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# *Note*

# Demography, morphometrics, and stomach contents of common ravens examined as a result of controlled take

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***Abstract:*** Common ravens (*Corvus corax*; ravens) are known nest predators that have the ability to negatively impact nesting birds, including imperiled species of seabirds and shorebirds. We conducted systematic necropsies of ravens that were lethally controlled in Monterey Bay, California, USA during 2013–2015, in or near western snowy plover (*Charadrius nivosus nivosus*) nesting areas, in an effort to better understand body condition, overall health, and diet of individual ravens. Raven predation of snowy plover nests has increased over the years in the Monterey Bay study area, and lethal removal of ravens has been employed to reduce predation. Most ravens examined in this study were in moderate to excellent body condition and also exhibited good organ health. There were statistically significant differences between male and female morphometrics (mass, culmen length, and wing length; $P < 0.05$). Stomach content analysis indicated a varied diet with consumption of animal remains and eggshell fragments, and anthropogenic sources of food (e.g., human food items and human-produced nonfood items). Our study provides evidence that lethal control of ravens targeted some individual ravens that were responsible for depredating snowy plover nests.

***Key words:*** California, *Charadrius nivosus nivosus*, common raven, *Corvus corax*, demographics, stomach content analysis, Monterey Bay, morphometrics, western snowy plover

**Common ravens** (*Corvus corax*; ravens) and other corvids are major nest predators of several avian species and have contributed to population declines of imperiled species of seabirds and shorebirds (Avery et al. 1995, Peery and Henry 2010, Burrell and Colwell 2012, Carle et al. 2017, Coates et al. 2021, Neuman et al. 2021). Due to many factors, including a high level of sociality, opportunistic and generalist foraging habits, and the ability to range over large areas, corvids have received focused attention from wildlife managers responsible for protecting at-risk species (Marzluff and Neatherlin 2006, Harju et al. 2021).

Raven populations have increased dramatically in the western United States in the past several decades (Sauer et al. 2017), and population increases have been especially notable in habitats with large amounts of anthropogenic subsidies and human infrastructure. Because of these characteristics, ravens are very successful habitat-edge specialists and efficient nest predators that thrive in areas with large human populations (Angelstam 1986, Andren 1992, Luginbuhl et al. 2001, Marzluff and Neatherlin 2006). Many studies have documented depredation of nests by corvid species; however, few studies have examined the post-mortem stomach contents of lethally controlled corvids to confirm the presence or absence of shell fragments and animal material, indicating that control efforts targeted the individual predators responsible.

Our overarching goal was to examine necropsy information to confirm predation events in lethally controlled ravens and to document overall health patterns of this human-commensal predator. Herein, we present the morphometrics, demography, and stomach content analysis of ravens ($n$ = 34) that were lethally controlled to protect threatened nesting western snowy plovers (*Charadrius nivosus nivosus*; snowy plover) in Monterey Bay, California, USA.

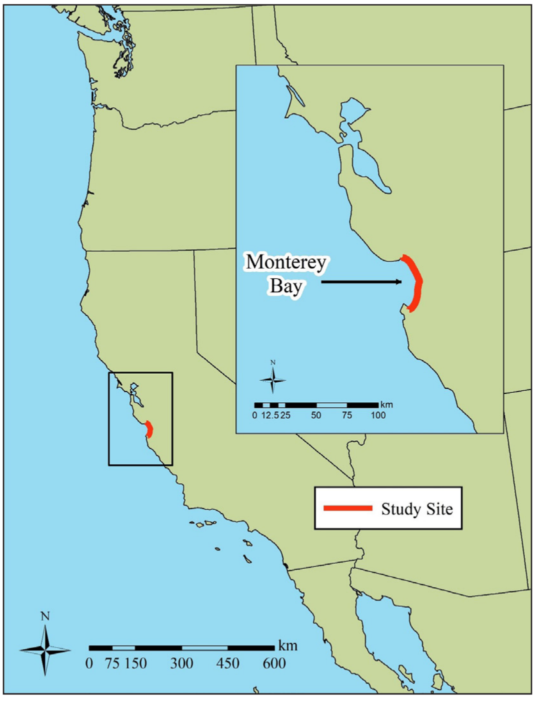


**Figure 1.** Map of the pacific coast of North America. The study area (Monterey Bay) is highlighted in red and located on the central coast of California, USA.

