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Original research article

## Factors influencing risk of predation by subsidized predators on juvenile Mojave desert tortoises (*Gopherus agassizii*)

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### ABSTRACT

A persistent lack of juvenile recruitment in populations of the imperiled Mojave desert tortoise (*Gopherus agassizii*) has been attributed to artificially inflated populations of coyotes (*Canis latrans*) and common ravens (*Corvus corax*) in some areas. Subsidized by resources in the form of road-killed prey, movement corridors, or nesting perches provided by ever-expanding road and powerline networks, these “subsidized predators” threaten tortoises and other species thanks to subsidies that help support their populations in areas where they might otherwise have been less abundant. Here, we quantified the risk of predation from these subsidized predators on juvenile Mojave desert tortoises by quantifying attack rates on 3D-printed replicas. We evaluated predation risk as a function of replica size, distance from powerlines, and season—variables that can inform release strategies of head-started and translocated tortoises. We found significantly greater risk of predation from ravens in the spring than in the fall. Replica size did not significantly influence predation risk from ravens or coyotes. Replica distance from a powerline or road also did not significantly influence predation risk, supporting previous studies that have found the risk of predation can persist for up to 1.6 km from raven nesting structures. Our results support recommendations for releasing juvenile head-started and translocated tortoises in the fall and away from areas close to raven nesting structures. Our study provides insight into the interactions of prey and subsidized predators and helps guide management on potential mitigation strategies for minimizing the impacts of subsidized predators on species like the imperiled Mojave desert tortoise.

### 1. Introduction

As global biodiversity declines and recovery efforts are implemented to mitigate loss, managers and conservationists must continually monitor conservation efforts and adapt to changing threats to ensure population viability (Burke, 2015, Germano and Bishop, 2009, Gibbons et al., 2000). As humans continue to encroach on natural areas, some generalist species can adapt to—or capitalize on—habitat changes that offer supplemental resources, potentially increasing in abundance (Goodrich and Buskirk, 1995). If these resource subsidies alter the density and distribution of predators, they can lead to “spillover predation” in which increased

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predation pressure on the surrounding landscape negatively affects populations of prey species (Casini et al., 2012, Schneider, 2001). If these “subsidized predators” are able to harness human-made resources or subsidies to a level that increases their abundance sufficiently (Soulé et al. 1988), they can jeopardize recovery efforts of imperiled species that historically may have served as only secondary prey, if at all (Loehr and Keswick, 2021, O’Neil et al., 2018, Smith and Quin, 1996). In some cases, targeted management action may be needed to control subsidized predators. The effects of predation by subsidized predators can vary spatially and temporally (Daly et al., 2019, Harju et al., 2018, Harju et al., 2022), however, and understanding how and why this predation risk varies can improve management outcomes (Goodrich and Buskirk, 1995).

The common raven (*Corvus corax*, hereafter “raven”) presents a challenge for the management and recovery of many at-risk species in North America, including Mojave desert tortoises (*Gopherus agassizii*, Harju et al., 2022, USFWS, 2011), marbled murrelets (*Brachyramphus marmoratus*, Peery and Henry, 2010), and greater sage-grouse (*Centrocercus urophasianus*, Harju et al., 2018), among others (Loehr and Keswick, 2021, Moldowan, 2023, Rees et al., 2020, Richter and Buhmann, 2021). Though ravens are native to western North America, their population densities have grown exponentially due to their ability to capitalize on food, water, and nesting subsidies associated with human encroachment into ex-urban areas (Boarman, 2003, Harju et al., 2022). In the deserts of western North America, for example, ravens historically had limited access to nesting structures in the sagebrush (*Artemisia tridentata*) and creosote (*Larrea tridentata*) vegetation communities that harbor greater sage-grouse or Mojave desert tortoises and were thus relegated to cliffs, high ledges within washes, and scattered Joshua trees (*Yucca brevifolia*). The placement of electrical transmission lines in these habitats, however, has created elevated structures that ravens use to nest and forage, facilitating their incursion into large, otherwise unfragmented landscapes (Boarman, 2003, Harju et al., 2018). Ravens exert the greatest predation pressures in spring (March–June), when nesting pairs forage around nests to feed their mates and offspring (Kristan and Boarman, 2003, Stiehl, 1985). During this time, ravens spend most of their hunting time within 400 m of the nest, but predation can extend >1 km from the nest (Daly et al., 2019, Sherman, 1993), contributing to landscape-scale predation risk to imperiled species. After nesting, predation risk generally declines as ravens leave nesting areas to forage elsewhere during late summer and fall (Boarman et al., 2006).

