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Research Paper

Reproductive success of Common Ravens influences nest predation rates of their prey: implications for egg-oiling techniques

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ABSTRACT. Abundance and distribution of Common Ravens (*Corvus corax*) have increased across western North America in recent decades, leading to conservation concern for sensitive prey species. Multiple management options have been proposed to reduce raven numbers or reduce the impacts of predation by ravens on sensitive species. We carried out a longitudinal study to evaluate the effects of experimentally manipulating the reproductive success of territorial ravens on the reproductive performance of their prey on Alcatraz Island across 6 years. Specifically, we employed remote video-monitoring on nests of predator and prey to document the effects of oiling raven eggs, a technique to prevent eggs from hatching, on raven reproduction, and to estimate impacts of raven hatching success on their predation of Black-crowned Night-Heron (*Nycticorax nycticorax*) nests. We used Bayesian multinomial logistic exposure models to estimate night-heron nest and chick survival and account for variation in nest failure across different life stages (i.e., egg versus nestling). We found daily predation rates on night-heron nests (median: 1.71%, 85% CI: 1.15–2.44%) and chicks (median: 0.57%, 85% CI: 0.27–1.03%) were the highest during years when ravens nested successfully. During years that raven eggs were oiled, daily predation rates on night-heron nests (0.98%, 85% CI: 0.55–1.57%) and chicks (0.00%, 85% CI: 0.0–0.00%) decreased, and we observed the lowest daily predation rates for nests (0.40%, 85% CI: 0.17–0.76%) during years when raven nesting was naturally absent on the island. The greatest probability of survival of night-heron eggs and chicks occurred during years when ravens were present but not nesting on Alcatraz. Our results suggest that manipulation of raven breeding success can influence predation and reproductive performance of their prey. These results also indicate that egg-oiling can be a viable localized method to reduce raven recruitment and possibly aid in the conservation of sensitive avian species.

Le succès de reproduction du Grand Corbeau a une incidence sur le taux de prédation des nids de ses proies : implications pour les techniques d'huilage des oeufs

RÉSUMÉ. Le nombre et la répartition des Grands Corbeaux (*Corvus corax*) ont augmenté dans l'ouest de l'Amérique du Nord dans les récentes décennies, soulevant des préoccupations de conservation pour les espèces proies au statut sensible. De nombreuses options de gestion ont été proposées pour réduire le nombre de corbeaux ou l'impact de la prédation de ceux-ci sur les espèces sensibles. Nous avons effectué une étude longitudinale visant à évaluer les effets de la manipulation expérimentale du succès de reproduction de corbeaux territoriaux sur le succès de reproduction de leurs proies sur l'île d'Alcatraz durant 6 années. Nous avons fait de la surveillance vidéo des nids des prédateurs et des proies pour décrire les effets du huilage d'oeufs de corbeaux - une technique empêchant les oeufs d'éclore - sur la reproduction de ceux-ci, et pour estimer les effets du succès d'éclosion des corbeaux sur leur prédation de nids de Bihoreaux gris (*Nycticorax nycticorax*). Nous avons utilisé des modèles logistiques multinomiaux d'exposition Bayésiens pour estimer la survie des nids et des poussins de bihoreaux et tenir compte des échecs de nidification aux différents stades de développement (c.-à-d. oeuf c. oisillon). Nous avons trouvé que les taux quotidiens de prédation sur les nids (médiane : 1,71 %, 85 % IC : 1,15-2,44 %) et les poussins (médiane : 0,57 %, 85 % IC : 0,27-1,03 %) de bihoreaux étaient plus élevés au cours des années où les corbeaux nichaient avec succès. Durant les années au cours desquelles les oeufs de corbeaux étaient huilés, les taux quotidiens de prédation sur les nids (0,98 %, 85 % IC : 0,55-1,57 %) et les poussins (0,00 %, 85 % IC : 0,0-0,00 %) de bihoreaux diminuaient, et nous avons obtenu le plus faible taux quotidien de prédation sur les nids (0,40 %, 85 % IC : 0,17-0,76 %) durant les années où les corbeaux ne nichaient pas naturellement sur l'île. La probabilité la plus élevée de survie des nids et des poussins de bihoreaux est advenue au cours des années durant lesquelles les corbeaux étaient présents mais ne nichaient pas sur Alcatraz. Nous résultats donnent à penser que la manipulation du succès de reproduction des corbeaux peut influer sur la prédation et le succès de reproduction de leurs proies. Nos résultats indiquent aussi que le huilage d'oeufs peut représenter une méthode localisée viable pour réduire le recrutement des corbeaux et peut-être aussi contribuer à la conservation d'espèces d'oiseaux sensibles.

