EGG DEPREDATION BY COMMON RAVENS *CORVUS CORAX* NEGATIVELY AFFECTS PELAGIC CORMORANT *PHALACROCORAX PELAGICUS* REPRODUCTION IN CENTRAL CALIFORNIA

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Received 30 December 2016, accepted 16 May 2017

ABSTRACT

CARLE, R.D., CALLERI, D.M., BECK, J.N., HALBERT, P. & HESTER, M.M. 2017. Egg depredation by Common Ravens *Corvus corax* negatively affects Pelagic Cormorant *Phalacrocorax pelagicus* reproduction in central California. *Marine Ornithology* 45: 149–157.

Many corvid (family Corvidae) populations have increased worldwide, and their predation sometimes threatens populations of other species. We studied the effects of depredation by Common Ravens *Corvus corax* on nesting Pelagic Cormorants *Phalacrocorax pelagicus* at Año Nuevo State Park, California. We monitored a Pelagic Cormorant subcolony located on the Año Nuevo mainland with an automated camera during April to August 2014, and monitored all Pelagic Cormorant nests on the mainland and at Año Nuevo Island (located ~1 km from the mainland) during weekly checks. We also monitored breeding population size and reproduction of Pelagic Cormorants at Año Nuevo State Park from 1999 to 2014. During the 2014 nesting season, ravens visited the camera-monitored Pelagic Cormorant subcolony on the mainland 165 times, averaging 1.6 (standard deviation [SD] 2.5) colony visits/d (n = 101 d), interacted with 100% of nests (n = 13), and removed at least 3.3 (SD 2.2) eggs from each nest. We observed no raven interactions with Pelagic Cormorant nests on the island in 2014. Pelagic Cormorant productivity in 2014 was five times greater on the island (2.45 [standard error 0.2]; n = 29 nests) than on the mainland (0.48 [SE 0.2]; n = 27 nests). Likewise, nests on the island had significantly greater hatching and fledging success rates than those on the mainland in 2014. We conclude that low breeding success on the mainland in 2014 was caused by egg depredation by ravens, and that a single pair of breeding ravens was responsible. Comparison of 2014 results with those from previous years suggests that extreme mismatches of hatching success between adjacent Pelagic Cormorant colonies may signal localized egg depredation. These results demonstrate the importance of regular monitoring of coastal seabird populations to better understand impacts of raven depredation.

Key words: Año Nuevo State Park, coastal California, Common Raven, egg depredation, Pelagic Cormorant, reproductive success

INTRODUCTION

Populations of many corvids (family Corvidae) have increased worldwide in response to human changes to the environment, as urbanization and fragmentation of vegetation have increased nesting sites and edge-habitat, and as human food has increased resources (Marzluff *et al.* 2001, Marzluff & Neatherlin 2006). Corvid predation is often identified as a threat to populations of prey species, including shorebirds and seabirds (Avery *et al.* 1995, Peery & Henry 2010, Burrell & Colwell 2012, McIver *et al.* 2016, West *et al*. 2016). To protect prey populations, corvid predation is sometimes managed by killing the birds (Parker 1984, Bodey *et al.* 2009, Fletcher *et al.* 2010) or deterring them (e.g., aversive conditioning; Avery *et al.* 1995, Gabriel & Golightly 2014), but the efficacy of these techniques and the actual impacts of corvid predation remain subject to debate (Madden *et al.* 2015). For example, in a recent review, >80% of studies found that corvid predation had no negative effect on population size or reproduction of avian prey species (Madden *et al.* 2015). Thus, research specific to situations and species is needed to quantify the effects of corvid predation on prey species before taking management action.

Common Ravens *Corvus corax* (hereafter "raven") are native to North America, and populations have increased continent-wide over the last 50 years (Sauer *et al.* 2014). In the Monterey Bay region, California, raven populations have increased rapidly, from being virtually absent before the mid-1980s to becoming common and widespread (Peery & Henry 2010). Ravens are managed in the region to limit depredation of nesting populations of threatened and endangered species, including Western Snowy Plovers *Charadrius nivosus nivosus* (Page *et al.* 2015) and Marbled Murrelets *Brachyramphus marmoratus* (US Fish and Wildlife Service 2004, Gabriel & Golightly 2014). Corvid predation of unlisted seabird species often goes unstudied, despite negative impacts on reproductive success or population trajectories of those species (Ewins 1991, Ekanayke *et al*. 2015, Hayward *et al.* 2015, McIver *et al.* 2016)

One such species is the Pelagic Cormorant *Phalacrocorax pelagicus* (hereafter "cormorant" unless noted), which ranges in North America from Alaska to Baja California, Mexico (reviewed by Hobson 2013), with a world population of ~400 000 birds (Siegel-Causey & Litvinenko 1993). The California population was last estimated at 14 345 birds (Carter *et al*. 1992). Cormorant population trends are uncertain due to a lack of data, but population trajectories appear to differ by region (Hobson 2013), and local populations have declined >50% in some areas since the 1960–1970s (Vermeer *et al.* 1992, Ainley *et al*. 1994, Carter *et al.* 2007, 2016). Potential threats to cormorant populations include pollution such as oil spills (Piatt *et al.* 1990, Cosco Busan Oil Spill Trustees 2012) and contaminants (Ohlendorf *et al.* 1982, Harris *et al.* 2003), reduced prey availability (Carter *et al.* 2007), mortality from fisheries interactions (King

1984), climate change (Sydeman *et al.* 2001), human disturbance (Verbeek 1982, Carter *et al.* 1984), and introduced predators or increases in native predators (Siegel-Causey & Hunt 1981, Verbeek 1982, Vermeer & Rankin 1984, Carter *et al.* 2016). Cormorants nest on cliffs, where they typically lay three-egg clutches in open nests and sometimes lay new clutches if the first clutch is lost (Hobson 2013). Cliff-nesting protects cormorant nests from terrestrial, but not avian, predators (Siegel-Causey & Hunt 1981).

