A desert tortoise-common raven viable conflict threshold

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Abstract: Since 1966, common raven (Corvus corax; raven) abundance has increased throughout much of this species' Holarctic distribution, fueled by an ever-expanding supply of anthropogenic resource subsidies (e.g., water, food, shelter, and nesting substrate) to ecoregion specific raven population carrying capacities. Consequently, ravens are implicated in declines of both avian and reptilian species of conservation concern, including the California (USA) endangered and federally threatened Mojave desert tortoise (Gopherus agassizii; desert tortoise). While ravens are a natural predator of desert tortoises, the inter-generational stability of desert tortoise populations is expected to be compromised as annual juvenile survival is suppressed below 0.77 through a combination of raven depredation and other sources of mortality. To estimate the extent to which raven depredation suppresses desert tortoise recruitment within the Mojave Desert of California, we collected data from 274 variableradius point counts, 78 desert tortoise decoy stations, and 8 control stations during the spring of 2020. Additionally, we complied a geodatabase of previously active raven nests, observed between 2013 and 2020. Raven density estimates from 4 monitoring areas ranged between 0.63 (eastern most) and 2.44 (western most) raven km⁻² (95% CI: 0.35–1.14 and 1.33–4.48, respectively). We used a Bayesian shared frailty model to estimate the effects of raven density and distance to the nearest previously active raven nest on the annual "survival" of juvenile desert tortoise decoys (75-mm Midline Carapace Length), which we then converted into survival estimates for 0- to 10-year-old desert tortoises by adjusting exposure to reflect natural activity patterns. At the 1.72-km median distance from the nearest previously active raven nest, the estimated annual survival of desert tortoises decreased as raven density increased, ranging among conservation areas from 0.774 (eastern most) to 0.733 (western most). Accordingly, our model predicts that desert tortoise populations exposed to raven densities in excess of 0.89 raven km², at a distance <1.72 km from a previously active raven nest, are not expected to exhibit inter-generational population stability, as excess additive juvenile mortality is expected to exceed the natural history limits of desert tortoise populations. These results also demonstrate that estimates of raven density, distance to the nearest previously active raven nest, and decoy "survival" rates can inform development of a desert tortoise-raven viable conflict threshold.

Key words: bird damage, Centrocercus urophasianus, common raven, Corvus corax, desert tortoise, Gopherus agassizii, greater sage-grouse, resource management, species conflict resolution, subsidized predator

successfully leveraged their intelligence, synanthropic capacity, and generalist nature to increase their abundance and expand their distribution throughout the biosphere (Perry and Dmi'el 1995, Marzluff 2001, Cunningham et al. 2015, Santoro 2017). Evidence suggests that human-subsidized *Corvus* spp. have been a key disrupter of many predator-prey relationships (Loehr 2017, Coates et al. 2020b, Coates et al. 2021, Moldowan 2021) that were once dictated by nonhuman related factors, such as

SEVERAL MEMBERS of the genus Corvus have evolution and abiotic climate conditions that influence seasonal and inter-annual patterns of resource availability. Accordingly, depredation pressure originating from human-subsidized *Corvus* spp. has the potential to be one of the most globally extensive threats to extant Chelonian species, of which at least 41.6% face the near-term prospect of either becoming endangered or going extinct, making Chelonians the most endangered group of vertebrates globally (Stanford et al. 2019). Increased depredation of Chelonians by Corvus spp. is a direct and indirect result of wildlife access to human garbage and compost; ornamental-ponds, groundwater recharge basins, canals, and irrigation systems; industrial agriculture; and importantly, human infrastructure (e.g., transmission towers, bridges, billboards, buildings; Perry and Dmi'el 1995, Cunningham et al. 2015, Xiong et al. 2020). Consequently, substantial impacts to sensitive species have been reported, particularly when anthropogenic sources of food, water, and nesting substrates change the timing and abundance of resource availability within once strongly seasonal ecoregions (Marzluff and Neatherlin 2006, O'Neil et al. 2018, Coates et al. 2020b).

Predator-prey interactions range between viable, even commensal, to inviable conflicts (Abrams 1992, Nevai and Van Gorder 2012, Urban et al. 2019). Inviable conflicts are expected to occur whenever a generalist predator has stable access to anthropogenic food, water, and habitat features (e.g., subsidies)-particularly in ecoregions characterized by strong seasonality and annual shifts in resource availability. In such instances, novel resource access, in time and spaces, facilitates a generalist like the common raven (C. corax; raven) to expand heedless of and beyond pre-subsidized carrying capacity oscillations and thus beyond coevolved pre-subsidized depredation rates, rendering some prey populations inviable (Nevai and Van Gorder 2012, Rominger 2018, Coates et al. 2020a). Viable predator-prey conflicts ensure viable prey populations, which we define as those prey populations that incur predation and background sources of mortality at rates that allow for long-term prey population stability, at the scale of both local and regions populations. Accordingly, depredation pressure from a viable predator-prey conflict is expected only rarely, if ever, and exceeds the vital rate threshold of the prey species, allowing maintenance of a stable demography, which populations of long-lived prey species, such as Chelonians, are predicated upon (Congdon et al. 1993, Gerlach 2008).

Implicit in this definition of a viable population is the notion that long-term stability in population trends can be increased to ≥ 1 by many combinations of life-stage specific vital rate targets. Nevertheless, adult desert tortoise (*Gopherus agassizii*) density has declined by ~90% in 4 of 5 desert tortoise recovery units during the last 3 desert tortoise generations (~90 years; Berry et al. 2021). Adult density is

below the 3.9 tortoise km⁻² viable tortoise population threshold for mate encounters within desert tortoise habitats in the Mojave Desert of California, USA (Doak et al. 1994, Allison and McLuckie 2018). The Western Mojave Recovery Unit exhibits the lowest proportion of juvenile (~40–180-mm Midline Carapace Length [MCL] or 0- to 18-20-year-old) observations to adult (>180 and >18-20-year-old) observations of 4 recovery units where 2-pass sampling was implemented (Allison and McLuckie 2018). Current threats to the vital rates of individuals thus threaten population stability (Darst et al. 2013), and budgetary realities will drive as well as limit the selection of vital rate targets appropriate for desert tortoise recovery. Consequently, attainable vital rate combinations suitable for recovering the desert tortoise within the Mojave Desert of California will be dictated by current threat realities and critically low (<3.9 tortoise km⁻²) adult desert tortoise densities.