Key Words: *Black-crowned Night-Heron; Common Raven; Corvus corax; egg-oiling; Nycticorax nycticorax; predation; reproduction*

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INTRODUCTION

Populations of Common Ravens (*Corvus corax*) (hereafter, raven), which are effective predators of many species, have increased substantially throughout the western United States (Sauer et al. 2017). Reasons for these population increases are well documented and include the species proclivity to exploit human resource subsidies. Ravens thrive in areas with roads (White and Tanner-White 1988), landfills (Boarman 2003, Webb et al. 2004, Boarman et al. 2006), power lines (Coates et al. 2014, Howe et al. 2014), and human population centers (Kristan and Boarman 2007), among others. Raven populations are increasing not only in numbers but also in distributional range, expanding into territories that were previously uninhabited. This is of conservation concern because raven predation has been linked to population declines of a number of threatened or endangered species. For example, ravens have been shown to be of conservation concern regarding their impacts on populations of desert tortoise (*Gopherus* spp.) (Boarman 2003, Kristan and Boarman 2003), Greater Sage-Grouse (*Centrocercus urophasianus*) (Coates and Delehanty 2010, Coates et al. 2016, Dinkins et al. 2016), and Snowy Plovers (*Charadrius nivosus*) (Burrell and Colwell 2012).

Multiple management options have been proposed to reduce the impacts of predation by ravens on sensitive species. For example, lethal removal has been shown to have short-term effectiveness in reducing the number of ravens in a population (Butchko 1990, Coates et al. 2007), sometimes resulting in increased productivity of local prey communities (Coates and Delehanty 2004). However, lethal management options often present ethical challenges (Boarman 1992), and long-term effectiveness has not been well-studied (Coates et al. 2007, Peebles and Conover 2016). Behavioral methodologies for controlling raven predation, such as conditioned taste aversion or the use of effigies, have been shown to be effective in reducing predation at local scales (Avery et al. 1995, Peterson and Colwell 2014). However, behavioral modification does not necessarily limit raven productivity, and effects often do not extend beyond study boundaries (Peterson and Colwell 2014).

Oiling eggs to prevent them from hatching is an alternative management strategy that has been studied primarily in regard to managing population growth in gull colonies (Blokpoel and Hamilton 1989, Blackwell et al. 2000). One of the primary goals of egg-oiling is to limit recruitment into populations, and it has been found to be more effective in preventing successful nesting than direct removal of eggs or nests because nesting birds continue incubation often beyond the typical hatch date, which reduces the probability of producing a second clutch (Blokpoel and Tessier 1991, Marzluff et al. 1995). For ravens, an efficient nest predator, egg-oiling could also affect raven predation on local prey communities as a result of the absence of caloric demands necessary to support growing nestlings. However, quantification of the effects of egg-oiling on raven nest success and raven nest predation rates are lacking. Such information can help guide raven management plans for reducing impacts of ravens on sensitive prey species.