This study was predicated on observations of raven depredation of cormorant eggs in 2012 at Año Nuevo State Park (ANSP), San Mateo County, California (Oikonos, unpubl. data). Cormorants at ANSP nest at two colonies, one on the Año Nuevo mainland (ANM) and the other on Año Nuevo Island (ANI), a wildlife reserve 1 km offshore (Fig. 1; note, Brandt's Cormorants *P. penicillatus* also nest at ANI). The ANSP cormorant population is among the five largest colonies of the species in central California, contributing ~4% of the central California population (Carter *et al.* 1992). Ravens first nested at ANSP in 1987, on cliffs within the ANM cormorant colony (Lewis & Tyler 1987). During 2004–2014, at least one raven nest was present at both ANM and ANI in all years when data were collected (no data at ANM in 2008, none at ANI in 2009), with the exception of 2006, when ravens did not nest at ANM (Oikonos/Point Blue Conservation Science [Point Blue], unpubl. data). Raven depredation of cormorant nests was first documented in 2012 (Oikonos, unpubl. data). On ANI, cormorant egg depredation has never been documented (Oikonos/Point Blue, unpubl. data), despite equal annual monitoring effort at ANM and ANI since 1999.

In 2014, we monitored a subcolony of cormorants at ANM with an automated camera to quantify raven interactions and their effect on cormorant reproduction. We compared reproductive success on ANI, with no observed raven predation, to ANM, with raven predation. We coupled this one-year camera study with a 16-year time-series of cormorant population and reproductive monitoring at ANSP to contextualize the impact of raven predation on long-term reproductive and population trends.

STUDY AREA AND METHODS

Our study took place at ANSP (37°07′N, 122°20′W). At ANM, cormorants nest on sheer cliffs at Point Año Nuevo. On ANI, cormorants nest on lower bluffs and on historic structures of a decommissioned lighthouse station.

Camera monitoring of raven nest predation

In April 2014, we installed a PlotWatcher Pro Trail Camera (Day6 Outdoors, Columbus, GA, USA) at East Cliff 2 (EC2), the largest of three ANM cormorant subcolonies (Fig. 1). With 13 active nests, EC2 accounted for 48% of nests on ANM. The camera took a still photo at 5 s intervals during daylight every day from 28 April to 7 August 2014. We used the program GameFinder version 1.6 (Day6 Outdoors) to rapidly review the photos. We documented all raven visits to the subcolony and raven interactions with nests. Visits were considered "new" if >30 s elapsed between a raven leaving the colony and returning. A nest interaction was defined as a raven coming within two nest lengths of a nest (Siegel-Causey & Hunt 1981). We recorded start and end time of each raven subcolony visit and nest interaction, whether a cormorant was flushed from its nest, and the length of time before the cormorant returned to its nest when forced off. We scored each colony visit and/or nest interaction based on the following outcome categories: raven 1) took an egg or chick, 2) flushed cormorant but did not take an egg or chick, 3) flushed cormorant but unclear whether egg or chick was taken, 4) interacted with nest but did not flush cormorant, 5) landed in subcolony but did not interact with any nests, or 6) flew over subcolony without landing.

We calculated the total number of raven interactions per cormorant nest, average number of raven nest interactions per day for the entire subcolony and by individual nest, minimum number of eggs taken by ravens per nest, average duration of raven nest interactions and colony visits, and average time cormorants spent off the nest when flushed by ravens. We calculated total video effort time for each day by recording when nests became visible in the morning