Coyotes (*Canis latrans*) are another subsidized predator affecting many at-risk species across North America. Facilitated by the loss of North American wolves (*C. lupus*, *C. rufus*, *C. lycaon*) and by anthropogenic modification of many landscapes, coyotes rapidly spread throughout North America over the last century (Hody and Kays, 2018). Coyotes, like ravens, are proficient at adapting to human-influenced environments and can take advantage of food and water subsidies like landfills or highway carrion (Esque et al., 2010). They have been identified as a potential threat to the recovery of several at-risk species, including the Mojave desert tortoise (USFWS, 2011), pygmy rabbit (*Brachylagus idahoensis*; Crawford et al., 2010), and least tern (*Sterna antillarum*; Atwood and Massey, 1988). Coyotes are highly mobile predators, with roads serving as corridors that facilitate travel through critical habitat for imperiled species or providing food subsidies through roadkill (Esque et al., 2010). In the western US, electrical and transmission lines are often accompanied by service roads (Kohl et al., 2019), causing predation risk from coyotes to vary spatially and temporally. Specifically, predation risk may decrease as distance from such infrastructure increases (Esque et al., 2010). When coyotes are reproducing (March–June), predation risk can also increase near denning areas where coyote pairs care for young (Way et al., 2001).

The Mojave desert tortoise (“desert tortoise”), native to the Desert Southwest of North America, was federally listed as “Threatened” in 1994 (USFWS, 1994) and was listed as “Endangered” by the state of California under the California Endangered Species Act in 2024 (California Natural Diversity Database, 2024). A significant challenge to its recovery has been increased predation by subsidized predators (Berry et al., 2020, Boarman, 2002, US Fish and Wildlife Service, 2011), especially ravens and coyotes. Although desert tortoises comprise a small proportion of the raven’s diet (Camp et al., 1993), the wide-ranging activity areas and increasing abundance of ravens can exert a large demographic impact on local populations of desert tortoises (Moldowan, 2023). Head-starting—the process of raising hatchling tortoises to a size less vulnerable to mortality from predators or harsh environmental conditions—is currently being explored as a recovery tool for desert tortoises (Burke, 2015, US Fish and Wildlife Service, 2011). However, predation by ravens can lead to the loss of up to 72 % of head-started tortoises released in some areas (Nagy et al., 2015a). At least one observation reported a raven nest with >250 juvenile tortoise shells scattered beneath (Woodman and Juarez, 1988). There is little information on the impact of raven predation on juvenile desert tortoises in the eastern Mojave Desert region, where raven populations are lower than those in the western Mojave Desert (Boarman and Kristan, 2006, Holcomb et al., 2021). Coyotes too can impart severe predation pressure on juvenile tortoises, resulting in limited recruitment and hampering tortoise recovery efforts (Esque et al., 2010). Additionally, predation by coyotes on desert tortoises may be exacerbated during drought or by spread of novel diseases (e.g., rabbit hemorrhagic disease, *Lagovirus europaeus*; Asin et al., 2021) that negatively affect rabbits—a preferred coyote prey (Hayward et al., 2023)—causing coyotes to switch to less common prey like desert tortoises (Esque et al., 2010, Lovich et al., 2014, Peterson, 1994).