During the mid-1990s, ravens first initiated nesting on Alcatraz Island, an important breeding area in the San Francisco Bay area for multiple avian species. Because ravens are effective hunters, raven recruitment was expected to be detrimental to the nesting bird colonies on the island. Studies indicate that the arrival of ravens on Alcatraz Island was followed by a precipitous decline in Black-crowned Night-Heron (*Nycticorax nycticorax*) (hereafter, night-heron) nest survival on the island (Hothem and Hatch 2004). Thus, egg-oiling procedures were adopted on Alcatraz Island with the goal of both limiting raven recruitment into the region and reducing the impacts of raven predation on multiple species of nesting birds. During 2010–2015, we carried out an experimental egg-oiling study between ravens and night-herons to better understand the impacts of egg-oiling on the reproductive success of an efficient generalist predator and its prey. Our specific objectives were to (1) evaluate raven nest success as a function of egg-oiling using an alternate year replicate design (i.e., during 2011 and 2014, eggs were oiled; in 2010 and 2013, eggs were not oiled; and 2012 and 2015 were considered lag years for effects of egg-oiling), (2) deploy microcamera and digital video recording (DVR) devices to qualitatively evaluate the impacts of egg-oiling on raven nest success and raven incubation behavior, (3) deploy microcameras and DVRs on night-heron nests to quantify causes of night-heron reproductive failure (predation versus abandonment), and (4) quantify differences in raven predation rates of night-heron nests as a function of raven hatch success. Inferences were based on Bayesian multinomial logistic exposure models. This analytical technique allowed for the estimation of effects of raven nest success on night-heron nest predation rates and overall reproductive success of night-herons while accounting for different outcomes of night-heron nest failure.

METHODS

Study area

The study site was on Alcatraz Island (hereafter, Alcatraz), a 9.1-ha island managed by the National Park Service (NPS) in San Francisco Bay, California (37.8°N, 122.4°W). Although now a historical landmark, Alcatraz has served as a harbor defense fort (1847–1907), military prison (1907–1933), and federal penitentiary (1933–1963). Alcatraz is characterized by historical buildings and primarily non-native vegetation (Martini 1990). In recent years, Alcatraz has become recognized as an important breeding area for many avian species (Adams and Leedy 1991, Kelly et al. 1993, Saenz et al. 2006), including night-herons, ravens, and Snowy Egrets (*Egretta thula*), as well as several seabird species, including Western Gulls (*Larus occidentalis*), California Gulls (*L. californicus*), Brandt's Cormorants (*Phalacrocorax penicillatus*), Pelagic Cormorants (*P. pelagicus*), Pigeon Guillemots (*Cepphus columba*), and Black Oystercatchers (*Haematopus bachmani*). American Crows (*Corvus brachyrhynchos*) are also frequently observed on Alcatraz, but no nesting has been documented.

Raven egg-oiling

We carried out a longitudinal study design whereby we measured before, during, and after effects of egg-oiling on two time occasions over a 6-y period (2010–2015). The indepth methodology of data collection used for this study (i.e., microcameras and DVRs) was too challenging logistically to replicate at other locations; thus, our experimental approach employed a time-for-space substitution by using two temporal replicates of three years. During each year of the study, we searched for raven nesting activity on Alcatraz Island. During the first year of each temporal replicate (2010 and 2013), raven nesting was allowed to proceed without experimental manipulation (egg-oiling). During 2011 and 2014, for any located raven nest, we carried out egg-oiling procedures to preclude ravens from successfully nesting. Egg-oiling was conducted after observation of raven nesting activity on the island. However, immediately following the first egg-oiling attempt in 2014, we found the clutch was incomplete; thus, a second egg-oiling procedure was implemented. Egg-oiling was carried out by professional tree climbers in cooperation with NPS on 25 March 2011, 22 March 2014, and 5 April 2014. Egg-oiling procedures were not implemented during 2012 and 2015 in order to measure the lag effects of egg-oiling from the previous breeding season.

Raven nest monitoring

During egg-oiling years (initiated in 2011), we video-monitored raven nests to measure impacts on raven behavior and egg hatching following egg-oiling procedures. Video systems consisted of microcameras (30 × 110 mm with a 3.6-mm lens; EZ Spy Cam, Los Angeles, California) connected to single-channel DVRs equipped with a 32-GB SD card. Each microcamera featured seven infrared light-emitting diodes to allow for recording during periods of darkness. The microcamera was disguised using vegetation to reduce researcher disturbance. The DVRs were powered using two 12-V deep-cycle rechargeable batteries and were concealed under camouflage burlap. We changed the batteries and SD cards weekly to ensure video-recordings were continuous. Video equipment was installed on 22 April 2011 and 5 April 2014.