Ravens have been expanding in the Warm Desert Ecoregions since at least 1966 (Harju et al. 2021), which is believed to have contributed substantially to critically low (<3.9 tortoise km⁻²) and declining adult desert tortoise densities observed in the Mojave Desert of California, particularly the Western Mojave (Allison and McLuckie 2018, Berry and Murphy 2019). Specifically, ravens seem to exhibit the greatest amount of pressure on 0- to 10-year-old tortoises (~40–139-mm MCL), which has the potential to skew demographic rates toward older, larger individuals and reduces or halts recruitment (Kristan and Boarman 2003, Nagy et al. 2015*a*, Daly et al. 2019).

Depredation from breeding and non-breeding ravens was initially suspected as a contributing cause of depressed juvenile desert tortoise vital rates at the Desert Tortoise Research Natural Area in the 1980s (K. H. Berry, U.S. Bureau of Land Management [BLM], unpublished report), prompting the BLM, in partnership with other interest groups as well as state and federal agencies, to begin implementation of an "Integrated Raven Control Program" (BLM 1989). This program, however, was halted in 1989 by a temporary restraining order due to public concerns that lethal raven management was being implemented without fully understanding all possible nonlethal alternatives (BLM 1990). Successive efforts to manage raven abundance and range expansions in the Mojave

and Colorado deserts of California were likewise halted due to a range of legal and public concerns (U.S. Fish and Wildlife Service [US-FWS] 2008). In 2008, however, the USFWS, in cooperation with the Desert Managers Group (Palm Springs, California), published the "Environmental Assessment to Implement a Desert Tortoise Recovery Plan Task: Reduce Common Raven Predation on the Desert Tortoise" (US-FWS 2008). The results presented herein are intended to inform the continued implementation of the Environmental Assessment (EA) as well as other monitoring and management programs for a range of agencies and nongovernmental organizations interested in aiding efforts to reduce the effects of raven depredation on desert tortoise recovery.

Previously, predator-prey conflicts such as those described above have been framed in terms of spillover- or hyper-predation (Kristan and Boarman 2003, Oro et al. 2013, Coates et al. 2020a). However, this approach runs the risk of creating an artificial dichotomy, which serves only to confound management decision making and obscure the most practicable solutions. Increased predation pressure by breeding ravens as an indirect effect of anthropogenic subsidies has been referred to as "hyper-predation" (Smith and Quin 1996, Oro et al. 2013, Coates et al. 2020a). Such effects are typically associated with ravens at relatively low density and near active raven nests. However, non-breeding ravens can also be subsidized by anthropogenic food and water sources and may move into surrounding undeveloped areas and encounter sensitive prey, resulting in "spillover-predation" (Kristan and Boarman 2003), which is typically associated with comparatively higher raven densities.

Although separate studies provide support for both types of predation effects (Bui et al. 2010, Howe et al. 2014, Coates et al. 2020*a*), a study that evaluates both phenomena would be highly informative to strategic management plans aimed at mitigating the effects of predation. Moreover, previous work described the viability of species-conflicts in terms of either hyper- or spillover-predation, but this dichotomy can result in spurious management recommendation when the effects of depredation to desert tortoise (or any other sensitive species) survival rates are not predicated on the breeding status of the raven (or any predator). Accordingly, the threshold we define herein combines the effects of both spillover- (nonbreeder and breeder density) and hyper-predation (distance to nest and intensity of territory defense) and seeks to demonstrate that the 2 concepts are neither independent nor discrete, as previously described (Kristan and Boarman 2003, Coates et al. 2020*a*).

To improve cost efficiency and robustness of the EA monitoring and adaptive management program, we explore whether a desert tortoiseraven viable conflict threshold exists. Such a threshold would enable depredation pressure to be estimated independently from the number of juvenile tortoises on the landscape (population size), the number of juveniles active (proportion of mean annual activity), and mean desert tortoise carcass persistence (Corvus Ecological Consulting, unpublished report) that confounded the initial adaptive management monitoring approach. Freedom from such factors is expected to improve the accuracy and efficiency of efforts to implement the EA, thus conserving the desert tortoise, raven, and Mojave Desert ecosystem. A desert tortoise-raven conflict threshold would build on a viable, predator-prey conflict threshold established for greater sage-grouse (Centrocercus urophasianus; sage-grouse), where raven densities >0.4 were linked to substantial impacts to sagegrouse nest survival, resulting in nest survival below average rates (Coates et al. 2020a).

Desert tortoise-raven viable conflict threshold development involved 6 primary objectives that were conducted within California's Mojave Desert of the western United States. Specifically, we: (1) reviewed historical and stable in silico population vitality rates of 0- to 10-year-old desert tortoises to define a survival probability threshold; (2) estimated raven densities throughout 4 conservation areas during the spring of 2020; (3) complied the location of all previously cataloged raven nests observed between March 2013 and July 2020; (4) estimated the effects of distance to nearest raven nest, raven density, and an interaction factor on desert tortoise survival by using 3-dimensionally printed desert tortoise decoys; (5) developed a desert tortoise-raven viable conflict threshold with respect to raven densities, distance to the nearest previously occupied raven nest, and their interactions; and (6) a derived annual survival target for 0- to 10-year-old des-



Figure 1. Mojave Desert as well as Mojave desert tortoise (*Gopherus agassizii*; desert tortoise) conservation areas in California's Mojave Desert (Kern, Los Angeles, and San Bernardino counties, California, USA). Graduated, color ramp symbols reflect the count of common ravens (*Corvus corax*; ravens) observed at individual point count locations during the spring of 2020. We calculated estimates of mean raven density and decoy derived estimates of desert tortoise survival from data collected in each conservation area during the spring of 2020. Raven nest observations, however, were made in each conservation area between March 2013 and June 2020.

ert tortoises. If a density- or distance-dependent depredation relationship and threshold similar to that established for sage-grouse (Coates et al. 2020*a*) applies to desert tortoises between the ages of 0 and 10 years old, such a value could be a useful tool for prioritizing efforts to manage the abundance of both subsidies and ravens. Such a threshold could also be used to effectively target habitat restoration efforts that enable the desert tortoise to use crypsis most effectively in times and locations where raven density are below a suggested threshold (Nafus et al. 2015, 2017).