## Study area

This study was conducted on the coast of Monterey Bay, a large open coastal embayment located on the central coast of California (Figure 1). The study area included approximately 30 km of continuous sandy beach within Santa Cruz and Monterey counties (122°17′W, 37°6′N to 121°52′W, 36°36′N), intersected by the Pajaro and Salinas Rivers. Coastal beach habitats were sparsely vegetated by sea rocket (*Cakile maritima*), beach bur (*Ambrosia chamissonis*), and American dune grass (*Leymus mollis*), with a moderate to extensive coastal dune system, grassland, shrubland, and wetland habitats, and agricultural areas located directly adjacent to the shoreline. Most topographic elevations are within 30.5 m of sea level, but some dunes in southern Monterey Bay range as high as 91.44 m above sea level. The mild Mediterranean climate of coastal Monterey Bay is characterized by low rainfall (<30 inches [approx. 76 cm] annually), mild summer temperatures rarely more than 70°F (21°C), and abundant coastal fog that provides the primary moisture for beach and dune flora.

## Methods

Ravens examined in this study were lethally controlled by firearm or were humanely euthanized after being captured in padded jaw leg hold traps in coastal habitats in the Monterey Bay. All were collected between the months of March and June 2013–2015.

Ravens that were lethally controlled were either present on sandy beaches where snowy plovers were nesting or were present in habitats directly adjacent to and within 500 m of sandy beaches where snowy plovers were nesting (e.g., sand dunes, agricultural fields) during the nesting season (approximately March through September). Because of confirmed predation of plover nests by ravens in previous years, ravens that were present in these areas were controlled preemptively once they were observed, although not all ravens that were observed were successfully controlled. All lethal control was conducted by U.S. Department of Agriculture, Wildlife Services biologists in 2013, 2014, and 2015 following their standard protocols and methods (Peebles and Spencer 2020).

After lethal control, ravens ($n$ = 34) were immediately collected and frozen for 4–10 weeks; subsequently, the carcasses were defrosted and examined via systematic necropsy at the California Department of Fish and Wildlife, Office of Spill Prevention and Response, Marine Wildlife Veterinary Care and Research Center (CDFW-OSPR MWVCRC) in Santa Cruz, California. Body condition was assessed for all birds examined in 2014 and 2015, and scores were applied on a scale of 0–3 as described in Van Franeker (2004; Table 1), where for subcutaneous and internal fat, 0 = no fat, 1 = some fat, 2 = fat, and 3 = very fat; and where for pectoral muscle condition, 0 = strongly emaciated, 1 = emaciated, 2 = moderate condition, and 3 = good condition. An overall condition index (CI) was calculated following Van Franeker (2004), where CI = subcutaneous fat score + internal fat score + pectoral muscle score (Table 1). Once calculated, CI can be interpreted following Van Franeker (2004), where score 0–1 = mortally emaciated, 2–3 = critically emaciated, 4–6 = moderate body condition, and 7–9 = good body condition.

We also assessed organ health. We applied organ health on a scale of 0–3 as described in Van Franeker (2004; Table 1), where 0 = heavily affected tissue, 1 = affected tissue, 2 = slight

