 2005, Millus et al. 2007, Goltsman et al. 2010, Lavers et al. 2009, 2010, Towns et al. 2011). Eradication of mostly introduced predators from islands has produced much data on the demographic consequences of predators on seabird populations. In a comprehensive meta-analysis of 800 predator removal case studies, Lavers et al. (2010) showed that removal of predators resulted in a 25% increase in productivity, with a concomitant increase in population size, suggesting that predators were suppressing the population. Suppressing effects were noted in the two case studies in which removal of native predators was assessed by Lavers et al. (2010), with removal of predators leading to increases in productivity. Furthermore, other studies such as the periodic arrival of Arctic foxes on the Gannet Islands, Labrador (Birkhead and Nettleship 1995) or on Funk Island, Newfoundland (Burke et al. 2011) showed similar reduction of breeding success, suggesting lowered rates of population growth. A single Arctic fox on Funk Island, caused breeding failures in ground-nesting (northern fulmars *Fulmarus glacialis*) or burrow-nesting birds (Atlantic puffins *Fratercula arctica*) (Burke et al. 2011). Likewise, a single Arctic fox on the Gannet Islands reduced breeding success of razorbills and other breeding birds (Birkhead and Nettleship 1995). The Canadian Wildlife Service culled the few individuals of Arctic foxes on the Gannet Islands that arrived over ice flows once every few summers to allow an increase in the populations of razorbills that had declined throughout eastern Canada during the 1900s. Removal of Arctic foxes, in this instance was justified by the fact that they are a widespread species and maintained high population sizes (IUCN - Least Concern, Angerbjörn and Tannerfeldt 2014) whereas razorbills remain near-threatened with consis-

tently declining population trends (IUCN- near-threatened, BirdLife International 2015).

Foxes represent an important cause of mortality to breeding Socotra cormorants on Siniya Island, with known effects on breeding success and population demography. The red fox is globally not threatened (IUCN - Least Concern; Hoffmann and Sillero-Zubiri 2016) and the population on Siniya Island persists between years. The cormorant population on Siniya Island appears to be stable and increasing, with fluctuations in numbers related to environmental conditions during breeding in a given year (Cook et al. 2017, Muzaffar et al. 2017a). If Socotra cormorant populations decline further throughout their range, then conservation measures, including greater protection of the colony on Siniya Island as well as active removal of foxes may be needed.

We recognize that the use of demographic parameter estimates based on other cormorant species could be problematic (Lavers et al. 2010). For example, razorbills in the Gannet Islands and Machias Seal Island exhibit different survival rates and reproductive success, most likely due to local food resource and environmental variability (Lavers et al. 2009). This influences their population demography (Lavers et al. 2009). We assume that survival of different age classes vary between species of cormorants as well as between populations of the same species. Similarly, reproductive success varies between years and between different colonies of Socotra cormorants, likely due to environmental variability (Jennings 2010, Muzaffar et al. 2012, 2017a). Therefore, the proper estimation of demographic parameters is warranted for Socotra cormorants breeding on Siniya Island. Unfortunately, there are no long-term studies examining population demography of the Socotra cormorant in any of the range nations. Thus, our effort here was to model the population of Socotra cormorant with available data to highlight the demographic threats faced by the population. Better understanding of environmental factors influencing survival and reproduction is required. This would help adjust parameters in models influenced by environmental variability and would aid in determining cumulative effects of factors that influence survival and reproduction in Socotra cormorants. Thus, further studies are needed to better estimate demographic parameters and improve population projections using models.

Management implications

We demonstrate that there is a healthy breeding population of foxes living at high densities, negatively affecting vulnerable Socotra cormorants which comprise a large proportion of their diet. If the population of cormorants becomes too low (e.g. less than 50 000 individuals) and extinction probabilities above 0.58 (corresponding to predation rates of over 4000 birds per season), control measures should be introduced. Translocation may be the most ethical conservation measure for controlling a native predator. Long term monitoring for foxes re-populating the island from the mainland is essential. If needed, further fox control measures may be put in place depending on the long-term population trends of Socotra cormorants breeding on Siniya Island.

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