Study area

We collected for this study in creosote bush (*Larrea tridentata*) scrub and Joshua tree (*Yucca brevifolia* and *Y. jaegeriana*) woodland ecosystems, found between approximately 300 and 2,000 m above mean sea level, within the Mo-

jave Desert of California (Kern, Los Angeles, and San Bernardino counties, California). These areas consist of sloping bajadas to generally flat valley bottoms as well as steep tortoise habitats arranged around the base of interspersed mountain ranges. Our study areas encompass approximately 8,660 km⁻², including the Fremont-Kramer Critical Habitat Unit (CHU), Fenner CHU, Ivanpah CHU, Mojave National Preserve, Ord-Rodman CHU, and Superior-Cronese CHU conservation areas (Figure 1). Most of these lands, with the exception of private in holdings, are managed for multiple uses by the BLM and for the public's enjoyment by the U.S. National Park Service.

Point count estimates of mean raven density and decoy-derived estimates of tortoise survival were calculated from data collected in each conservation area between March 15 and July 1, 2020. Spring of 2020 produced annual and perennial flowering displays consistent with a "superbloom," due to above-average precipitation received between October 2019 and March 2020. March through July monthly average temperatures expected in Barstow, California, near the geographic center of our study areas, range from a March low of approximately 6°C to a July high of approximately 39°C, which annually form 4 regular seasons. Sampling was conducted outside of wilderness areas, in compliance with all wilderness protections and prohibitions related to the use of camera traps in wilderness. All applicable permits were acquired for work on U.S. National Park Service administered lands. Additionally, the location of active raven nests were documented between March 2013 and July 2020.

Methods Distance to previously active common raven nests

We recorded the location of large predatory bird nests, including ravens, red-tailed hawks (Buteo jamaicensis), and golden eagles (Aquila chrysaetos), during raven breeding seasons between March 2013 and July 2020. Nest searches were conducted during daylight hours by driving established open routes and by walking to point counts, camera-station points, or previously identified raven nests, and consisted of scanning suitable raven nesting substrates with and without binoculars. Nests were also found by watching raven behavior from a vantage point that enabled the use of either a rangefinder or compass and map to mark possible nests in Joshua Tree Woodlands. Nest surveys were conducted within desert tortoise critical habitat and other tortoise conservation areas. Searches were conducted by 1- or 2-person crews (preference determined by consultant). Vehicle surveys conducted on dirt and paved roads never exceeded 32 km/hour or the posted speed limit, respectively. Once a potential raven nest was identified, a spotting scope was used to inspect the nest in question and nest data were recorded.

The location of all raven nests observed as active between March 2013 and July 2020 were used to estimate desert tortoise decoy "survival" as a function of distance to the nearest raven nest. Using locations for all years compensated for imperfect raven nest detection, particularly within a single season, which resulted from raven management program efficiency measures (e.g., focusing monitoring efforts first on anthropogenic nest substrates). Moreover, spring of 2020 was a boom-year for raven nest occupancy due to abundant precipitation received during November and December 2019 as well as January and February 2020.

Common raven density estimation

We conducted 274 variable-radius point counts (hereafter point counts) following published methodology described in Ralph et al. (1995) and Brussee et al. (2021). Point counts consisted of randomly placed 10-minute surveys for all visible raven clusters throughout the 4 separate areas. We also arranged point counts with respect to a minimum 2 km spacing to avoid overlapping survey areas. Moreover, observations were truncated to a maximum distance of 2 km within package "distance" in "Program R," using the truncation argument and were also binned by the following distances: 0.0, 0.25, 0.5, 0.75, 1, 1.25, 1.5, 1.75, and 2 km. The best fitting model was then tested with a Cramer-von Mises tests, to ensure goodness of fit between the observed and modeled values.

Point counts were integrated into nest location surveys as well as nest phenology monitoring routines. Point counts could be moved ≤10 m from the exact location of the randomly assigned Universal Transverse Mercator northing and easting, to a location with a maximally unobstructed view of the landscape and sky. Using a 10-m buffer helped ensure that large objects (e.g., tree, shrub, cliff) did not block a substantial portion of the view. If the view of the sky, however, was still blocked by >40% after exhausting all potential alternative vantage points, then surveys were still conducted, but a record of percent obstruction was noted. Cluster counts and corresponding distances were then converted to mean density estimates as well as upper 95% confidence intervals for each conservation area, using a hazard rate distance estimator of detection probability in "Program R" version 4.0.3 (R Development Core Team 2018) with package "distance" (Buckland et al. 2015, Miller et al. 2019).

Surveys were performed in suitable desert tortoise habitat as well as adjacent areas contained within each conservation area between sunrise and 1400 hours from April 1 to May 19, 2020, which coincides with southern California's raven breeding season. We did not conduct surveys when wind speed exceeded 40 km h⁻¹ or when precipitation (e.g., rain, sleet, snow, hail) limited the observer's ability to detect ravens out to 2 km.

Desert tortoise decoy and control "survival" probability

During the 2020 raven nesting season, we placed 19–20 desert tortoise decoy stations, 0–2 novel-object stations, and 0–1 camera-trap only station 250 m (\leq 10 m) due north of randomly placed point count locations throughout 4 separate conservation areas (78 total decoy stations, 5 novel-object bait-stations, and 2 camera-only stations). Yet, only 66 of the decoy stations were used in this analysis because in 12 instances, the closest nest to the randomly placed decoy station was addled using food-grade oil in 2020 (Shields et al. 2019) and we wanted to remove as much of this effect as possible.

Each desert tortoise decoy station consisted of a 75-mm MCL 3-dimensionally printed Techno-Tortoise TM (Hardshell Labs, Inc., Joshua Tree, California); decoy anchoring stake, wired-washer, and monofilament anchor tether; Moultrie D-300 Kit (passive infrared [PIR] triggered camera, SD card, and 8 AA batteries) set with a trigger delay of zero and burst capture of 3 "high" quality still images; and a 48-inch (~121 cm) Poly Step-in fence post, cut to ~54 cm (placing the camera lens 24 cm above the ground, if the bottom of the step-in is flush with the ground) and painted with "satin oregano" spray paint. Two zip ties were also used to attach the camera to the post, plus a small wooden block placed between the camera and the post to ensure that the center of the field of view remains perpendicular to the step-in fence post. Novel-object bait-stations differed only in that the desert tortoise decoy was replaced with a novel object (e.g., rectangular box, painted with irregular shapes in a color palette matching that of desert tortoises).