**Table 1.** Necropsy findings and organ health in examined common ravens (*Corvus corax*), 2013–2015, Monterey Bay, California, USA. Body condition was coded as described by Van Franeker (2004), where for fat scores for subcutaneous fat (SubQ fat) and internal fat are denoted as follows: 0 = no fat, 1 = some fat, 2 = fat, 3 = very fat. Pectoral muscle score (Pec score) is denoted as follows: 0 = strongly emaciated, 1 = emaciated, 2 = moderate condition, 3 = good condition. Organ health was scored similarly as described by Van Franeker (2004), where 0 = heavily affected tissue, 1 = affected tissue, 2 = slight or somewhat affected, 3 = unaffected and healthy looking. If a bird was not assessed or data were unknown, it was left blank in the table. An overall condition index (CI) was calculated following Van Franeker (2004), where condition index = subcutaneous fat score + internal fat score + pectoral muscle score. Once calculated, CI can be interpreted following Van Franeker (2004), where score 0–1 = mortally emaciated, 2–3 = critically emaciated, 4–6 = moderate body condition, and 7–9 = good body condition. U represents an unknown value, Juv represents a juvenile individual, and SA represents a sub-adult individual. M represents a male individual, and F represents a female individual.

| ID | Age | Sex | Mass (g) | Culmen (mm) | Wing (mm) | SubQ fat | Internal fat | Pec score | CI | Stomach | Liver | Gut | Kidney | Lung |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 13-0990 | Adult | F | 760 | NA | 389 | | | | | | | | | |
| 14-0601 | Adult | F | 815 | 63.5 | 395 | 0 | 2 | 2 | 4 | 1 | 3 | 3 | 3 | |
| 14-0605 | Adult | F | 650 | 63.8 | 401 | 2 | 3 | 3 | 8 | 3 | 3 | 2 | 3 | 3 |
| 14-0606 | Adult | F | 865 | 62.6 | 402 | 2 | 3 | 3 | 8 | 3 | 3 | 3 | 3 | 3 |
| 14-0608 | Adult | F | 755 | 69.4 | 404 | 1 | 3 | 3 | 7 | 3 | 2 | 3 | 3 | 3 |
| 14-0611 | Adult | F | 430 | 64.7 | 400 | 3 | 3 | 3 | 9 | 3 | 3 | 3 | 3 | 3 |
| 14-0615 | Adult | F | 715 | 58.6 | 390 | 1 | 3 | 3 | 7 | 3 | 3 | 2 | 3 | 3 |
| 15-0607 | Adult | F | 820 | 65.4 | 392 | 0 | 2 | 2 | 4 | 3 | 3 | 2 | 3 | 1 |
| 15-0609 | Adult | F | 735 | 61.6 | 397 | 0 | 2 | 3 | 5 | 3 | 3 | 3 | 3 | 3 |
| 15-0613 | Adult | F | 820 | 63.7 | 401 | 1 | 3 | 3 | 7 | 2 | 3 | 3 | 3 | 3 |
| 15-0616 | Adult | F | 915 | 64.4 | 405 | 1 | 3 | 3 | 7 | 3 | 3 | 3 | 3 | 3 |
| 13-0989 | Adult | M | 860 | 64.9 | 412 | | | | | | | | | |
| 14-0600 | Adult | M | 840 | 71.1 | 427 | 0 | 0 | 2 | 2 | 3 | 2 | 2 | 3 | 3 |
| 14-0603 | Adult | M | 1035 | 68.3 | 396 | 2 | 3 | 3 | 8 | 3 | 3 | 2 | 3 | |
| 14-0614 | Adult | M | 935 | 72.2 | 396 | 2 | | 3 | | | | | | |
| 14-0616 | Adult | M | 920 | 61.6 | 400 | 2 | 3 | 3 | 8 | 3 | 3 | 3 | | |
| 14-0618 | Adult | M | 1010 | 68 | 418 | 2 | 3 | 3 | 8 | 3 | 3 | 2 | | |
| 14-0619 | Adult | M | 870 | 68.1 | 407 | 1 | 1 | 3 | 5 | 3 | | 3 | 3 | |
| 15-0608 | Adult | M | 910 | 66.6 | 415 | 0 | 2 | 2 | 4 | 3 | 3 | 2 | 3 | 1 |
| 15-0611 | Adult | M | 910 | 66.4 | 408 | 0 | 1 | 3 | 4 | 3 | 3 | 2 | 3 | 3 |
| 15-0614 | Adult | M | 725 | 60.6 | 394 | 0 | 3 | 2 | 5 | 3 | 3 | 3 | 3 | 1 |
| 15-0615 | Adult | M | 910 | 67.3 | 405 | 2 | 3 | 3 | 8 | 3 | 3 | 3 | 3 | 2 |
| 14-0604 | SA | M | 925 | 63.8 | 431 | 0 | 2 | 3 | 5 | 3 | 3 | 2 | 3 | |
| 14-0607 | SA | M | 795 | 71.5 | 405 | 1 | 3 | 3 | 7 | 3 | 3 | 2 | 3 | |
| 14-0609 | SA | M | 760 | 61.8 | 417 | 1 | 2 | 3 | 6 | 3 | 3 | 2 | 3 | 3 |
| 13-0519 | Juv | F | 700 | 56.1 | 368 | | | | | | | | | |
| 14-0613 | Juv | F | 915 | 60.7 | 394 | 2 | 3 | 3 | 8 | 3 | 3 | 3 | 3 | |
| 14-0617 | Juv | F | 665 | 62.2 | 372 | 3 | 3 | 3 | 9 | 3 | 3 | 3 | 3 | 3 |
| 13-0520 | Juv | M | 850 | 67.2 | 381 | | | | | | | | | |
| 14-0610 | Juv | M | 790 | 58.2 | 378 | 2 | 3 | 3 | 8 | 3 | 3 | 3 | 3 | |
| 14-0612 | Juv | M | 985 | 68.2 | 415 | 2 | 3 | 3 | 8 | 3 | 3 | 2 | 2 | 3 |
| 15-0612 | Juv | M | 850 | 67.2 | 413 | 2 | 2 | 3 | 7 | 3 | 3 | 2 | 2 | 1 |
| 14-0602 | U | U | 835 | 59.9 | 401 | 2 | 3 | 3 | 8 | 3 | | 3 | | |
| 15-0610 | U | U | 805 | 62.4 | 392 | 1 | 3 | 3 | 7 | 3 | 3 | | | |