Night-heron nest monitoring

We conducted weekly intensive island-wide searches for night-heron nests during peak nesting time from April to mid-June during 2010–2015. We attempted to locate all active night-heron nests in the early periods of incubation. We used video-monitoring techniques on a sample of night-heron nests to identify causes of nest failure and estimate nest predation rates by ravens on night-heron eggs and chicks. We simultaneously deployed up to 24 microcameras connected to 4-channel H.264 DVR systems (AV Tech Corp., Hong Kong, China). Microcameras were mounted 0.5–1.0 m on nearby vegetation or to a camouflaged iron stake and were connected to a 100-m coaxial cable disguised with camouflage tape and vegetation. We set DVRs to record nests at 15 frames per second continuously to capture all predation events, and housed them in camouflage boxes under vegetation. Extension cords were used to connect video systems to available power outlets on Alcatraz Island. Although video-monitoring was limited by available power, we stratified samples across nesting habitat areas to account for variation in habitat types. Additionally, subsampled areas were consistent across years. Microcameras were maintained at each monitored nest until the nest failed or until chick departure. Cameras were then redeployed on nearby randomly chosen active nests.

Statistical analyses

We processed video data in a laboratory to observe causes of night-heron nest and chick failure. Specifically, we documented nest fate as hatch, predation by ravens, destruction by night-herons, abandonment, and failure to hatch. For the nestling phase, causes of failure were predation by ravens, destruction by night-herons, abandonment, and unknown causes of chick mortality (e.g., starvation, exposure). We considered nestlings successful if they reached 20 days post-hatch. After this time frame, chicks are difficult to track and ultimate fate might occur away from the nest. Scavenged nests were not considered raven predations in the analysis because they were not the direct cause of nest failure for night-herons. Dates and times of all predation events were recorded and predator behaviors were described.

We created encounter histories for nests, which consisted of the date the nest was located and the date of the nest fate (i.e., hatched or failed). For chicks, encounter histories consisted of the date the chicks hatched and the last date the chicks were observed (i.e., alive or dead). Failed nests consisted of exposure time for both time survived and time failed. That is, nests were successful until the time interval that they failed. Except for nests that failed to hatch despite being consistently incubated, video-monitoring allowed us to determine the exact dates of nest and chick fates. Thus, interval times were always 1 day for depredation or abandonment events.

We used a Bayesian multinomial logistic exposure model (Darrah et al. 2017) to estimate the likelihood of each nest fate and to examine raven predation on night-heron nests as a function of different treatment scenarios. For nests, the model took the form:

$$y_{ij} \sim \\ multinomial\left(\left[P_s(t_j)_{ij}, P_p(t_j)_{ij}, P_a(t_j)_{ij}, P_h(t_j)_{ij}, P_f(t_j)_{ij}\right], 1\right)$$

where the nest fates y_{ij} of each nest i at interval j, with an interval length of t days, follow a multinomial distribution. Possible nest fates, as determined by video data, were survive (s), predation by ravens (p), abandonment (a), nest destruction by night-herons (h), and failure to hatch for unknown reasons (f). The model for nestlings took the same form, with possible nest fates of survive (s), predation by ravens (p), abandonment (a), nestling destruction by night-herons (h), and chick death for unknown reasons (f). This multinomial distribution was applied once for each nest interval. We then regressed the predictor of raven reproductive success on the likelihood of predation of night-heron eggs and chicks and overall reproductive success of night-herons. We did not consider raven nest manipulation to be a factor that influenced other types of nest and chick failure (e.g., abandonment).

To assess the predictive value of egg-oiling treatments, we created indicator variables with a Bernoulli distribution with a prior of 0.5. The βt parameters (k) associated with raven nest treatment were multiplied by the indicator variable w_k. For each iteration, w_k is 1 if the variable was included in the model and 0 if it was not included in the model, resulting in a posterior distribution for variable inclusion. Using the mean of the posterior distribution of w_k, we calculated Bayes Factor, which represents the odds ratio for the inclusion of the variable in the model. Because prior distribution can influence model selection, and to ensure that uncertainty was constant for all models regardless of complexity, total model variance of the priors was scaled to V/K where K represents the number of coefficients in the model and V follows a Gamma distribution with 3.29 and 7.8 as parameters (Link and

Barker 2006). This is considered a vague prior, which assumes no previous knowledge of the estimated parameter.