We deployed bait stations between April 6 and 17 and retrieved them between April 22 and May 13, 2020. We sought to place the desert tortoise decoy in open areas or under the edges of shrub driplines, ≤ 10 m of the assigned point. We then located an area approximately 5 m (±2 m) south of the anchor spike to stake the pre-mounted PIR camera, making sure that this location had an unobscured view of the desert tortoise decoy location. To obscure the camera from ravens as well as humans, we placed the camera against a backdrop of shrub canopy or underneath the canopy of rigid perennials (e.g., cactus, yucca, and ephedra) so that it blended with the surroundings and was entirely obscured from aerial predators. This also minimized direct solar insolation, preventing overheating of the camera and batteries. In the final step, we mounted the desert tortoise decoy in place and ensured that footprints and other signs of their presence were erased.

Mojave desert tortoise-common raven threshold analysis

We carried out a Bayesian shared frailty model (Halstead et al. 2012) to estimate the effects of raven density and distance to the nearest previously active raven nest on the probability of desert tortoise decoy survival. We then corrected decoy "survival" for use as a proxy of annual survival for 0- to 10-year-old desert tortoises inhabiting the Mojave habitat within California. Images containing ravens were split into 2 12-hour sampling periods. Period I extended from 0001-1200 hours and period II from 1201–2400 hours. In order of collection time, we then converted image results into a binary response variable, where the decoy was assumed to be "depredated" if a raven was recorded within a 1.5-m radius, hemispherical area centered on the decoy – or the novel object in the case of control stations. All other images containing ravens were accordingly scored as "survived." In this manner, each period was scored as "survived" or "depredated." These binary trials were then used to estimate survival of actual juvenile (0- to 10-year-old) desert tortoises under the assumption that predation will occur on all occasions when a raven is within 1.5 m of a juvenile desert tortoise. We think this is a conservative assumption because an actual juvenile desert tortoise has no defense mechanisms against raven depredation once seen, and then approached to within 1.5 m. We then generated at least 1 encounter history for each desert tortoise decoy station (n = 66) and additional encounter histories (n = 11) for desert tortoise decoys that were attacked 1 or more times during the study period. We used repeated measures on the assumption that different ravens were attacking the same decoy.

We think this assumption is reasonable because only 1 attack was permissible during each 12hour period. Moreover, multiple tortoise shells have been found below a single raven nest, meaning that a single raven or pair of ravens can depredate multiple desert tortoises emerging from a nest or nearby shelter.

Encounter histories were constructed using the date of deployment or reset date following an attack, the date the desert tortoise decoy was last observed in a state of non-disturbance (i.e., no depredation occurred up to that point), and the date the desert tortoise decoy was "depredated." We adopted a daily encounter history and estimated the unit hazard (*UH*) of each desert tortoise decoy as:

$$UH_{dst} = exp(\alpha + \beta_{dist} * X_{dist} + \beta_{dens} * X_{dens} + (1))$$

$$\beta_{int} * X_{dist} * X_{dens} + \gamma_s),$$

$$\alpha \sim Uniform(-20,0), \qquad (2)$$

$$\beta_{dist} \sim Normal(0, 100),$$
 (3)

$$\beta_{dens} \sim Normal(0, 100),$$
 (4)

$$\beta_{int} \sim Normal(0, 100),$$
 (5)

$$\gamma_s \sim Normal(0, \sigma_\gamma^2), \tag{6}$$

$$\sigma_{\gamma} \sim Uniform(0, 10), \qquad (7$$

where subscripts *d*, *s*, and *t* reference day of study, desert tortoise decoy bait station, and trial, respectively. Parameters estimated from the model included the baseline log-hazard (α), random effect for desert tortoise decoy (γ), and log hazard ratios for distance to the nearest previously active raven nest (β_{dist}), raven density (β_{dens}), and an interaction between distance and density (β_{int}) variables. The random effect of desert tortoise decoy station was treated as a nuisance parameter and its inclusion was meant to account for any within-individual correlations that may have existed in the data.

The cumulative hazard (*CH*) and probability of desert tortoise survival (*S*) were derived using the equations:

$$CH_t = \sum_{1}^{D_t} UH_{1:d,t},$$
 (8)

$$S_t = e^{-CH_t}, (9)$$

where *D* represents the duration of the exposure period for each trial (*t*).

The discrete outcome of each trial (y_t) , coded 1

("survived") or 0 ("depredated"), served as the response variable and S_t the probability of success:

$$y_t \sim Bernoulli(S_t)$$
 (10)

To derive posterior estimates of annual survival for actual 0- to 10-year-old desert tortoises using daily encounter histories constructed from desert tortoise decoy stations, we multiplied the daily unit hazard by the total number of exposure days in a calendar year (E). E is a function of 2 types of temporal exposure: (1) the total number of calendar days spent above ground in any given year (T_{days}) , and (2) the proportion of diurnal hours in a single day spent above ground (P_{day}). For the total number of calendar days that a typical desert tortoise spends above ground, we used a value of 168 (Agha et al. 2015). Had we modeled survival from actual desert tortoises, the parameter representing daily exposure (P_{day}) would have been accounted for as an intrinsic property of the data. However, the desert tortoise decoys do not employ the behavioral mechanisms of actual desert tortoises and incur the full value of a daily exposure rate (i.e., $P_{day} = 1$). To correct for behavioral mechanisms associated with thermal regulation and predator avoidance (e.g., use of burrows) we adjusted the daily exposure rate to 0.19, which is the mean estimate for the proportion of daily above-ground activity presented in Daly et al. (2019). Based on correction factors, the full equation for the cumulative hazard of actual 0- to 10-year-old desert tortoise (CH_{IT}) becomes:

$$CH_{JT} = UH * T_{days} * P_{day}, \tag{11}$$

and the annual survival probability, which accounts for other sources of non-raven related mortality ($O_{mortality} = 0.152$; McGovern et al. 2020), becomes:

$$S_{JT} = \exp(-CH_{JT}) - O_{mortality}.$$
 (12)