**Table 2**. Stomach contents of examined common ravens (*Corvus corax*), where animal items represent mammal, bird, reptile, and insect fragments, Monterey Bay, California, USA, 2013–2015. If nothing was found in a particular category, it was left blank in the table.

| ID | Anthropogenic rubbish | Animal items | Eggshell fragments | Plant material |
|---|---|---|---|---|
| 13-0990 | | Mammal remains | Snowy plover eggshells | |
| 14-0601 | watermelon, hot dog | Reptile remains, skin | | |
| 14-0605 | | Mammal remains, trachea | | |
| 14-0606 | | Bones, fur | | |
| 14-0608 | Tissue fragment, foil | | | |
| 14-0611 | | | | |
| 14-0615 | | Tissue with adhered feathers | | |
| 15-0607 | | Mammal remains, fur, tissue, insects | Snowy plover eggshells | |
| 15-0609 | | 2 bones, 1 talon, larvae, insects | Waterfowl eggshells | Plant matter |
| 15-0613 | | White, black, and gray feathers | | Tomato, seeds |
| 15-0616 | Unknown rubbish | Feathers, 1 avian foot, bones, tissue | | |
| 13-0989 | | Mammal remains, egg yolk | Snowy plover eggshells | |
| 14-0600 | | | | |
| 14-0603 | | Tissue | Waterfowl eggshells | Pea seed |
| 14-0614 | | | | |
| 14-0616 | Bones (human food) | Tissue, 1 feather | | Plant matter |
| 14-0618 | | Tissue | | |
| 14-0619 | Unknown rubbish | Tissue | | |
| 15-0608 | | 1 talon, 16 bones, tissue, 30 feathers, insects | Snowy plover eggshells | Plant matter |
| 15-0611 | | 25 bones, tissue, fur, insects | Waterfowl eggshells | Plant matter |
| 15-0614 | | 41 bones, tissue | | |
| 15-0615 | 2 pieces plastic thread | Bones | | |
| 14-0604 | Unknown rubbish | Tissue with adhered fur | Waterfowl eggshells | Pea seed |
| 14-0607 | | Bones, fur | | |
| 14-0609 | | | | |
| 13-0519 | Paper | | | Plant matter |
| 14-0613 | | | | |
| 14-0617 | | | | |
| 13-0520 | | Bones | Snowy plover eggshells | |
| 14-0610 | | | | |
| 14-0612 | | | | |
| 15-0612 | | 1 mouse, tissue, fur, bones, jaw, teeth | | |
| 14-0602 | | Tissue | | |
| 15-0610 | | 1 tooth (molar), bones, tissue, fur | | Plant matter |