To evaluate the risk of predation by subsidized predators on juvenile desert tortoises, we examined how attack rate on 3D-replicas varied based on replica size, distance from powerlines (and associated roads), and season of year. Juvenile tortoise survival has been shown to generally increase with size (Candal, 2021, McGovern et al., 2020, Nagy et al., 2015b), as common ravens can kill juveniles up to 90 mm in midline carapace length (MCL) via entry into the carapace or plastron using their bills (McGovern et al., 2020, Nagy et al., 2015b). We thus predicted that attack rate on replicas from ravens would decrease as tortoise size increased. We also predicted that raven attack rate would decrease with distance from powerlines (i.e., potential nesting structures), as predation has been shown to increase with proximity to raven nests and perch structures (Daly et al., 2019). We also predicted that the attack rate from ravens would be greater in the spring (raven nesting season) than the fall (non-nesting season) because ravens hunt and forage intensively around their nesting areas in the spring (Boarman, 2003, Daly et al., 2019). We predicted that the attack rate from coyotes would not change as replica size increased because all size classes of desert tortoises are vulnerable to predation by coyotes (Woodbury and Hardy, 1948). We also predicted that attack rate from coyotes would decrease with distance from the powerline as coyotes may preferentially travel on roads associated with powerlines (Esque et al., 2010). We predicted that attack rate from coyotes would not

differ between the spring and the fall. Though coyotes reproduce in the spring, possibly leading to increased predation risk near denning areas (Way et al., 2001), pups disperse in the fall (Koehler and Hornocker, 1991). Thus, coyotes may pose a year-round predation risk to tortoises. Understanding how risk of raven and coyote predation vary with tortoise size can inform management practices for ideal size at release for head-starting efforts to maximize survival probability. Additionally, knowing how predation risk varies spatially and temporally will help to identify high-priority release sites and optimal release times to boost juvenile recruitment and effectiveness of head-starting outcomes, as well as tailor predator management to protect wild juvenile tortoises.

## 2. Methods

### 2.1. Study Site

We conducted this study in the Mojave National Preserve (MNP), San Bernardino County, California, USA, in the southern portion of the Ivanpah Valley. The study site occurs in the Mojave Desert Tortoise's Eastern Mojave Recovery Unit, where juvenile recruitment has experienced the biggest declines (Allison and McLuckie, 2018, Nussear et al., 2009, USFWS, 2011). The study area is characterized by open flats interspersed by desert washes, with vegetation dominated by creosote, white bursage (*Ambrosia dumosa*), little-leaf ratany (*Krameria erecta*), big galleta (*Pleuraphis rigida*), Mojave yucca (*Yucca shigidera*), and cholla cacti (*Cylindropuntia* sp.; Todd et al., 2016). The area has low densities of wild juvenile tortoises and has served as a release site for head-started tortoises (Allison and McLuckie, 2018, Daly et al., 2019). Post-release monitoring of head-started desert tortoises has revealed occasional high mortality risk from ravens near powerline transmission towers, which ravens use as roosting and nesting substrates and near which they hunt prey to provision their young (Daly et al., 2019). Raven densities in the range of the desert tortoise have increased over the last 50 years, with raven abundance in the eastern Mojave Desert increasing by 1 % per year, with a density of 0.63 ravens/km<sup>2</sup> in 2021 (Boarman and Kristan, 2006, Harju et al., 2022, Holcomb et al., 2021). Three power lines (two Southern California Edison (SCE) 200 kV lines, and one SCE 500 kV line) extend 10 km through our study area and are supported with lattice H-frame towers and lattice horizontal structure towers, respectively. A service road runs below these towers; the road is rarely trafficked by vehicles (<1 per day) but is frequently used by wildlife, including desert tortoises and potential predators like coyotes and badgers (*Taxidea taxus*; pers. obs).