A modeling assumption stemming from Equations 11–12 is the alignment of raven breeding season phenology (Kristan and Boarman 2007; when nest initiation is possible = 70–170 days since January 1) and above ground activity periods for desert tortoise (Berry et al. 2016; when desert tortoise activity is possible = 45–319 days since January 1). That assumption is supported by the number of days that a breeding pair of ravens and their offspring can Figure 2. Expected survival probability (see Equation 12) for 0- 10-year-old Mojave desert tortoises (Gopherus agassizii; desert tortoise) exposed to common raven (Corvus corax; raven) depredation for a calendar year, at various raven densities (raven km⁻²) and distances (km) to the nearest active or previously active raven nest. The red vector bisects the survival plane into a viable (behind) and inviable (in front) conflict regions, where different combinations of raven density and distance to the nearest nest dictate alternative management strategies to reach the target juvenile desert tortoise survival rate (0.77). The gray point depicts the target density at the 1.72-km median distance to the nearest raven nest observed between March 2013 and July 2020 in California's Mojave Desert (Kern, Los Angeles, and San Bernardino counties, California, USA). Point count estimates of mean raven density and decoy derived estimates of tortoise survival were calculated from data collected in each conservation area during the spring of 2020.

associate with a nest within the Mojave Desert. Following nest initiation, the breeding season life history of ravens includes periods of incubation (20-25 days; Cornell Lab of Ornithology 2019), pre-fledging (28–50 days; Cornell Lab of Ornithology 2019), post-fledging initial natal dispersal (\bar{x} = 46 days; Webb et al. 2009), and post-fledging final natal dispersal (\bar{x} = 21 days following initial dispersal; Webb et al. 2009). The cumulative time associated with a nest location for a breeding pair/family unit under maximal values could theoretically extend out to the second week of November (312 days since January 1). A more conservative estimate based on mean initiation, incubation, and prefledging dates would place final nest associations around the last week of August (239 days since January 1). It is therefore our position that the model described reasonably reflects seasonality and ecology of both ravens and desert tortoises within the Mojave Desert.

To relate desert tortoise annual survival to observed raven density and distance to nearest previously active raven nest, prediction vectors and posterior parameter estimates were combined within the *UH* function used in Equation 11. In the case of the prediction vector for distance (natural log of m), we restricted the maximum value to the upper quartile of the observed data (3.33 km), which was based on initial plots that revealed uninformative survival estimates beyond that distance.

Historical life-stage specific annual survival probabilities observed from desert tortoise populations near Goffs, California, and throughout the western Mojave during the late 1970s to mid-1980s (Turner et al. 1987b, Doak et al. 1994) were used to set a maximum and minimum pre-raven expansion survival probability. Survival rates designed to create a stable in silico desert tortoise populations (Table 7 in Peaden 2017) were then compared with reports of historical survival by running 4 10-year simulations to calculate the number of recruits expected year⁻¹ 1,000 yearlings⁻¹ (year 0) exposed to a constant mean survival probability from individual studies or the variable survival probability mean calculated from these 3 studies (supplemental materials Table 1 and Figure 2). On average, 75.06 tortoise recruits year⁻¹ 1,000 yearlings⁻¹ (32.1–117.1 tortoise recruits year⁻¹ 1,000 yearlings⁻¹) are expected to survive from 0-10 years when exposed to age-class specific mean and constant mean vital rates reported in supplemental material Table 1. The mean number of tortoise recruits year⁻¹ 1,000 yearlings⁻¹ expected from the average vital rate estimated by Doak et al. (1994) and from averaging all life-stage specific rates equaled 75.2 and 75.9, respectively. The mean survival probability of 0.772 (Doak et al. 1994) is nearest the grand average among all estimates (even when average life-stage specific results are excluded from the calculation of the mean) and was thus selected (≈ 0.77) as a survival probability threshold for age-classes 0–10. More importantly, the mean survival rate of 0.709 for 0- to 10-year-old desert tortoises reported in Peaden (2017) requires immature 2 through adult 2 (44–139-mm MCL; Turner et al. 1987a) and beyond to experience survival rates in excess of those reported in either Doak et al. (1994) or Turner et al. (1987b), which is very unlikely given current distribution of threats on the landscape causing an ongoing demographic and density collapse with-



Table 1. Yearling through stage-1 immature (0- to 10-year-old) Mojave desert tortoise (*Gopherus agassizii*; desert tortoise) annual survival estimates for calendar year 2020 (see equation 12) by conservation areas and thus raven density, at 500 m and the 1.72-km median distance between random points and the nearest previously active common raven (*Corvus corax*; raven) nest. Nest observations were made in California's Mojave Desert between 2013 and 2020 (Kern, Los Angeles, and San Bernardino counties, California, USA). Point count estimates of mean raven density and decoy derived estimates of tortoise survival were calculated from data collected in each conservation area during the spring of 2020. CHU = Critical Habitat Unit.

Conservation area	Annual survival estimates for 0- to 10-year-old tortoises at 500 m	Annual survival estimates for 0- 10-year-old tortoises at 1.72 km	Estimated 2020 mean common raven density (ravens km ⁻²)	2020 mean common raven density-threshold (ravens km ⁻²)
Fenner CHU, Ivanpah CHU, Mojave National Preserve	0.752	0.774	0.63	-0.26
Ord-Rodman CHU	0.705	0.767	1.08	0.19
Superior-Cronese CHU	0.636	0.758	1.56	0.67
Fremont-Kramer CHU	0.430	0.733	2.44	1.55
Average	0.631	0.758	1.43	0.54

in tortoise populations throughout California (Allison and McLuckie 2018).

The 0- to 10-year-old (44-139-mm MCL; Turner et al. 1987a) desert tortoise age-size class represents the life-stage when tortoises have been reported as vulnerable to raven predation (Hazard et al. 2015, Nagy et al. 2015b). While desert tortoises of all sizes appear to be exposed to some level of raven depredation risk (Woodman et al. 2013), we assumed raven depredation of late sub-adult and adult age-size classes (11- to >80-year-old or 140 to >240-mm MCL) was negligible. That assumption could increase the conservative nature of model predictions should actual risk faced by extant desert tortoise populations exceed expectations. Using the survival probability threshold to identify a desert tortoise-raven viable conflict threshold was problematic in that multiple distance-density combinations produced similar survival estimates when rounded to the nearest thousandth. To overcome this feature, we restricted the initial subset to the distance value nearest the observed median for our study area (1.72 km). We chose to use the median over the mean due to the positive-skew of our distance variable and the higher likelihood of juvenile desert tortoises encountering a raven nest at closer distances. The resulting distance-density combination represented our desert tortoise-raven viable conflict threshold. For managers that may, nevertheless, only be able to control for a single raven metric (i.e., distance or density), we provide the full table of combinatorial survival estimates and highlight those that meet the viable conflict threshold.