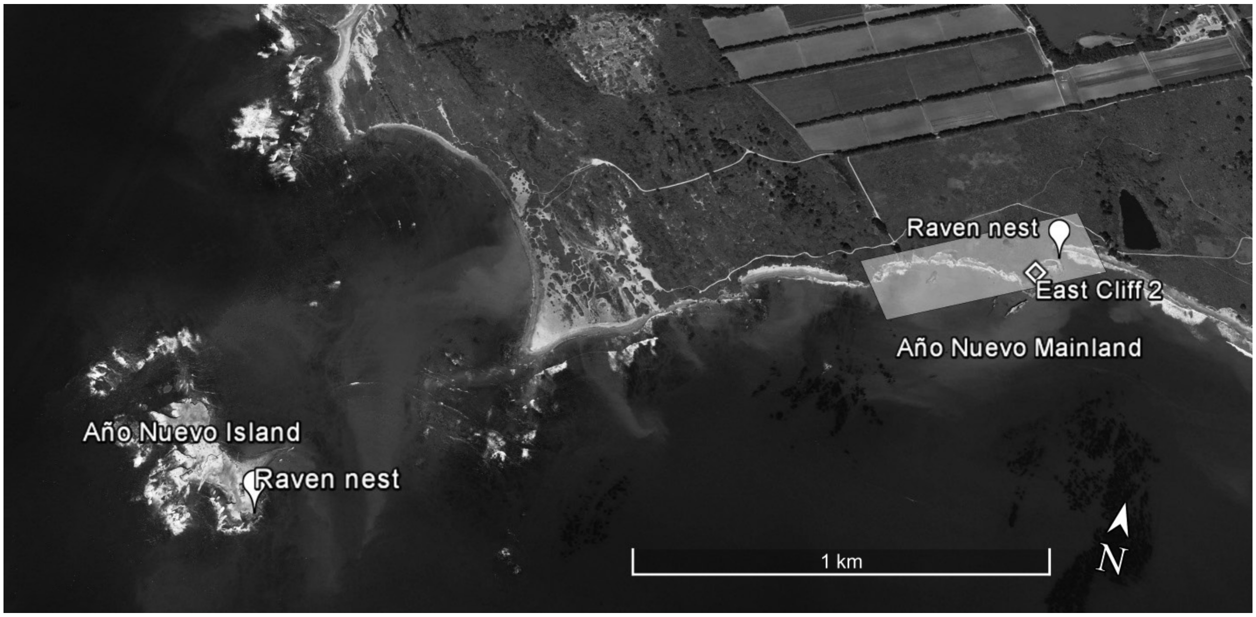

Fig. 1. Pelagic Cormorant and Common Raven breeding locations at Año Nuevo State Park, California. Map pins marked "Raven nest" were active in 2014. Satellite image from Google Earth, Google, Mountain View, CA.

and when good visibility ended at dusk. Periods during which some or all of the nests were not visible (e.g., because of fog or glare, or because we were changing memory cards on the camera) were subtracted from video effort time.

Cormorants at ANI were not monitored by camera, but nests were checked weekly from 1 April to 5 August 2014 to monitor reproduction and for opportunistic sightings of raven interactions. Approximately one hour was spent closely observing cormorant nests between 09h00 and 11h00 (the peak time for raven visits at ANM in 2014) during weekly ANI trips. Thus, we closely monitored cormorant nests on ANI for approximately 19 h in 2014. All opportunistic raven sightings and raven behaviors during sightings on ANI were recorded.

Reproductive success and population

We conducted weekly checks of all visible cormorant nests at ANM and ANI between April and August 1999–2014 to determine the following outcomes on an annual basis: 1) breeding population (number of reproductively active nests), 2) productivity (number of chicks fledged per breeding pair), 3) fledging probability (proportion of nests that fledged at least one chick), 4) hatching probability (proportion of nests that hatched at least one chick). We define hatching or fledging probability as the proportion of breeding pairs that fledged at least one chick in a given year; this differs from hatching or fledging success, which are more quantitative (i.e., actual number of eggs or fledglings per nest). Nests on ANI not visible from island observation points were checked via boat at least monthly and included in the population estimates. Weekly nest checks were conducted from land using binoculars or a spotting scope. We considered nests active if eggs or chicks were observed, or if adults were observed in incubation posture for two consecutive weeks. Relay or second clutch attempts were defined as a lapse of incubation behavior for at least two consecutive weeks at nests that had previously been observed with adults incubating eggs, followed by a resumption of incubation behavior or observation of new eggs. Cormorant chicks were considered fledged if they survived to 25 d of age or were fully feathered. Nests for which the number of chicks hatched or fledged was unknown were excluded from hatching probability calculations, or productivity and fledging probability calculations, respectively.

In 2014, the raven nest at ANM was monitored for reproductive activity weekly, whereas the raven nest on ANI was inaccessible by land and was irregularly monitored by boat.

Statistical analyses

We calculated annual productivity at ANM and ANI colonies and tested differences between the colonies over the entire time-series (1999–2014) using a paired *t*-test. To examine the magnitude of annual differences in productivity between ANM and ANI, we calculated *Z*-scores (the number of standard deviations below or above the mean) on the absolute value of the difference between ANI and ANM productivity for each year.

We tested differences in fledging probability between ANM and ANI for each year in the time-series using likelihood-ratio χ^2 tests. For years in which fledging probability significantly differed between breeding colonies, we also compared hatching probabilities using likelihood-ratio χ^2 tests. We hypothesized that, if differences in fledging probability between colonies were driven by egg depredation by ravens, this pattern would show up in the hatching probability metric.

We tested overall population trends at ANSP using linear and quadratic regression models, and compared models using Akaike's Information Criterion (AIC). Population and productivity data were checked for auto-correlation using Ljung-Box tests with time lags for the length (years) of each time-series. Test-residuals were checked for normality using Shapiro–Wilk goodness-of-fit tests for the normal distribution. Means are reported ± one standard deviation unless otherwise noted. We defined statistical significance as $P < 0.05$.

RESULTS

Video monitoring effort

We reviewed all photos taken during daylight hours, 28 April to 7 August 2014, totalling 1,424.6 h and averaging 14.1 ± 1.5 h/d ($n = 101$ d). On average, 0.39 ± 0.75 h/d ($n = 101$ d) were excluded from analysis because of poor visibility.