### 2.2. Replicas and camera trials

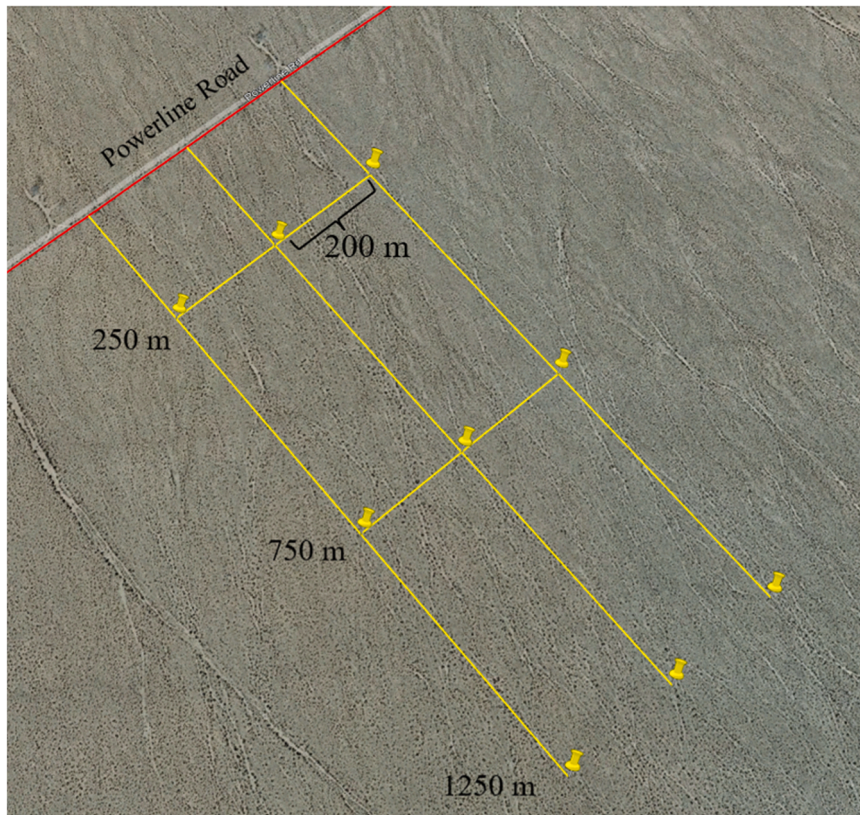
We quantified the risk of predation by ravens and coyotes on juvenile tortoises by measuring attack rates on 3D-printed model replicas ("Techno-Torts"; Hardshell Labs, Inc. Joshua Tree, CA), which were composed of hard plastic and painted to resemble a live tortoise with their legs retracted into their shell (Fig. 1). We compared attack rate as a function of tortoise size (75, 100, or 125 mm MCL), distance from powerline (250, 750, and 1250 m), and season of year (spring vs. fall, corresponding to the raven nesting and non-nesting season, respectively) using wildlife camera arrays. We deployed two arrays per 14-day period, constituting two trials per period. We conducted consecutive trials through the raven nesting (April–June) and non-nesting season (September–October) in 2020 and 2021.

Each array contained nine stations (Fig. 2). At each station, we placed a replica of each size (75, 100, 125 mm) at each of three distances (250, 750, 1250 m) from the powerline, randomly assigning each replica to one of the nine stations corresponding to each replica size-by-distance combination. We anchored the replicas into the ground using thick, clear monofilament line tied to a 20 cm galvanized steel spike driven into the ground and covered with soil.

We measured attack rate at each replica using a Cuddeback H-1453 Wildlife Camera (Cuddeback 2016, De Pere, WI, USA) placed



**Fig. 1.** The three sizes of tortoise replicas: 75 mm, 100 mm, and 125 mm MCL, from left to right used to examine risk to predation by common ravens (*Corvus corax*) and coyotes (*Canis latrans*) on Mojave desert tortoises (*Gopherus agassizii*) during spring and fall of 2020 and 2021 in Mojave National Preserve, California, USA.



**Fig. 2.** Map of one array showing the 9 camera stations, with 3D tortoise replicas placed at three different distances from the powerline for 14-day trials examining risk to predation by common ravens (*Corvus corax*) and coyotes (*Canis latrans*) on Mojave desert tortoises (*Gopherus agassizii*) conducted in spring and fall of 2020 and 2021 in Mojave National Preserve, California, USA. The powerline road is displayed in red.