or somewhat affected, and 3 = unaffected and healthy looking. Examined birds with a low level of freshness or completeness (due to gunshot wounds) were recorded as unknown and/or not assessed (Table 1). Birds examined in 2013 were considered part of a pilot study and were not assessed for body condition and organ health.

We recorded morphometric parameters (culmen length, body mass, wing length) and demographic parameters (sex and age class) for all birds (2013, 2014, 2015) during necropsy (Table 1). Sex was determined by internal examination and identification of the gonads. We determined age by 2 factors: presence or absence of the bursa of Fabricius (hereafter bursa), and gonadal development. Age classes were divided into 3 groups: juvenile, subadult, and adult. Birds with a bursa present were considered to be juvenile, birds without a bursa but with underdeveloped gonads were considered to be subadult, and birds without a bursa and with developed gonads were considered to be adults (Van Franeker 2004).

Mouth color is often thought of as an indicator of age in ravens; however, this metric has been debunked due to inaccuracy (Heinrich and Marzluff 1992), and therefore (although recorded at time of necropsy) was not used in this assessment. We measured morphometrics following Van Franeker (2004), where culmen length was recorded in millimeters from first feather-base to tip of bill, body mass was recorded in grams for all fresh and complete birds, and wing length was measured in millimeters in all birds with full-grown outer primary p10 feathers (Table 1). To estimate statistical differences in morphometrics between sex classes, we used a 2-sample $t$-test for unequal variances ($\alpha = 0.05$), and an $f$-test to estimate unequal variances ($\alpha = 0.05$) in the data (calculated with Microsoft Excel, Microsoft Corporation, Redmond, Washington, USA).

To analyze stomach contents, we opened the proventriculus and ventriculus and rinsed them through a 0.5-mm mesh sieve to retrieve contents, which were sorted and categorized as: anthropogenic material, animal items (including mammal, bird, reptile, and insect), eggshell fragments, or plant material (Table 2). We scored food items visually and then categorized them. Fragments that were too small and/or too digested to allow for visual analysis were excluded. Eggshell fragments were identified as snowy plover if they exhibited the distinct spotted pattern and size range (pale buff spotted with black; Kaufman 2005, Page et al. 2009); if eggshells were without a distinct color or pattern or were larger than the size range of the snowy plover, they were categorized as unknown waterbird.

Gut content analysis can be biased in numerous ways, including incomplete consumption of prey, regurgitation of prey before necropsy (through the formation of pellets by ravens, specifically; Laudet and Selva 2005), full digestion of some materials before necropsy, which may lead to an emphasis on smaller particles, or an emphasis on particles that were left undigested (Hart et al. 2002). In addition, high frequency of occurrence of items in gut analysis does not necessarily correlate with relative importance in the diet (Pinkas 1971). Because of these biases and our limited sample size, we intend this stomach content analysis to provide a qualitative overview of the diet of the birds that were sampled.