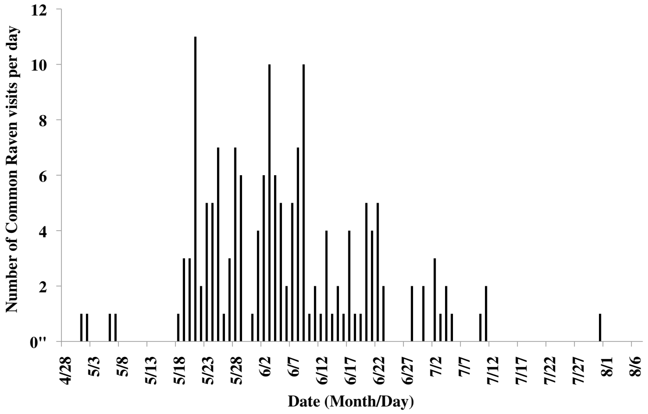

Fig. 2. Common Raven visits to EC2 in 2014, determined by automated camera-based monitoring.

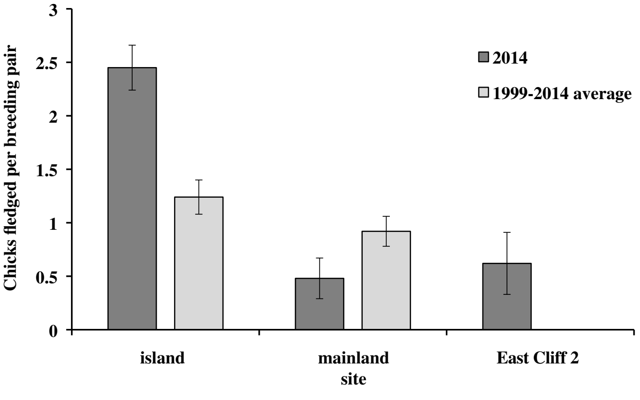

Fig. 3. Productivity (mean and standard error [error bar]) of Pelagic Cormorants on Año Nuevo Island (island), all mainland sites (mainland), and the East Cliff 2 site on the mainland monitored by camera in 2014.

Raven interactions with cormorant colonies

Camera-monitored subcolony (EC2). In 2014, ravens took at least one egg from 100% of the 13 cormorant nests at EC2. No depredations of cormorant chicks were recorded. During the 101 d we monitored, ravens visited EC2 165 times, averaging 1.6 ± 2.5 subcolony visits/d. Most raven visits occurred in May (1.9 ± 2.8 visits/d) and June (3.1 ± 2.8 visits/d), with fewer visits in July (0.4 ± 0.8 visits/d; Fig. 2), and none during camera monitoring in late April (*n* = 3 d) or early August (*n* = 7 d; Fig. 2). One pair of ravens nested on the bluffs within the ANM colony in 2014 (Fig. 1). Eggs were laid in this raven nest between 14 April and 21 April, and at least two chicks fledged between 30 June and 7 July.

During the 165 documented colony visits, ravens interacted with cormorant nests 201 times, flushed cormorants from nests 89 times (54% of visits), and took eggs at least 43 times (26% of visits). Ravens would typically stand adjacent to the targeted nest before lunging at the cormorant, sometimes making physical contact, after which cormorants would flush from the nest. The same raven, or less often a second raven, would then return to the nest and fly off with an egg. An individual raven was responsible for the majority of colony visits (85% of visits). Two individuals were present during 15% of visits (*n* = 165 visits). No more than two ravens were ever seen visiting cormorant nests at EC2.

Raven visits to EC2 (*n* = 165) occurred during all daylight hours, from 05h00 to 21h00, except from 17h00 to 18h00. The majority of raven visits (73%) occurred between 08h00 and 13h00, and within that period, the hour with the most visits (22%) was 10h00 to 11h00.

During the 2014 breeding season, each cormorant nest at EC2 had 15.5 ± 8.5 raven interactions, was flushed by ravens 6.8 ± 5.5 times, and had ravens remove at least 3.3 ± 2.2 eggs. The maximum number of confirmed egg thefts for a single nest was eight and the minimum was one. The maximum number of times ravens flushed birds from a single nest was 21 and the minimum was two.

The duration of raven colony visits was 85 ± 71 s (*n* = 165). The duration of individual nest interactions was 39 ± 35 s (*n* = 201), and 52 ± 37 s for interactions in which a raven ultimately flushed the cormorant (*n* = 89). The duration of interactions that ended in confirmed egg thefts was 50 ± 39 s (*n* = 43).

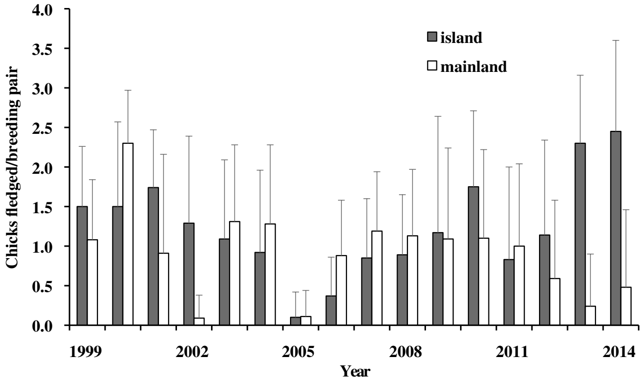

Fig. 4. Productivity (mean and standard deviation [error bar]) of Pelagic Cormorants at Año Nuevo Island and mainland, 1999–2014.

When cormorants were flushed by ravens, they returned to their nest after 53 ± 48 s (maximum: 5 min 25 s, minimum: 10 s; *n* = 89 flushings). No opportunistic depredation by other predators was observed when cormorants were away from nests.