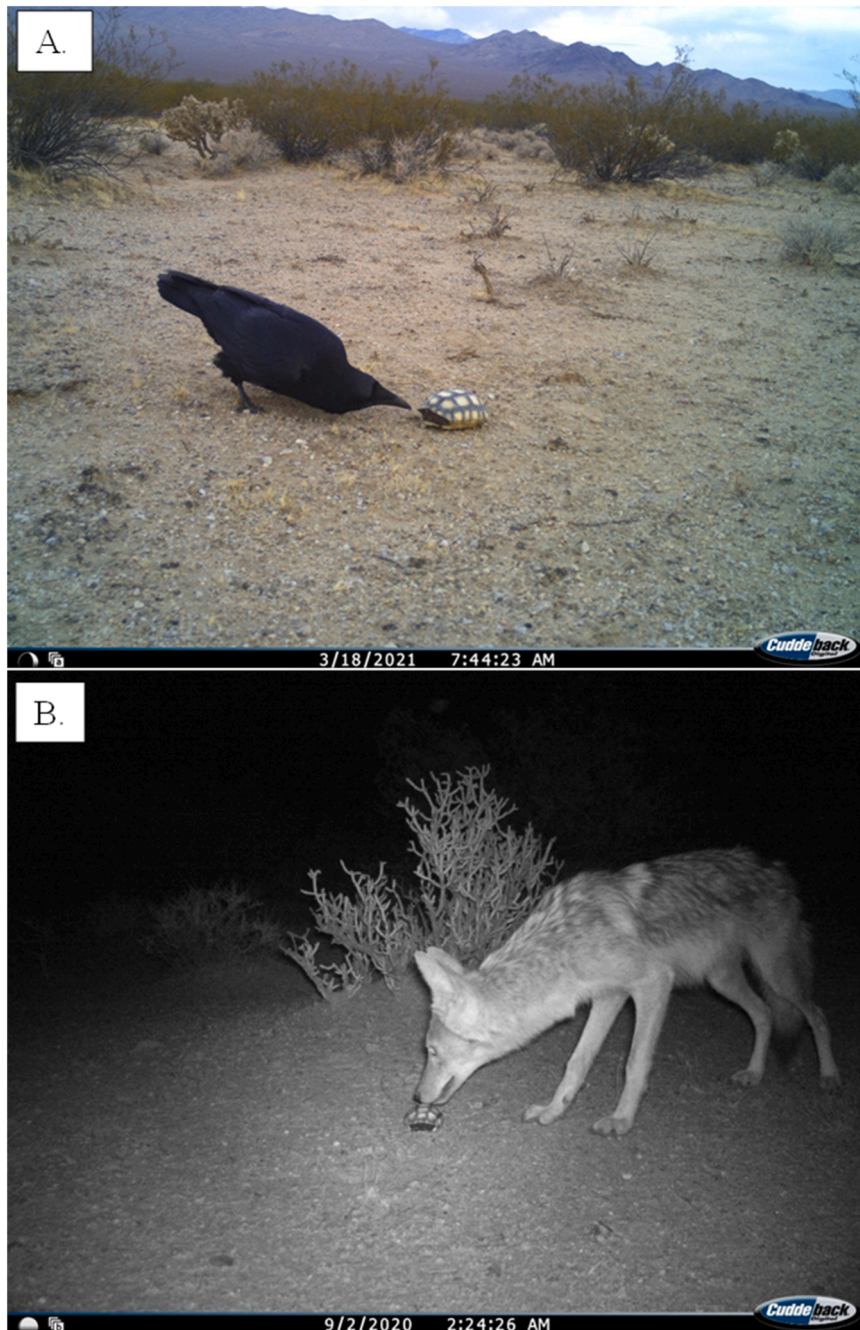
2 m from the replica (Fig. 3). We set the cameras to record a two-photograph burst when triggered, followed by a 30-second video to capture predator interactions with the replica. We mounted the cameras 60 cm aboveground on a 1 m U-Post on the opposite side of a creosote shrub from the power line to help conceal it from ravens scanning the landscape from the powerline, though we did not fully



**Fig. 3.** Trail camera and tortoise replica station used to examine risk to predation by common ravens (*Corvus corax*) and coyotes (*Canis latrans*) on Mojave desert tortoises (*Gopherus agassizii*) during spring and fall of 2020 and 2021 in Mojave National Preserve, California, USA.

camouflage the cameras from ravens as has been done in other studies (Coates et al., 2008). As the replicas were set completely in the open at each location, we felt that concealment of the cameras behind shrubs was sufficient to ensure ravens were approaching due to attraction or curiosity for the replicas rather than the cameras. Within an array, we set stations 200 m apart from one another at each distance from the powerline to ensure independence of observations. We fit 16 arrays along the northwest and southeast sides of the powerline road. We separated arrays by 600 m to ensure independence in observations among arrays.