## Results

Out of the 34 examined ravens, 22 were adult (22/34; 65%), 3 were subadult (3/34; 9%), 7 were juvenile (7/34; 20%), and 2 were unknown age due to the state of completeness of the carcass (2/34; 6%; Table 1). Fourteen of the examined birds were female (14/34; 41%), 18 were male (18/34; 53%), and 2 were classified as unknown sex if the gonads were missing or damaged from gunshot wounds (2/34; 6%; Table 1). Morphometric differences were evident between sex classes. There were differences between male and female mass ($P = 0.002$), culmen length ($P = 0.013$), and wing length ($P = 0.007$), where males on average had a higher mass and a longer culmen and wing length. The mass of female birds ranged between 430–915 g, while the mass of male birds ranged between 725–1,035 g (Table 1). The culmen length of female birds ranged from 56.1–69.4 mm, while the culmen length of male birds ranged from 58.2–72.2 mm (Table 1). The wing length of female birds ranged from 368–405 mm, and the wing length of male birds ranged from 378–431 mm (Table 1).

The CI scoring (2014, 2015 only) showed that most ravens examined in this study were in overall good body condition. Examination of the CI showed that 0 birds were mortally emaciated (0/29; CI score 0–1), 1 bird was critically emaciated (1/29; 3%; CI score 2–3), 9 birds were in moderate condition (9/29; 31%; CI score 4–6), 19 birds were in good body condition (19/29; 66%; CI score 7–9), and 1 bird (14-0614; Table 1) was not assessed for CI due to decomposition.

Organ health (examined in 2014 and 2015 only) also was rated highly in examined birds, showing that birds were generally in good health; 93% of examined birds had excellent stomach health, 93% had excellent liver health, 54% were considered to have excellent gut health, 92% had excellent kidney health, and 72% had excellent lung health. Scoring for stomach condition was as follows: 0 birds were scored as 0 (severe lesions; 0/29; 0%), 1 bird was scored as 1 (affected tissue; 1/29; 3%), 1 bird was scored as 2 (minorly affected tissue 1/29; 3%), 27 birds were scored as 3 (unaffected tissue; 27/29; 93%), and 1 bird was not assessed due to decomposition (14-0614; Table 1). Scoring for liver condition was as follows: 0 birds were scored as 0 (severe lesions; 0/27; 0%), 0 birds were scored as 1 (affected tissue; 0/27; 0%), 2 birds were scored as 2 (minorly affected tissue; 2/27; 7%), 25 birds were scored as 3 (unaffected tissue; 25/27; 93%), and 3 birds were not assessed for liver condition due to decomposition (14,0602, 14-0614, and 14-0619; Table 1).

Scoring for gut health was as follows: 0 birds were scored as 0 (severe lesions; 0/28; 0%), 0 birds were scored as 1 (affected tissue; 0/28; 0%), 13 birds were scored as 2 (minorly affected tissue; 13/28; 46%), 15 birds were scored as 3 (unaffected tissue; 15/28; 54%), and 2 birds were not assessed for gut health (14-0614 and 15-0610; Table 1). Scoring for kidney health was as follows: 0 birds were scored as 0 (severe lesions; 0/25; 0%), 0 birds were scored as a 1 (affected tissue; 0/25; 0%), 2 birds were scored as 2 (minorly affected tissue; 2/25; 8%), 23 birds were scored as 3 (unaffected tissue; 23/25; 92%), and 5 birds were not assessed for kidney health due to decomposition (14-0602, 14-0614, 14-0616, 14-0618, and 15-0610; Table 1). Scoring for lung health was as follows: 0 birds were scored as 0 (severe lesions; 0/18; 0%), 4 birds were scored as 1 (affected tissue; 4/18; 22%), 1 bird was scored as 2 (minorly affected tissue; 1/18; 6%), 13 birds were scored as 3 (unaffected tissue; 13/18; 72%), and 12 birds were not assessed (14-0601, 14-0602, 14-0603, 14-0604, 14-0607, 14-0610, 14-0613, 14-0614, 14-0616, 14-0618, 14-0619, and 15-0610; Table 1) due to the state of the lungs that were affected by gunshot wounds or euthanasia.