Año Nuevo Island. During approximately 19 h of nest observations on ANI in 2014, no raven interactions with cormorant nests were documented. However, ravens were observed on ANI on 44% of days that researchers were present that year (*n* = 25 d). Raven sightings included one pair that attempted to nest on the historic lightkeeper's house structure (Fig. 1); other individuals were observed, but the length of time they spent on the island was unknown. The highest daily count was seven ravens observed at once on 15 April 2014. Groups of ravens were observed feeding on California sea lion *Zalophus californianus* stillborn fetuses during April and May, and one raven was observed being chased by nesting Black Oystercatchers *Haematopus bachmani* in June.

Cormorant reproductive success

2014 reproductive success. In 2014, at EC2 cormorant productivity was 0.62 ± 1.04 chicks fledged per pair (*n* = 13 nests), and at the other ANM subcolonies it was 0.36 ± 0.93 (*n* = 14 nests). Neither hatching nor fledging probability differed significantly between EC2 and the neighboring subcolonies of ANM (hatching *P* = 0.2,

TABLE 1
Annual fledging probabilities for Año Nuevo Island (ANI) and mainland (ANM) Pelagic Cormorant breeding colonies, 1999–2014

Year	ANI	ANM	χ^2 (*df* = 1)	*P* value	Number of pairs	Less successful colony[a]
1999	0.88	0.77	0.38	0.54	21	
2000	0.75	0.71	0.03	0.86	22	
2001	0.89	0.41	11.30	0.0008	41	ANM
2002	0.66	0.08	22.94	<0.0001	65	ANM
2003	0.66	0.69	0.78	0.08	73	
2004	0.49	0.76	5.84	0.016	74	ANI
2005	0.10	0.11	0.01	0.94	19	
2006	0.37	0.73	7.48	0.005	60	ANI
2007	0.59	0.81	2.70	0.10	53	
2008	0.67	0.71	0.11	0.74	56	
2009	0.50	0.58	0.13	0.72	44	
2010	1.00	0.61	3.72	0.05	37	
2011	0.50	0.55	0.06	0.81	44	
2012	0.52	0.23	5.18	0.023	60	ANM
2013	0.95	0.15	36.99	<0.0001	53	ANM
2014	0.90	0.22	28.59	<0.0001	56	ANM

[a] The less successful colony is listed for years with significant differences between colonies.

$df = 1$, $n = 26$, $\chi^2 = 1.8$; fledging $P = 0.3$, $df = 1$, $n = 27$, $\chi^2 = 1.1$). Given the similar or poorer performance of other ANM nests compared with EC2 for all reproductive metrics, it appeared that raven predation was impacting all of ANM, not just EC2. Thus, we combined EC2 with the other ANM subcolonies to compare reproductive metrics between ANM and ANI.

Cormorants at ANI fledged on average five times more chicks than at ANM in 2014 (Fig. 3). Productivity on ANI was nearly double the ANI 1999–2014 average, whereas productivity at ANM was just above half the ANM 1999–2014 average (Fig. 3). Cormorant fledging probability was over four times greater at ANI than at ANM, a highly significant difference ($P < 0.0001$, Table 1). Likewise, in 2013, cormorant fledging probability was over six times greater at ANI than at ANM (Table 1); during that year, raven activity was frequently observed at ANM but was not quantified.

Of the cormorant pairs monitored weekly at ANM in 2014, 40%–60% attempted a second clutch after egg loss (11 pairs confirmed and five pairs suspected). No monitored pairs laid a second clutch on ANI ($n = 29$), as 100% of ANI nests hatched chicks on the first clutch that year (Table 2). Of the six pairs that fledged at least one chick at ANM, four fledged chick(s) from a replacement clutch, one from a first clutch, and one from an unknown clutch but with a late egg lay date.

Long-term reproductive success. Over the 16-year time series, annual cormorant productivity was slightly, but insignificantly, greater on the island than the mainland ($P = 0.15$, $t = -1.5$, $df = 15$; Fig. 4). Residuals of this test were normally distributed ($W = 0.90$, $P = 0.096$) and were not auto-correlated (Ljung-Box Q test, $P > 0.05$ for all time lags). Only in 2013 and 2014 was the Z-score >2 for the difference in absolute values of ANI productivity and ANM productivity (Fig. 5). This indicated that divergence in production at the two colonies in 2013 and 2014 exceeded 2 standard deviations from the mean annual difference. No other years had Z-values >1, and only the year 2005 had a Z-score < -1 (Fig. 5), indicating that production at ANM and ANI converged more than usual that year (Fig. 4).

Cormorant fledging probability significantly differed between ANI and ANM during seven years of the 16-year time series, with 2013 and 2014 having the most significant differences in fledging probability ($P < 0.0001$ for both years; Table 1). In all but two years (2004 and 2006) with significantly different fledging probability between colonies, hatching probability also significantly differed (Table 2). In each significant case, hatching was lower at ANM (Table 2). The magnitude of the difference in hatching was greatest in 2013 and 2014 ($P < 0.0001$ for both years; Table 2), years when raven depredation was confirmed at the ANM colony.