We recorded the following for each photo or video obtained by cameras: replica size, distance from powerline, image date and time, the potential predator species that appeared in the photographs or videos, and whether the predator “attacked” the replica. We



**Fig. 4.** (A.) Predation attempt by a common raven (*Corvus corax*) on a replica of a Mojave desert tortoise (*Gopherus agassizii*) during spring and fall of 2020 and 2021 in Mojave National Preserve, California, USA. The raven attempts to remove the plastic legs of the 3D-printed plastic tortoise replica. (B.) Predation attempt by a coyote (*Canis latrans*) on a replica of a Mojave desert tortoise during spring and fall of 2020 and 2021 in Mojave National Preserve, California, USA. The coyote sniffs the 3D-printed plastic tortoise replica.

considered any appearance on camera by a raven or coyote as an attempted predation event—i.e., an “attack”—if the animal approached the replica within 1.5 m (Fig. 4), which would likely result in an attack had the animal encountered a live tortoise. Because we could not identify individual ravens or coyotes, any raven or coyote that left the camera frame for 20 min between photos or videos was considered a unique individual. This research was conducted in accordance with permits issued by the U.S. Fish and Wildlife Service (TE-17838A-3), U.S. National Park Service (MOJA-2018-SCI-0016 [under study MOJA-00258]), and California Department of Fish and Wildlife (SC-0011221). No permission from the Institutional Animal Care and Use Committee was necessary for this research.

### 2.3. Statistical analysis

To examine the effects of replica size, distance from the powerline, and season on attack rates on replicas during each 14-d trial, we ran a generalized linear mixed-effects model (GLMM, family = Binomial, link = Logit) using the “lme4” package in R (Bates et al., 2015). We included repeated attacks on replicas as additional counts of attacks if they were separated by at least 20 min as described above. We confirmed that a zero-inflated regression was not needed by testing our data for an inflated number of zeros compared to the predicted value using the “MASS” package (Venables and Ripley, 2002). We built a model set for ravens and coyotes combined, as well as separate model sets for ravens and coyotes. Each model set included a null model as well as univariate models for replica size, distance from the powerline, season, and year (Suppl Table 1). We also built an additive model for replica size, distance from the powerline, and season. We also included a candidate model exploring the potential for an interactive effect between replica size and distance from powerline to examine if location can lead to a preferential selection of replica size. To capture inter-year variability in weather conditions, we considered two models with an interaction between year and season: one with the interaction term only and one that also included size and distance as additive variables. We included “array” as a random effect in each candidate model. We used AIC<sub>c</sub> in the “AICmodAvg” package to identify the most parsimonious model ( $\Delta\text{AIC}_c < 2.0$ , Mazerolle, 2020, Suppl Table 2). We then evaluated directionality of the variables included in the most parsimonious models based on their coefficients, assessing variable significance at  $\alpha=0.05$  (Suppl Table 3). If the null model was within 2  $\Delta\text{AIC}_c$ , we considered the predictors uninformative, though we still interpreted their coefficients.

## 3. Results

Over the course of 44 trials (28 Spring, 16 Fall), we monitored a total of 396 replica stations. A total of 43 replicas were “attacked” a total of 61 times over the course of the study; 26 (42.6 % of attacks, nine in 2020, 17 in 2021) were by ravens, whereas the remaining 35 (57.4 % of attacks, 21 in 2020, 14 in 2021) were by coyotes. Several possible predators of desert tortoises that are not typically considered subsidized predators were captured by cameras over the course of the study, including kit foxes (*Vulpes macrotis*), badgers (*Taxidea taxus*), bobcats (*Lynx rufus*), and red-tailed hawks (*Buteo jamaicensis*). None of these animals were photographed showing any predatory interest toward the replicas. Kit foxes, however, often marked the replica with urine or feces before leaving the frame of the camera and did not damage the replicas. Black-tailed jackrabbits (*Lepus californicus*), one of the most frequently observed species on the cameras, also showed some interest in the replicas, often sniffing them, but never caused damage to the paint or plastic.