All analyses were run using program JAGS 4.3 (Plummer 2003) and program R version 4.0 (R Development Core Team 2018). We ran the model for 100,000 iterations using 3 independent chains and discarded the initial 70,000 iterations (burn-in) from each chain. The remaining 30,000 iterations were thinned by a factor of 10, resulting in 3,000 inferential, posterior samples for each parameter. We evaluated chain convergence via visual inspection and requiring an R-hat Gelman statistic <1.2 (Gelman et al. 2014).

Results Distance to previously active common raven nests

We identified 2,477 nest territories and entered them into the previously active nest geodatabase. Of those, 724 territories were previously or consistently occupied by ravens and were used in this analysis. The median distance between the nearest previously active nest and our random decoy and control stations was 1.72 km, when analyzed among all conservation areas.

Common raven density estimation

Among all conservation areas, ravens were observed at 198 point count surveys (~72%), at an average rate of 1.35 ravens per count (range = 0-29), for a total of 370 ravens observed at 274 counts (Figure 1). These observations were also analyzed as clusters, which resulted in 258 raven cluster observations at 274, raven cluster encounter rate of 0.94, and expected raven cluster size of 1.4. The average observation distance was 952.7 m (SD = 763.6) before and 823.5 m (SD = 621.1) after truncation. Ravens were not observed at 76 points (~28%). Twenty-four points were not reachable due to terrain or landownership and were thus removed from the study. Mean area density and upper 95% confidence interval (CI) estimates ranged from 0.63-2.44 ravens km⁻² (95% CI: 0.35–1.14 and 1.33–4.48, respectively; Table 1) and 0.52–1.35 raven clusters km⁻² (95% CI: 0.29–0.93 and 0.81–2.23, respectively). This estimate was made using a hazardrate key function, and no adjustments, which fit our binned observation well (2-tailed Cramervon Mises tests, P = 0.11135, df = 5). It is notable that the average raven density in the western Mojave Desert, particularly near highway US 395, was approximately 287% higher than that of the Fenner, Ivanpah, Mojave National Preserve conservation area (Figure 1; Table 1).

Desert tortoise decoy and control "survival" probability

Among the 4 conservation areas and all halfday depredation periods (see the "Mojave desert tortoise-common raven threshold analysis" section of the methods), we recorded 21 individual raven depredation events at decoy stations, during 77 depredation trials, with a range of 0-5 predation events per decoy. Ten (~15%) desert tortoise decoy stations accounted for all depredations observed within the study (1 decoy station with 5, 2 stations with 3, 3 stations with 2, 4 stations with 1, and 56 stations with 0 depredations). This resulted in a daily decoy "survival" rate of 0.986 (range = 0.757-0.999). We also recorded a raven ≤1.5 m from 1 novelobject station (1/5), while no ravens were recorded <5 m of any camera-only control (0/3). Consequently, an attraction to the camera-trap correction was not applied to our raw decoy results, and the larger, more conspicuously positioned (always in the open) novel-objects demonstrate that design, color value, and decoy placement all influence the attractiveness of objects used to measure the depredation potential of an aerial predator.

Mojave desert tortoise–common raven threshold analysis

Aided by exposure rates and estimates of background (non-additive) mortality, we estimate that the annual survival probability for 0- to 10-year-old tortoises averaged 0.758 among the 4 conservation areas at the median distance of 1.72 km from all previously active raven nests (range = 0.733–0.774; Table 1). Conversely, this results in an average annual chance of mortality equal to 0.242 among all areas at the median distance of 1.72 km. Therefore, our results suggest maintaining a life history and current threats dictated minimum 0.77 annual survival probability for 0to 10-year-old desert tortoises could involve reducing and maintaining raven densities to at or near 0.89 km⁻² throughout desert tortoise habitat as well as concurrent annual treatments of active raven nests ≤1.72 km from tortoise habitat (Figure 1). Alternatively, an annual survival probability of 0.77 for 0- to 10-year-old desert tortoises could be achieved by increasing the median distance between tortoise habitat and previously occupied nests, as indicated by the red vector bisecting the survival plane. This approach would entail targeted nest exclusion areas, maintained by removing all nests and nesting material upon identification.

Discussion

Our decoy-derived estimates of annual cumulative hazard (CH_{JT}) experience by wild yearling through stage-one immature (~40–139mm MCL or 0- to 10-year-old) desert tortoises $(CH_{JT} = UH * T_{days} * P_{day}; \text{ see Equation 11}) \text{ are con-}$ servative relative to those reported for 20 direct released desert tortoises and 28 indoor as well as 20 outdoor head-started desert tortoises released in Ivanpah Valley, which is located in our study's Fenner, Ivanpah, MNP conservation area (Daly et al. 2019). In March of 2016 (2008 EA Phase I), the MCL averaged 48.8 mm (range = 44.7–52.8) for direct release desert tortoises, 78.2 mm (range 54.6-87.1) for indoor headstarted desert tortoises, and 50.6 mm (range 45.4-55.7) for outdoor head-started desert tortoises, which closely approximates the 75-mm MCL desert tortoise decoy used in this study. For context, free-living desert tortoises hatched in the Mojave Desert take approximately 7 and 10 years, respectively, to reach an MCL of 110 mm or 139 (Turner et al. 1987a, Germano 1993,

Medica et al. 2012, Nagy et al. 2015b).

By October 27, 2016, 18 (~0.26) of the 68 desert tortoises tracked as part of Daly et al. (2019) were depredated, apparently by a single nesting pair of ravens. Our decoy-derived estimate of cumulative hazard for actual, 0- to 10-yearold desert tortoises (CH_{JT} ; see Equation 11) for Fenner, Ivanpah, MNP conservation area is 0.079, at the 1.3-km mean distance between an active raven nest and all release points reported in Daly et al. (2019) and at the 2020 raven density estimate of 0.63 ravens km^{-2,} clearly demonstrating that our derived estimate of annual mortality due to raven depredation only (CH_{IT}) is more than 3 times less than that reported in Daly et al. (2019). This discrepancy is partially explained by the release of approximately 0.94 (64 of 68) of these desert tortoises <1.2 km from an active and undisturbed raven nest, while ≥0.5% of our decoys were placed ≥1.72 km (median distance) from a previously active nest. Moreover, approximately 0.71 of the desert tortoises monitored as part of Daly et al. (2019) were released during the beginning of the local raven nesting season, which amplified the negative impact of initial post-release movements. As such, it appears that Daly et al. (2019) describes a worst-case scenario, while our estimate can be viewed as a conservative estimate.