TABLE 2
Hatching probabilities for the Año Nuevo Island (ANI) and mainland (ANM) Pelagic Cormorant colonies in years when fledging probabilities significantly differed

Year	Hatching probability (Less successful colony)	Hatching probability (More successful colony)	χ^2 ($df = 1$)	P value	Number of pairs
2001	0.70 (ANM)	1.00 (ANI)	9.053	0.0026	39
2002	0.55 (ANM)	0.82 (ANI)	5.164	0.0231	61
2004	0.61 (ANI)	0.81 (ANM)	0.04	0.8509	59
2006	0.63 (ANI)	0.78 (ANM)	1.829	0.1763	60
2012	0.44 (ANM)	0.79 (ANI)	6.335	0.0118	55
2013	0.15 (ANM)	0.95 (ANI)	35.486	<0.0001	52
2014	0.12 (ANM)	1.00 (ANI)	28.085	<0.0001	55

Cormorant population trends

Overall breeding population size of cormorants at ANSP (Fig. 6) showed a significantly increasing linear trend from 1999 to 2014 ($r^2 = 0.33$, $P = 0.02$, $\beta = 4.33$). A linear model was the best fit model (linear model AICc = 160.44, quadratic model AICc = 163.73). Residuals of this test were not auto-correlated (Ljung-Box Q test, $P > 0.05$ for all time lags), and were normally distributed (linear $W = 0.97$, $P = 0.77$, quadratic $W = 0.96$, $P = 0.57$).

In 2014, 158 cormorants bred at ANSP, which was the highest population on record from 1999 to 2014 at ANSP (Fig. 6). The number of cormorants that attempted to breed increased 34% on ANI (104 birds total) and decreased 18% on ANM (54 birds total) from 2013 to 2014 (Fig. 6).

DISCUSSION

Cormorant and raven interactions

Ravens depredated 100% of the nests at EC2, the subcolony monitored by camera at ANM, and were the only egg-predator detected. Other avian predators such as Glaucous-winged Gulls *Larus glaucescens* and Northwestern Crows *Corvus caurinus* are known to take cormorant eggs (Siegel-Causey & Hunt 1981, Verbeek 1982), but we did not observe these species. Our observations at ANSP (2012–2014) are the first documented occurrences of raven depredation affecting cormorants of which we are aware.

Notably, ravens in this study were never observed taking chicks. However, because egg theft was so successful, only six nests in all of ANM (including EC2) contained chicks, and the majority of these (86%) were from second clutches laid late in the season (lay dates 23 May–23 June). The harassment behaviors exhibited by ravens in this study (lunging and causing adults to flush) could

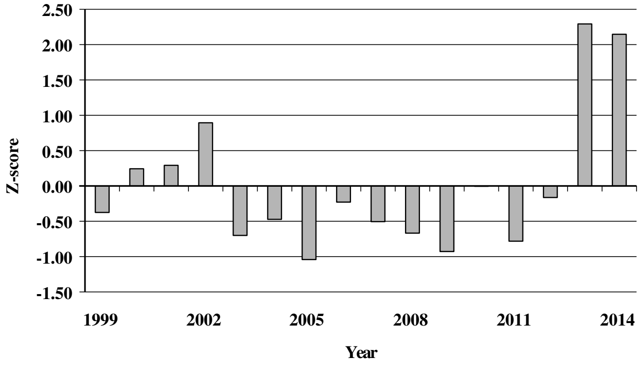

Fig. 5. Z-scores of the absolute value of the difference between annual Pelagic Cormorant productivity at Año Nuevo Island and at Año Nuevo Mainland, 1999–2014.

also be used to steal young chicks. We suggest that differences in phenology between cormorant and raven incubation and chick-rearing may have resulted in predatory pressure affecting only eggs in 2014.

Egg depredation at the camera-monitored subcolony was likely carried out exclusively by one nesting pair of ravens, and possibly their young, although we were unable to mark the ravens to study this directly. Several observations suggest that one pair was responsible: 1) no more than two ravens were observed at once at a cormorant nest; 2) many cormorant eggshells were found at a single cache near the ANM raven nest (D. Calleri, pers. obs.); and 3) raven interactions with cormorant nests declined after raven chicks fledged from the ANM nest (30 June–7 July; Fig. 2). There has been evidence of a single pair of ravens causing damage in other seabird colonies. Experimental control of a nesting pair of ravens in Point Reyes, California, resulted in cessation of raven depredation of Common Murre *Uria aalge* eggs for three years (Press 2013). Thus, egg depredation of cormorant nests may have been a specialized behavior of the raven pair that nested at ANM.

As further evidence that the ANM raven pair exhibited specialized predatory behavior, there were ravens on ANI throughout the 2014 breeding season, including another nesting pair, but no interactions with cormorant nests were documented, and cormorant productivity was well above average (Fig. 4). The peak in raven depredation at ANM occurred during the hours when ANI nests were monitored (approximately 09h00–11h00), suggesting that raven depredation would have been observed on ANI, had it happened. Ravens observed on ANI in 2014 were feeding on pinniped carcasses, suggesting that ravens had other more easily obtained sources of food on ANI than cormorant eggs. In central California, breeding pairs of ravens traveled on average <1.0 km from the nest, and during their incubation and fledging stage they traveled <0.4 km (Roth *et al*. 2004). Thus, ANI was likely too distant (1.8 km away) for the ANM raven pair specializing on cormorant eggs to impact both colonies.

In addition, nesting ravens and groups of non-breeding ravens were documented close to cormorant colonies at ANM and ANI for multiple previous years, with no observed harassment until 2012 (Oikonos/Point Blue, unpubl. data). However, this was the first study designed to quantify raven and cormorant interactions, and past impacts could have been missed during the 16-year time series of monitoring cormorant nesting at ANSP. This study provides data to identify past years when ravens could have been a factor in reproductive failures.