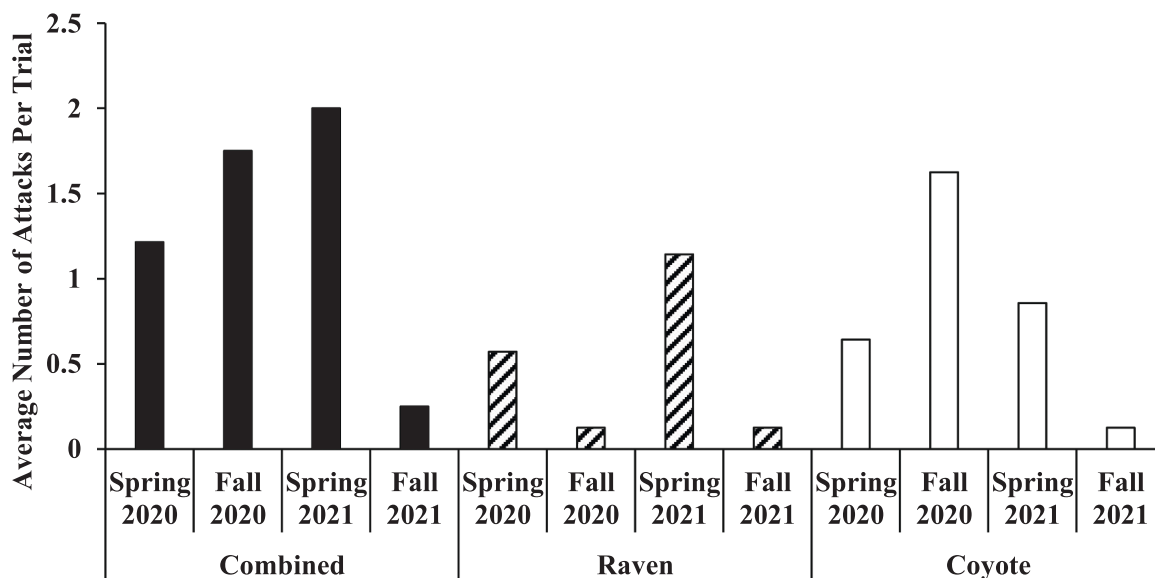


Fig. 5. Average number of attacks per trial for combined predators, common ravens (*Corvus corax*), and coyotes (*Canis latrans*) on 3D-printed plastic tortoise replicas during spring and fall of 2020 and 2021 in Mojave National Preserve, California, USA. The average number of attacks was significantly higher in Spring 2021 than Spring 2020 and Fall of 2020 and 2021 for combined predators.

Attacks occurred on every replica size (75 mm: 26 attacks, 100 mm: 13 attacks, 125 mm: 22 attacks) and at every distance (250 m: 18 attacks, 750 m: 30 attacks, 1250 m: 13 attacks). Attacks occurred both in spring and fall (spring: 43 attacks, fall: 16 attacks).

When considering attacks by both ravens and coyotes combined, the model that included just the year\*season interaction was the most parsimonious model, garnering 78 % of the AICw ( $\beta = 2.92$ ,  $p < 0.01$ , Suppl Table 2, Suppl Table 3), indicating that the change in attack rate between season and year differed in slope, with attack rates being highest in spring of 2021 (Fig. 5). The addition of size and distance to the interactive model did not improve the model fit (Suppl Table 2). Attack rates did not differ significantly based on season alone ( $\beta = 0.15$ ,  $p = 0.67$ , Suppl Table 3). Attack rates also did not differ significantly with tortoise size ( $\beta = -0.01$ ,  $p = 0.33$ ) or distance from the powerline ( $\beta = 0.00$ ,  $p = 0.69$ , Suppl Table 3).