We estimated daily probability of nest predation by ravens for each of the three raven nesting scenarios (i.e., years when ravens were successful, years when raven nesting was unsuccessful as a result of egg-oiling, and years of no raven nesting activity). We also estimated daily probability of abandonment, failure from unknown causes, and destruction by night-herons for both nests and chicks. In addition, we calculated daily survival probability for both nests and chicks given probabilities of nest failure and success. We calculated cumulative night-heron nest survival given a 25-d incubation period (Hothem et al. 2010) by exponentiation of the posterior distribution of daily survival rate to the total length of the incubation period (Powell 2007). Similarly, we calculated cumulative chick survival to fledging (i.e., 40 days) (Hothem et al. 2010). We calculated overall reproductive success (from laying to fledging) by multiplying cumulative nest survival and cumulative chick survival for each of the three raven nesting scenarios. For all results, we report effects when the 85% credible intervals (CI) of the posterior distribution excluded zero. Given the uncertainty around our model parameters, we chose the 85% CI because it incorporates the most probable values of the effects while discarding the extreme tails of the distribution. All analyses were conducted in R 3.2.1 (R Core Team 2014) and JAGS 4.2.0 using the package rjags (Plummer 2016). We ran 10,000 iterations of 3 chains with a thinning rate of 2 and a burn-in of 1000. We assessed convergence of chains visually and using the Gelman-Rubin test. We used uninformative priors for all parameters.

RESULTS

Raven nest manipulation

During 2011, we identified one active raven nest on Alcatraz, which had a clutch of seven eggs. Given raven nesting activity beginning around mid-March (estimated 17 March) and an incubation period of approximately 21 days (Stiehl 1985), the expected hatch date for the eggs was 7 April. When the camera was installed on 22 April (15 days after expected hatch date), only four of the seven original eggs remained in the nest. However, ravens continued to actively incubate and tend to the nest. We observed ravens consume three of the four eggs, from 28 April through 1 May, at which point incubation concluded.

In 2014, we identified one active raven nest on Alcatraz, which had seven eggs. Given nesting activity beginning around 21 March (one egg present on 22 March), the expected hatch date for the eggs was 11 April. We observed ravens consume three of the eggs between 19 and 23 April. Incubation concluded on 4 May, approximately three weeks past the expected hatch date.

During 2010, one pair of ravens successfully hatched two chicks on 13 April, one of which survived to fledging. In 2013, one pair of ravens successfully hatched three chicks in early April, all of which survived to fledging. During 2012 and 2015, we did not identify any raven nesting activity on Alcatraz.

Night-heron nest and chick survival

Throughout the course of the study, we video-monitored 159 night-heron nests and observed 26 predation events by ravens on night-heron nests and seven predation events on night-heron nestlings up to 20 days post-hatch. Ravens were the only predator identified on video. We did not consider egg destruction by night-herons to be predation events because the contents were not typically consumed.

These data provided evidence that nest success of ravens influenced predation rates on night-heron nests and chicks. Namely, probability of nest predation during years when ravens were raising young was substantially greater than during years when raven nests were unsuccessful or ravens were not observed nesting on Alcatraz Island (Table 1, Fig. 1). Daily probability of nest predation rates was 1.7 times greater during years when ravens successfully nested (median: 1.71%, 85% CI: 1.15–2.44%) than those years when nesting was unsuccessful following egg-oiling (0.98%, 85% CI: 0.55–1.57%). However, 85% CI of the β

Fig. 1. Estimated median cumulative predation probability (a) and median cumulative survival probability (b) of Black-crowned Night-Heron nests (before dashed vertical line) and chicks (after dashed vertical line) during years when Common Ravens were raising young (solid line), egg-oiling years (dashed line), and years when raven nesting was absent (dotted line) on Alcatraz Island, 2010–2015. Shaded area represents 85% credible intervals. Vertical dashed line is hatch day. For illustrating cumulative predation, all other causes of nest failure were held at their median values.