Impact on cormorant reproductive success

In 2014, the high rate of raven egg depredation was the cause of poor hatching and fledging probabilities at EC2, where egg theft by ravens resulted in only 38% of nests hatching one or more chicks and in only 31% fledging at least one chick. Hatching and fledging probabilities were even lower at the neighboring cliff faces, resulting in only 22% of all nests at ANM fledging a chick (*n* = 27 nests). It is likely that egg theft by ravens caused this low reproductive success across all ANM nests, a conclusion supported by 1) the proximity of other ANM subcolonies to EC2 (within 0.6 km; Fig. 1); 2) direct observations of ravens interacting with other ANM subcolonies in 2014 (Oikonos, unpubl. data); and 3) similarly low reproductive values at EC2 and at ANM compared with above average values at ANI (Fig. 3, Tables 1, 2), where no raven interactions were observed.

Because 52% of the ANM colony was not observed with the camera, differences in cormorant reproduction observed between ANM and ANI in both 2013 and 2014 (Fig. 4) may have been driven by site-specific pressures rather than raven depredation. However, a number of factors indicate otherwise. Annual productivity between ANM and ANI did not differ significantly during 1999–2014 (Fig. 4), despite different nest-site characteristics (e.g., high mainland cliffs at ANM vs. low bluffs and manmade structures on ANI). Furthermore, the differences in productivity between ANM and ANI were much greater in 2013 and 2014 (*Z*-score >2), when raven depredation was observed at ANM, than any other year in the time-series (all *Z*-scores <1; Fig. 5). Differences in productivity in 2013 and 2014 were unlikely to have been caused by differing prey availability, because ANM and ANI are separated by only 1–2 km, and the maximum foraging range of cormorants is 9 km, according to a previous study (Kotzerka *et al*. 2011). Furthermore, trawl studies indicated exceptionally high abundance of juvenile rockfishes (*Sebastes* spp.) in central California waters in 2013 and 2014 (Leising *et al.* 2014). Likewise, Rhinoceros Auklet *Cerorhinca monocerata* diet at ANI indicated that juvenile rockfishes and northern anchovy *Engraulis mordax* were available near ANSP in 2013 and 2014 (Carle *et al.* 2014, 2015). Previous studies have shown that cormorant reproductive success is strongly linked to availability of prey, especially juvenile rockfishes (Ainley *et al.* 1990, 1994). Thus, high regional abundance of juvenile rockfishes and other prey in 2013 and 2014 (Leising *et al.* 2014, Carle *et al.* 2014, 2015) probably contributed to high cormorant productivity on ANI (Fig. 4), although we did not study this directly. Given the proximity of the ANM and ANI, similar productivity might have been expected at ANM during those years, in the absence of egg theft by ravens.

It appears that the 22% of cormorant nests at ANM that fledged chicks in 2014 did so by laying new clutches to replace those lost to raven depredation. At EC2, at minimum 3.3 ± 2.2 eggs were taken from each nest, representing more than the typical three-egg clutch. In 2014, 40%–60% of the cormorant pairs at ANM (EC2 included) re-laid after losing the first clutch, and five of the six pairs that successfully raised a chick at ANM fledged those chicks from replacement clutches. In contrast, on ANI all chicks hatched from first clutches in 2014. Birds at ANM might have been able to

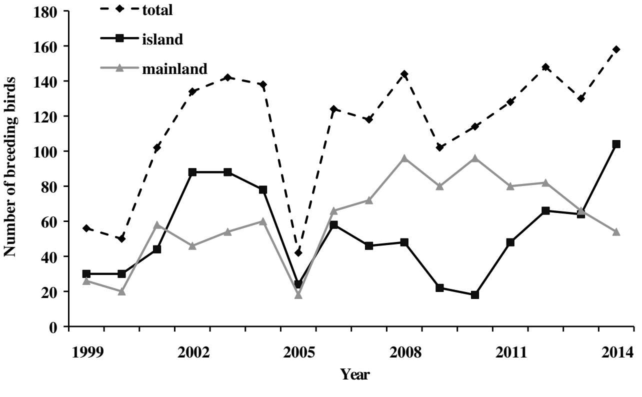

Fig. 6. Population of Pelagic Cormorants breeding at Año Nuevo State Park, 1999–2014.

re-lay in 2014, despite repeated harassment, because of high local availability of quality prey that year (Carle *et al*. 2014).

The highly significant differences in hatching probability between ANM and ANI in 2013 and 2014 (Table 2) support our supposition that, in years with heavy raven depredation, breeding failure would be driven by low hatching success. The other years with significant differences in fledging probability between ANM and ANI (2001, 2002, 2006, and 2012; Table 1) did not show a clear difference in hatching (Table 2). Hatching probability differed significantly in 2001, 2002, and 2012, but was not catastrophically low at the less successful colony (e.g., the lowest was 44% at ANM in 2012). In comparison, hatching probability was 15% in 2013 and 12% in 2014 at ANM, vs. 95% and 100%, respectively, at ANI (Table 2). In 2012, raven depredation was observed at ANM but was not quantified; however, hatching probability was not as low that year as in 2013 and 2014 (Table 2). The pair of ravens that nested at ANM successfully fledged chicks in 2012 and was present throughout the cormorant incubation period (Oikonos, unpubl. data). Thus, perhaps the raven pair at ANM relied on other food sources more during 2012 than during 2013 and 2014. The ANM raven nest was located on the same ledge during 2012–2014, although the birds were not individually marked.