Our range of decoy-derived estimate of cumulative hazard includes the estimate reported in Kristan and Boarman (2003), who monitored 100 62-mm styrofoam desert tortoise decoys between March 27 and May 25, 2000 throughout the western portion of Edwards Air Force Base, approximately 5 km west of this study's Fremont-Kramer Conservation Area. After 4 days of exposure during staggered trials, 29 (0.29) styrofoam decoys had been attacked by ravens. Our decoy derived estimates of cumulative hazard range approximately 0.05–0.63 at 3.33 and 0.00 km from a previously active nest, respectively. It is likely that denser raven populations during our 2020 study combined with a more realistic decoy that has caused our estimate of cumulative hazard to exceed that reported for raw results in Kristan and Boarman (2003).

Finally, our annual raven depredation estimates are conservative to the 0.72 (2007) and 0.43 (2004) annual raven depredation rates reported in Nagy et al. (2015*a*). Consequently, we expect our estimates of raven mortality risk to

be conservative to actual risk experienced by wild desert tortoises, but accurate and sensitive enough to be useful—particularly because the effects of conservation on ravens and tortoises will be monitored closely each future year.

Congruence between our decoy-derived estimates of juvenile desert tortoise annual survival probability and those previously reported for live tortoises and closed-cell extruded polystyrene foam decoys suggests that our 3-dimensionally printed tortoise decoys are indeed a useful proxy for measuring raven depredation risk to juvenile desert tortoises, and possibly other Chelonian species experiencing, or in the future likely to experience, unsustainably low annual survival due to a human-subsidized avian predator (Fincham and Lambrechts 2014). It is thus also reasonable to suggest from our results that tortoise populations experience the synergistic effects of hyper- and spilloverpredation as a result of human-subsidized raven abundance in exurban and remote areas during the raven breeding season. Therefore, desert tortoise juveniles hatched in habitats occupied by >0.89 raven km⁻² or ≤1.72 km of the nearest previously active raven nest may experience mortality in excess of the desert tortoise's annual mortality threshold of 0.23 (Turner et al. 1987b, Doak et al. 1994, Peaden 2017; see the "Mojave desert tortoise-common raven threshold analysis" section in the methods).

Both Kristan and Boarman (2003) and Nagy et al. (2015a) reported data supporting raven depredation as the result of the combined effect of spillover- and hyper-predation (see Figure 3 in Nagy et al. 2015*a* and Figures 2 and 3 in Kristan and Boarman 2003). Results presented in Daly et al. (2019) as well as herein also suggest inviable desert tortoise-raven conflicts occurring in the Mojave Desert of California are most likely the result of a synergy between both spillover- and hyper-predation effects that should not be viewed independently or as discrete categories of depredation risk, at least in the context of risk to desert tortoise vital rates and ultimately population stability as well as species persistence. Furthermore, the synergies between spillover- and hyper-predation are supported as a key driver of inviable conflicts by the observation that raven nest density increases (a proxy for defended territory) from eastern to western regions of the Mojave Desert

of California (Xiong 2020). This positive correlation with an east-west gradient of raven densities reported herein thusly demonstrates that distance to nest (i.e., hyper-predation risk) is influenced by both breeding and non-breeding raven density. Finally, traditional point count estimates of raven density do not and cannot delineate between breeding and non-breeding segments of the raven population, at least as currently designed. As such, this information is prudent to developing the most efficient treatment approaches to humanely and cost-effectively manage species conflicts, particularly those between migratory bird species and species of conservation concern.

Unfortunately, maintaining a stable desert tortoise population with an annual rate of juvenile (>139) desert tortoise mortality equal to either 0.23 or 0.20 (supplemental material Table 1) requires an adult survival rate in excess of 0.92 and 0.90, respectively. Otherwise, survival rates ≤0.91 and 0.89, respectively, result in only 3 43-year-old tortoises year⁻¹ 1,000 yearlings⁻¹, which is below the 4-6 tortoises expected from exposure to life-stage specific and average survival rates reported for a stable desert tortoise population in silico (Peaden 2017; supplemental material Table 2). Expected desert tortoises year⁻¹ 1,000 yearlings⁻¹ was examined at age 43 (≥240 mm MCL), as this is the reported average age of the long-term surviving desert tortoises (Medica et al. 2012). Moreover, desert tortoise habitats currently supporting adult survival rates ≥91 and 89% are likely only to occur in remote tortoise habitats and are likely unrealistic outside of backcountry and wilderness areas when we consider the current threats facing desert tortoise populations in California (e.g., unfenced transportation arteries, intensive offhighway vehicle recreation, and other subsidized predators; Darst et al. 2013, Peaden et al. 2017, Berry and Murphy 2019). Therefore, we estimate that the desert tortoise-raven viable conflict threshold equals 0.89 ravens km⁻² at the median distance of 1.72 km from previously active nests, highlighting the need to manage both hyper- and spillover-predation and their combined effects in tandem to restore viable desert tortoise-raven conflict levels and to restore the ecological stability to the Mojave Desert Ecoregion throughout the Mojave Desert of California.

More importantly, raven abundance in the Warm Deserts Ecoregion was 4.7 times higher in 2018 than in 1966 and increased 110.4% more within tortoise habitat as opposed to areas outside tortoise habitat (Harju et al. 2021), and raven depredation continues to have substantial impacts on the vitality rates of 0- to 10-year-old desert tortoises (Nagy et al. 2015a, Daly et al. 2019). Interestingly, inviable species conflicts may help explain why clearance surveys conducted ~35 km west of our study, during 2003 and 2004 (M. Vaughn, Sundance Biology, Inc. unpublished report) as well as 2019 and 2021 (USFWS, unpublished data) found a combined total of 33 adult tortoises (the smallest was a 227mm MCL female, ~21 to ≥25-year-old) throughout approximately 50 km⁻² (or 0.66 tortoise per km⁻²) of desert tortoise habitat in the westernmost portion of this species' range. This is >3 tortoises per km⁻² below previously suggested adult density threshold for mate encounter rate (USFWS 1994). More broadly, the Western Mojave Recovery Unit has had the smallest ratio of juvenile to adult desert tortoises observed for all recovery units, while portions of the Eastern Mojave Recovery Unit contained in our study experienced the largest declines in the relative proportion of juveniles observed (Allison and McLuckie 2018).