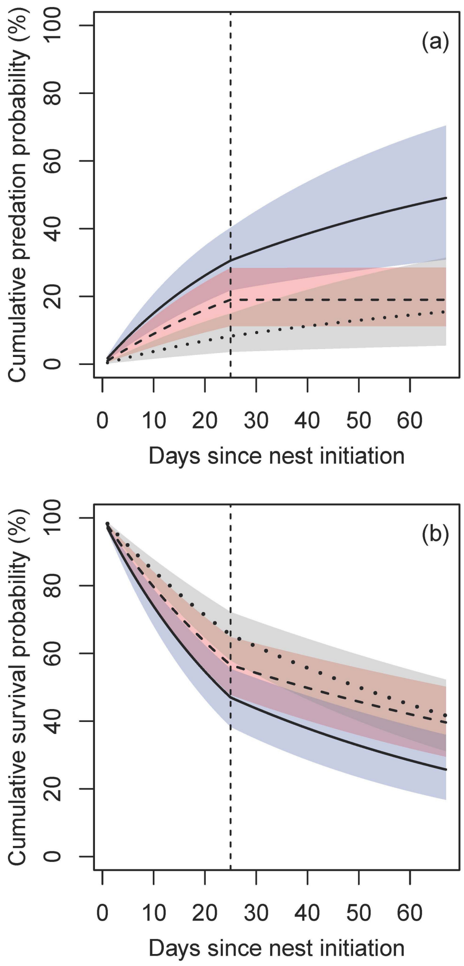

Table 1. Median estimates (85% credible interval) of posterior distributions from multinomial logistic exposure models modeling the effects of Common Raven reproductive success on predation rates and reproductive survival (i.e., nests, chicks, and overall) of Black-crowned Night-Herons on Alcatraz Island, 2010–2015.

Life stage	Parameter	Median (85% Credible Interval)
Nests	Daily predation probability, ravens successful (%)	1.71 (1.15–2.44)
	Daily predation probability, raven eggs oiled (%)	0.98 (0.55–1.57)
	Daily predation probability, no raven nesting (%)	0.40 (0.17–0.76)
	Daily probability of abandonment (%)	0.92 (0.67–1.23)
	Daily probability of failure to hatch (%)	0.19 (0.09–0.34)
	Daily probability of destruction by night-heron (%)	0.15 (0.06–0.29)
	Cumulative survival probability, ravens successful (%)	46.99 (38.34–55.44)
	Cumulative survival probability, raven eggs oiled (%)	56.58 (47.77–64.84)
	Cumulative survival probability, no raven nesting (%)	65.48 (57.95–72.23)
Chicks	Daily predation probability, ravens successful (%)	0.57 (0.27–1.03)
	Daily predation probability, raven eggs oiled (%)	0.00 (0.00–0.00)
	Daily predation probability, no raven nesting (%)	0.20 (0.05–0.51)
	Daily probability of abandonment (%)	0.11 (0.04–0.24)
	Daily probability of failure to hatch (%)	0.52 (0.34–0.76)
	Daily probability of destruction by night-heron (%)	0.19 (0.09–0.35)
	Cumulative survival probability, ravens successful (%)	54.66 (43.75–64.83)
	Cumulative survival probability, raven eggs oiled (%)	70.01 (61.73–77.39)
	Cumulative survival probability, no raven nesting (%)	63.61 (53.73–72.34)
Fledging	Cumulative survival probability, ravens successful (%)	25.40 (18.93–32.67)
	Cumulative survival probability, raven eggs oiled (%)	39.29 (31.99–46.84)
	Cumulative survival probability, no raven nesting (%)	41.32 (33.77–48.99)

estimate slightly overlapped zero (median: -0.57, 85% CI: -1.25–0.06). We found 90.4% of the posterior distribution of the β estimate was less than zero. Thus, there was a 90.4% probability that predation rates on nests were lower during years when raven eggs were oiled than during years when they successfully hatched. Furthermore, we found daily probability of nest predation was 4.3 times more likely when ravens successfully nested compared with years when raven nesting activity was absent on the island (0.40%, 85% CI: 0.17–0.76%). Based on the posterior distribution of the β estimate (median: -1.49, 85% CI: -2.39 – -0.71), we found a 99.8% probability that predation rates on nests were lower during years when ravens were not nesting than when ravens nested successfully, indicating strong evidence for immediate and 1-y lag effects from egg-oiling procedures.