Stomach content analysis revealed a varied diet. Twenty-seven birds had stomach contents available for examination (27/34; 79%), and 7 birds had empty stomach chambers (7/34; 21%). Of the birds with stomach contents available, 8 birds had anthropogenic material (8/27; 30%), 25 birds had animal remains (25/27; 93%), 9 birds had eggshell fragments that were identified as snowy plover (5/27; 19%) or other waterbird (4/27; 15%), and 9 birds had plant material (9/27; 33%; Table 2). Seven out of 22 adults (32%), 1 out of 3 sub-adults (33%), and 1 out of 7 juveniles (14%) had evidence of eggshell fragments. More specifically, 4 of the 22 adults (18%), 0 of the 3 sub-adults, and 1 of the 7 juveniles (14%) had evidence of snowy plover egg consumption.

## Discussion

Our study provided insights into the overall health of ravens in Monterey Bay, California and confirmed that targeted lethal control of ravens successfully removed individuals that were depredating nests of sensitive plover and waterbird species. Lethal predator removal is a widespread strategy employed to promote conservation of rare and threatened wildlife species (Tapper et al. 1996, Côté and Sutherland 1997, Treves and Naughton-Treves 2005, Dinsmore et al. 2014). Burrell and Colwell (2012) showed that ravens are a primary factor contributing to snowy plover reproductive failure. Strong et al. (2021), more specifically highlights the threat of ravens to nesting snowy plovers in the Monterey Bay area, a threat that has increased in magnitude since 2007. The authors note that prior to 2007, ravens were responsible for <2% of all nest failures; however, by 2020, ravens were associated with the loss of up to 27% of all failed snowy plover nests in the area (Strong et al. 2021). Ravens examined in this study were lethally controlled because they were hunting in or adjacent to snowy plover habitat. Our results provide evidence that the predator control employed here successfully targeted specific ravens that were depredating snowy plover nests.

Our study also provided interesting insights into the health of ravens that were lethally controlled. These ravens had a broad generalist diet and were in overall good physical health, both of which are consistent with their status as a human-commensal predator that is thriving in the human-altered landscape where they were controlled. They consumed waterbird eggs (both shorebirds and waterfowl) and a variety of other animals, including mammals and reptiles, as well as human-subsidized food resources.

Although our data are limited, adults and sub-adults may have been more successful at securing eggs (snowy plover and other waterbird) than the juvenile age class, which may further support the idea of hyperpredation in ravens. We expect most adults to be breeding individuals, while a larger proportion of juveniles/sub-adults may be non-breeding transients. Kristan and Boarman (2003), in their study on raven predation on a threatened species (desert tortoise, *Gopherus agassizii*), found that the breeding population of ravens in the Mojave Desert have become abnormally and artificially high due to food subsidies from anthropogenic sources (Madden et al. 2015). In turn, an elevated risk of predation was found to occur when large persistent flocks of breeding individuals amassed, and ravens use areas of both developed and undeveloped habitat (Kristan and Boarman 2003). In hyperpredation, the predator becomes unaffected by the population size of their prey and continues to depredate the same prey resource even at very low numbers (Kristan and Boarman 2003). This hyperpredation phenomenon has also been noted in other studies that highlight nest predation events by ravens to be mostly accountable to resident breeding adult birds versus transients (Bui et al. 2010, Howe et al. 2014, Howe and Coates 2015).

Most examined birds (97%) were in good or moderate body condition and had good to excellent organ health (Table 1). They also comprised a variety of ages, sexes, and body condition and were confirmed to have depredated waterbird nests (Table 2). Along with stomach content analysis (Table 2), our data further support that ravens were generally consuming waterbird eggs as a nutritive diet source and using anthropogenic sources of food as an additional ancillary food source.

In addition to being in good health, we found that most birds examined were identified as adult birds (22/34; 65%; Tables 1 and 2). The rest of the examined birds were either sub-adult (3/34), juvenile (7/34), or unknown (2/34). As with many species, adult ravens have greater foraging success than juvenile and sub-adult birds; they are better at food-caching (Beck et al. 2020), do not have to rely on group foraging as a tactic for gaining food (Marzluff and Heinrich 1991), and have greater success keeping the food they have captured (Gallego-Abenza et al. 2020). It is then, perhaps, not surprising that most birds that were lethally controlled in this study were adults. As is the case with adults being more likely to be associated with hyperpredation, adults are also generally considered to be superior foragers relative to other age classes. Additionally, we found statistically significant differences in the morphometric parameters (mass, culmen, wing length) we examined between male and female ravens. Bedrosian et al. (2008) also found statistically significant differences in mass between male and female ravens but did not examine wing length between males and females and did not find a statistically significant difference in culmen length.