Further support for our desert tortoise-raven conflict threshold is provided by a sagegrouse-raven threshold, which has been estimated to equal 0.4 ravens km⁻² (Coates et al. 2020a), suggesting that a threshold between 0.4 and 0.89 ravens km⁻² could be an applicable starting point for other species of conservation concern. It is of note that the lower threshold value established for sage-grouse within the Great Basin corresponded with raven densities that were likewise, comparatively lower (range = 0.00-1.86 ravens) than those established for the Mojave Desert Ecoregion. This suggests that demographic rates of sensitive prey species and abundance estimates of raven populations must be jointly considered when establishing novel conflict thresholds. Additionally, the threshold established in Coates et al. (2020a) was not developed in relation to overall population stability as carried out here but instead based on densities above and below average nest survival for sage-grouse. Increased survival across other life stages (e.g., chick, juvenile,

and adult) may compensate to some degree for below average nest survival from ravens. Thus, it follows that a higher density threshold will likely result when considering overall population stability rather than average value of a single life stage. Nevertheless, continued research to develop a broadly applicable threshold that meets minimum requirements for a community of sensitive prey species could lead to landscape application of conservation planning relative to inviable predator-prey conflict resolution for entire ecoregions. A tangible benefit of this approach would be enabling managers to develop recovery plans with defensible and definable management targets and intensities. Management targets and intensities would further be selected and evaluated using raven density alone or a combination of raven density and distance to known raven nests, thus lending to a tiered management system, one that leverages uncertainty from statistical models to inform an adaptive management process as well as a geospatial definition of predation risk from both hyper- and spillover-predation (Dettenmaier et al. 2021).

We can thus deduce that at a current density of 2.44 ravens km⁻², a majority of the Fremont-Kramer desert tortoise Critical Habitat Unit and indeed much of the extreme West Mojave Desert is expected to have supported inadequate recruitment during the last 20 years due solely to raven depredation (Doak et al. 1994, Kristan and Boarman 2003, Peaden 2017). It is, however, understood that many factors contributed to the decline of desert tortoise viability in the Western Mojave Desert, but our model suggests that in the theoretical absence of these other sources of mortality, raven depredation alone could stifle recruitment. Furthermore, at a density of 0.63 ravens km⁻², desert tortoises inhabiting the Fenner and Ivanpah Critical Habitat Units as well as the Mojave National Preserve, our easternmost and least subsidized conservation area, are expected to experience an annual juvenile desert tortoise survival probability that ranges from 0.745 at the center of frequently active raven territories (nest) to 0.774 at the observed median distance of 1.72 km from the nearest known previously active nest. As a result, only small, isolated portions of the easternmost conservation area >1.72 km from previously active nests are expected to sustain tortoise recruitment, at least during periods and at locations not overwhelmed by drought, road mortality, and invasive species (Doak et al. 1994, Darst et al. 2013, Peaden et al. 2017).

Management implications

Our results suggest that desert tortoise recruitment is insufficient to sustain species viability throughout critical portions of the California Mojave Desert. While we continue to study this situation in the Mojave Desert of California, we are also establishing programs in tortoise habitats located in southern Nevada and Utah, USA, to determine if, and to what degree, inviable desert tortoise–raven conflicts are threatening population level vital rates for 0- to 10-year-old desert tortoises in these habitats as well.

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Supplemental material

Supplemental material can be viewed at https://digitalcommons.usu.edu/hwi/vol15/ iss3/14.

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KERRY L. HOLCOMB is currently a fish and wildlife biologist in the Palm Springs, California U.S.



Fish and Wildlife office. He is interested in restoring and conserving natural ecosystems faced with the myriad threats posed by climate change, fragmentation, and human subsidized predators to species and ecosystem function stability and thus persistence. Specifically, he seeks to

understand the impacts that roads (from interstates to single-tracks) and subsidized predators have on the demography of extant tortoise and turtle populations. He currently leads or advises road mortality and common raven depredation mitigation programs throughout the Mojave desert tortoise's (*Gopherus agassizii*) 4-state distribution (Arizona, California, Nevada, and Utah), where he leverages adaptive management, statistical decision theory, and prioritization strategies to ensure program efficiencies. For fun, he and his wife and daughter recreate in one of California's greatest outdoor spaces.

PETER S. COATES is a research wildlife biologist for the U.S. Geological Survey, Western Ecological



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y western Ecological Research Center. He holds a bachelor's degree in biology from Northerm Illinois University and an M.S. degree in avian sciences from the University of California, Davis. His work focuses on movement and population ecology, resource selection, wildlife monitoring, and predator–prey dynamics with emphases on sage-grouse and sagebrush ecosystems. **TIMOTHY SHIELDS**, after a 35-year career as a desert tortoise conservation researcher, began



work on non-lethal avian management methods to address the threat posed by ravens to tortoises, other wildlife, and agricultural products. Hardshell Labs, his company, uses emerging technology for specific conservation and resource protection cases. Current efforts involve drone and laserbased raven repulsion, remote egg oiling to limit pest bird reproduction, and the use of 3D printed juvenile tortoise models equipped to aversively train ravens that attack them.

WILLIAM I. BOARMAN, Ph.D., founder and owner of Conservation Science Research &



Consulting, and former research wildlife scientist with the U.S. Geological Survey and Bureau of Land Management, has >35 years of experience working in the field, conducting scientific research, and providing technical support to many state and Federal government agencies in the fields of wildlife

ecology and conservation biology. He has authored >40 peer-reviewed publications and >50 technical reports. His expertise is in desert wildlife, and he has performed research on desert tortoise conservation and ecology, common raven biology and management, and terrestrial vertebrate ecology within the Mojave Desert. He has performed and published broad-scaled, extensive evaluations of wildlife threats, management, surveying methodology, and conservation strategies. As director for science at Hardshell Labs, Inc., he is helping to develop and test various emerging technologies for use in wildlife conservation and resource management. The use of aerial drones for oiling bird eggs and 3-D printing of tortoise shells to study and manage raven preda-tion on tortoises are 2 technological approaches that have been field tested and ready for broader application. He and Hardshell Labs are also working on field tests and refining methodologies for the use of multispectral lasers, automated ground-based rovers, and Artificial Intelligence to deter ravens and other avian pests from accessing and damaging endangered species and other valuable resources.