The mismatch in productivity in 2002 was similar to that in 2013 and 2014 (Fig. 4), suggesting that raven depredation was the cause of low productivity at ANM in 2002. However, cormorant hatching probability was not strikingly low at ANM in 2002 (55% of nests hatched chicks), and biologists monitoring the nests weekly that year never observed raven interactions (D. Calleri, pers. obs.). It appears that low ANM productivity in 2002 (Fig. 4) was driven by both egg failure and chick death, and we are uncertain of the cause.

In 2005, there was markedly low productivity (Fig. 4) and hatching probability at both colonies (40% at ANI, 11% at ANM), as well as a low overall breeding population at ANSP (Fig. 6). This unique pattern resulted in productivity values between ANM and ANI that were more similar than the averages in the time-series (Fig. 5). Extremely low overall cormorant productivity at ANSP in 2005 was driven by lack of upwelling, which created El Niño-like conditions and a widespread lack of prey. These conditions resulted in the breeding failure of many seabirds in the California Current that year (Peterson *et al.* 2006). During this 2005 event, there was also complete breeding failure of Pelagic Cormorants at Southeast Farallon Island in the central California Current (Peterson *et al.* 2006).

Based on the patterns observed in 2013 and 2014 of extremely low hatching probability at the colony with documented raven depredation (Table 2), we suggest that significant differences in hatching success between adjacent colonies of cormorants may be a signal of egg depredation.

Potential impacts on population stability

To assess the population-level impacts of continued raven depredation on cormorant nests at ANSP, analyses of population viability and habitat availability are needed. At ANM, this study demonstrated a significant negative effect on reproductive success from egg theft by a single raven pair, but no chick or adult mortality. The cormorant population at ANSP increased from 1999 to 2014 (Fig. 6), although it remained lower than a 1980 estimate of 210 nesting birds at the ANM colony alone (Sowls *et al.* 1980). Breeding effort and reproductive success vary among years in cormorants, depending on oceanographic conditions and prey availability (Boekelheide *et al.* 1990, Sydeman *et al*. 2001). However, the three consecutive years of low productivity at ANM, 2012–2014 (Fig. 4), driven by raven depredation, were unprecedented in this time-series. Population-level effects of low productivity during 2012–2014 would not be expected to be observable for two to three years, until the young from those years recruit into the breeding population (Van Tets 1959). Discerning any population-level effects from low ANM productivity during 2012–2014 will be further complicated by the above-average breeding success at ANI in those years (Fig 4) and the potential of birds to move between nearby nesting colonies at ANM and ANI.

Nesting distribution patterns at ANM and ANI colonies have been variable (Fig. 6). The ANM population declined from 2012 to 2014 as the ANI population grew (Fig. 6), suggesting that cormorants abandoned raven-vulnerable ANM nest sites in favor of ANI. Also, within subcolonies at ANM (i.e., different cliff faces in various coves; Fig. 1), the distribution of nests suggested that cormorants relocated to sites and cliffs further away from the raven nest (Oikonos, unpubl. data). The consequences of relocating nest sites to avoid harassment could include mate loss, a lower-quality site, and/or new disturbances. For example, moving from ANM to ANI might expose cormorants to new interactions with nesting Western Gulls *L. occidentalis*, and disturbance from researchers at less visually protected nest sites at ANI (Carle *et al.* 2014).

Quality habitat for cormorants is limited at ANSP. At ANM, nest sites are limited to completely vertical cliffs to avoid mammalian predators, and in recent years a number of these cliff sites have been lost during winter storms (Carle, pers. obs.). At ANI, nest sites are limited to a few low bluffs and vertical ledges on a deteriorating house. In 2014, 31% of nests at ANI ($n = 52$) were on the historic lightkeeper's house, which will likely collapse soon. To evaluate the stability of the ANSP population, future studies could model consequences of repeated reproductive failure and estimate dynamics of habitat availability among colonies.

Raven predation clearly resulted in near-total failure of reproduction at the cormorant colony at ANM in 2014. Currently, depredation by ravens has been observed only at the ANM colony, and we know of no reports of this behavior elsewhere, although ravens have recently nested adjacent to Pelagic Cormorant colonies in northern California (Ron LeValley, pers. comm.). Due to the widespread distribution and increased densities of ravens in California (Peery & Henry 2010), raven depredation could become a factor for cormorant reproduction in other areas. More study is needed on region-wide Pelagic Cormorant population size and reproduction trends to monitor the species' conservation status and understand emerging threats such as raven depredation.

ACKNOWLEDGEMENTS

We would like to thank Año Nuevo State Park staff and docents for access to study sites and support for this study. Thanks to Point Blue for the use of cormorant population and reproduction data before 2008, and to all the biologists and volunteers who collected those data. Thanks to Adam Fox for assistance with fieldwork in

2014. Big thanks to Gwen Larrow for many hours reviewing camera footage. Thanks to David Ainley and two anonymous reviewers, whose comments and insights greatly improved this manuscript. Thanks also to Emily Coletta, Nathaniel Smith, and Alayne Meeks for help with the manuscript. We also acknowledge and thank Gary Strachan for his pioneering work on seabirds and ravens at ANSP.

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