Prior to being lethally controlled, the ravens examined in this study were observed to have completed foraging trips along beaches in the Monterey Bay area within snowy plover nesting habitat or in adjacent habitats. Raven abundance and reproductive rates increase with human settlements and recreation areas, with anthropogenic food sources as the main influencing factor (Marzluff and Neatherlin 2006). The Monterey Bay area is densely populated (Monterey County, 44.84 people per km$^2$; Santa Cruz County, 227.57 people per km$^2$; U.S. Census Bureau 2019), and in areas where the population is more sparse, agricultural fields are widespread, providing many opportunities for corvids to access anthropogenic food and water sources, as well as nesting sites. This is likely a major contributing factor to the abundance of ravens found in this area. Because of the anthropogenic factors driving raven population increases in the Monterey Bay area, lethal control of ravens will likely be necessary to benefit nesting plovers into the foreseeable future.

Lethal predator control is often unpopular with the general public (Messmer et al. 1999) and has had varying levels of success depending on anticipated outcomes but has been promoted in a number of predator removal studies (Ivan and Murphy 2005; Shwiff et al. 2005; Smith et al. 2010*a*, *b*). Our findings support the use of lethal control to target specific individuals that are directly responsible for nest loss. This may be a useful tool in targeting predatory individuals when other means of predator control, such as individual nest exclosures, are not viable.

The use of individual nest exclosures has been successful at increasing snowy plover hatch rates but may lead to nest abandonment and lower adult survival and requires time-intensive implementation and monitoring that may not be feasible for some wildlife managers (Neuman et al. 2004, Hardy and Colwell 2008, Gaines et al. 2020, Strong et al. 2021). Reducing the availability of anthropogenic subsidies that attract generalist predators has been shown to reduce the number of generalist predators (Peery and Henry 2010, Walker and Marzluff 2015, Brunk et al. 2021); however, in densely populated areas (such as Monterey and Santa Cruz counties), this may not be a viable option because it would require large efforts at regional coordination, management, and considerable funding for planning and implementation. Lethally removing predators has been shown to be especially beneficial to populations of breeding birds, with increases in breeding population size as well as hatching and fledging success (Smith et al. 2010*a*, *b*).

In an economic analysis by Shwiff et al. (2005), increased spending for predator removal before and during the nesting period was associated with increased nesting success for another imperiled beach nesting species, the California least tern (*Sternula antillarum browni*); when predator removal was combined with nest monitoring activity, there was an associated increase in eggs laid and the number of breeding adults. Not all ravens that were examined in this study had direct evidence of waterbird eggshell fragment ingestion. Because ravens regurgitate nondigestible materials such as eggshells in pellet form (Boarman and Heinrich 1999), we cannot confirm or rule out that ravens lacking eggshell remains in their guts were waterbird nest predators.

## Management implications

Our findings support the strategy of targeting ravens that are foraging in or adjacent to waterbird nesting areas as an aid in removing individuals that are responsible for waterbird nest loss. Targeted lethal removal proved to be a successful strategy based on stomach content analysis, and while our data are limited and provided by opportunistic lethal control, verification of predation by a controlled species on a federally threatened species is novel and important. Continued intensive monitoring of both waterbird nests and raven impacts on these nesting populations will be necessary for managers to determine which predators to control and to provide a better perspective on the overall success of lethal control.

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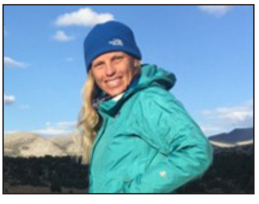

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