For chicks, probability of daily predation was higher during years when ravens successfully nested (median: 0.57%, 85% CI: 0.27–1.03%) compared with years when nesting was unsuccessful following egg-oiling procedures (0.00%, 85% CI: 0.00–0.00%), and years when ravens did not attempt to nest at all (0.2%, 95% CI: 0.05–0.51%) (Fig. 1). We found a 99.9% and 89.3% probability that daily predation rates on chicks were lower during years when raven eggs were oiled (β median: -23.07, 85% CI: -57.37 – -4.89) and when nesting was absent (β median: -1.04, 85% CI: -2.47–0.15), respectively, than during those years of successful nesting. Based on Bayes Factor calculations, the model that included a covariate for raven nesting status on predation of night-heron nests and chicks was 2.5 and 2.1 times more likely than a model that did not include raven nest success as a predictor for predation of night-heron nests and chicks, respectively. Overall reproductive success of night-herons was greatest during years when raven nesting activity was absent on Alcatraz (Table 1, Fig. 1). Estimates of probabilities for other forms of nest and chick failure are reported in Table 1.

DISCUSSION

This study provides clear experimental evidence of how a predatory generalist's reproductive success can influence the reproductive performance of its prey. Using an egg-oiling technique, we successfully manipulated the reproductive response of ravens and identified predictable impacts on colonial nesting night-heron reproduction. Specifically, our study reveals that when ravens reproduced successfully, they exhibited increased predation on eggs and chicks of night-herons, which likely resulted in decreased overall productivity. Furthermore, during years when ravens were active on the island but raven nests were not observed, night-herons exhibited the greatest overall nest and chick survival, resulting from low predation rates. These findings could help inform conservation and management decisions for sensitive prey species in areas where nesting ravens are present.

The incubation and nestling phases for altricial birds are particularly energetically demanding for parent birds (Martin 1987), and night-heron eggs might fulfill important daily caloric needs for reproducing ravens on Alcatraz Island. Following hatch of ravens' clutches (average clutch size 3–7 eggs) (Boarman and Heinrich 1999), nestling requirements for growth and development must also be met, which might have substantial impacts on nearby nesting birds. For example, one pair of ravens requires approximately 721 kcal/day (Shank 1986). Given an energy density of 7.22 kcal/g (SE = 0.05 kcal/g), an average mass of 31.8 g for a night-heron egg (Carey et al. 1980), and assimilation metabolism of 75% (Castro et al. 1989) in order to satisfy the energetic needs of a pair of ravens, they would need to consume 4.2 night-heron eggs/day. Average clutch size for night-herons on Alcatraz is 2.87 eggs (Hothem and Hatch 2004), and average number of night-heron nests from 2010 to 2015 was 133 (SE = 14). Thus, the number of eggs needed to support a successful raven nest (adults and young) to fledging (~40 days) (Boarman and

Heinrich 1999) can quickly exceed the number of eggs produced within the night-heron colony on Alcatraz, which leads to the potential for ravens to completely destroy nesting bird colonies, as has happened at other nesting colonies in San Francisco Bay (Kelly et al. 2005). Additionally, growing night-heron nestlings are likely an important dietary component for ravens that are raising young. For example, we observed predation on night-heron nestlings during the 2 years when ravens successfully hatched chicks (2010 and 2013), whereas predation on nestlings was not observed during 3 years when the ravens were not raising young (2011, 2012, and 2014).

Although we observed reduced nest predation by ravens during years when raven eggs were oiled and hatch was prevented, the lowest predation rates occurred in the year following oiling procedures when raven nesting was absent. These different patterns in predation rates among years is likely explained by raven reproductive behavior and spatial constraints associated with territorial breeding ravens. First, breeding ravens are efficient nest predators, and they capitalize on available resources by caching eggs (Howe and Coates 2015) for later consumption or to feed growing nestlings, which could lead to higher predation rates during years of active incubation (including years of egg-oiling). Additionally, although ravens are capable of 40-km movements (Boarman 2003), during nesting, they are territorial and act as central-place foragers (Roth et al. 2004), concentrating most of their hunting within approximately 400 m of their nests (Kristan and Boarman 2003). Thus, during years of egg-oiling, while ravens continued incubating their nests, they were restricted to hunting close to their nest sites (i.e., avian nesting colonies on Alcatraz). In contrast, nonbreeding ravens are not limited to an area surrounding a nest; thus, they can use a larger home range (Linz et al. 1992) to acquire food from multiple sources. These findings offer support to the overarching hypothesis that breeding ravens are more of a conservation concern to sensitive species than are nonbreeding ravens (Bui et al. 2010, Howe and Coates 2015). Additionally, the potential observed lag effects from egg-oiling (i.e., the absence of raven nesting in years following egg-oiling procedures) was contrary to the findings of Marzluff et al. (1995), in which manipulation of raven nests (i.e., clutch removal) did not have any influence on breeding propensity the following year. It is possible that ravens nested near Alcatraz but not on the island. Several avian species have been shown to change nesting locations after an unsuccessful reproductive attempt during the previous season (Haas 1998, Clark and Shutler 1999). The potential for egg-oiling to have impacts for more than one reproductive season has considerable significance for the effectiveness of egg-oiling as a management technique, and warrants further study.

This study was not without caveats and constraints. First, although our study was replicated temporally, the findings of the treatment effect should be interpreted with caution because they are likely based on a single pair of ravens and potentially are unique to Alcatraz Island. Ravens are highly territorial, are known to reuse nest structures or nest close to previous nests, and can reproduce for up to 10 years in the wild (Boarman and Heinrich 1999). Second, additional raven nests may have been present but undetected during 2012 and 2015. However, we did not observe any ravens exhibiting typical nesting behaviors during those years (e.g., hunting by a single member of a pair or repeated visits to a localized nest location), and extensive weekly surveys did not reveal any areas that likely contained new nests. Lastly, it is possible that ravens, a generalist predator known for prey-switching (Boarman and Heinrich 1999), might have preyed on species other than night-herons during the years that night-heron predation was reduced, considering that Alcatraz Island is a breeding area for a variety of seabird species. This should not detract from the effect that was observed for night-herons, but it is an important consideration for the use of egg-oiling in environments with multiple prey species because effects may vary across species. Although similar egg-oiling studies within other environments are warranted, these initial findings demonstrate that egg-oiling appears to be a viable conservation tool to reduce predation impacts, and could be especially important for sensitive prey. It should be noted that Alcatraz Island provided an ideal setting to carry out a longitudinal experimental design because this system appeared closed and consisted of few ravens, which allowed us to effectively quantify nest survival responses of their prey as a function of raven reproductive success.

In conclusion, these findings indicated that egg-oiling procedures, if timed appropriately, can have immediate and delayed favorable effects on reducing nest success of ravens and nest predation rates by ravens on local prey communities. Such findings could have broad implications for conservation of sensitive species by improving their nest survival and fledgling rates, and might be most valuable for species in which reproduction has strong influences on population growth. However, the success of egg-oiling as a management tool is likely dependent on characteristics associated with the treatment area and might merit careful planning prior to implementation (e.g., number of ravens, prey species involved). For example, finding nests and oiling eggs can be labor intensive, and thus, might not be a viable option for large areas with a substantial number of territorial ravens. Nevertheless, to our knowledge, this study represents the first to quantify the efficacy of this potential nonlethal raven management action by using more than 6 years of intensive video-monitoring to gain insight into these questions.

Responses to this article can be read online at:
http://www.ace-eco.org/issues/responses.php/1207

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