When considering just attacks by ravens, the top model again included an interaction between year and season, suggesting that attack rate was higher in spring of 2021 ( $\beta = 1.64$ ,  $p = 0.31$ , Suppl Table 3), though the difference was not statistically significant. In this case, the top model garnered just 26 % AICw (Suppl Table 2), and several candidate models were within 2  $\Delta$ AIC<sub>c</sub>, reflecting some ambiguity in the most parsimonious model. The addition of size and distance to the year\*season interactive model did not improve the model fit (Suppl Table 2). The model that included just season, however, garnered the third highest AICw at 15 % (Suppl Table 2). The “season only” model indicated that attack rates by ravens were significantly higher in spring compared to fall ( $\beta = 1.94$ ,  $p = 0.03$ , Suppl Table 3). Attack rates by ravens were not significantly associated with tortoise size ( $\beta = -0.02$ ,  $p = 0.11$ ) or distance from the powerline ( $\beta = 0.00$ ,  $p = 0.34$ , Suppl Table 3).

When considering just attacks by coyotes, the top model again included an interaction between year and season and in this case, garnered 85 % AICw (Suppl Table 2). The interaction of year and season was significant, indicating that the change in attack rate between seasons and years differed significantly in slope ( $\beta = 3.45$ ,  $p < 0.01$ , Suppl Table 3, Fig. 5). The addition of size and distance to the interactive model of year and season did not improve the model fit (Suppl Table 2). Attack rates did not differ significantly by tortoise size ( $\beta = 0.00$ ,  $p = 0.89$ ) or distance from the powerline ( $\beta = 0.00$ ,  $p = 0.34$ ), and did not differ by season ( $\beta = -0.35$ ,  $p = 0.39$ , Suppl Table 3).

#### 4. Discussion

Increased predation by subsidized predators represents a significant obstacle in desert tortoise recovery as it reduces population persistence by limiting juvenile recruitment (Boarman, 2003, USFWS, 2011). We aimed to quantify the risk of predation from ravens and coyotes to juvenile desert tortoises and examine how that risk varies with tortoise size, distance from potential raven nesting structures (powerline towers) or coyote travel corridors (powerline service roads), and season to inform future desert tortoise conservation efforts. Combined attack rates from both ravens and coyotes were primarily associated with the interaction of season and year, though attack rates decreased slightly as replica size increased and were higher in the spring compared to fall. We observed a total of 61 attacks on replicas over the course of this study. The overall low visitation rate by predators may have masked any significant patterns of combined predation risk from both predators overall. Additionally, patterns may have been masked due to the differences in raven and coyote foraging strategies, as ravens are flighted, diurnal, visual predators, whereas coyotes are terrestrial, hunt by day and night, and rely on olfaction and visual acuity to hunt (Boarman, 2003, Grinder and Krausman, 2001, Wells, 1978). Fluctuations over the course of the study in the populations of primary prey items of coyotes, such as jackrabbits (*Lepus californicus*), may have also contributed to variation in attack rates on replicas.

Variation in attack rates, indicated by the top model including just an interaction of year and season in all three model sets, was likely due to the severe drought conditions in our study area beginning in the Fall of 2020. During this time, our study area received no precipitation (US Department of Commerce, 2022), leading to extremely harsh conditions experienced by head-started tortoises (Richter et al., 2024) and by the mammal prey preferred by coyotes (Hayward et al., 2023) and consumed heavily as roadkill by ravens in the Ivanpah Valley. Consequently, the greater number of attacks on tortoise replicas in Spring 2021 was likely influenced by a lack of primary prey available for coyotes and ravens compared to Spring and Fall 2020 and Fall of 2021.

We found that risk of predation by ravens was generally greater in spring than fall. Each spring, breeding ravens select nesting sites and spend their time hunting near their nest to feed offspring (Sherman, 1993). Previous studies have shown that predation risk from ravens often decreases in fall as juveniles fledge and adults move away from nesting territories (Daly et al., 2019, Stiehl, 1985). During this time, ravens often join larger flocks and will move away from nesting areas to more productive feeding grounds (Boarman et al., 2006). Ravens are seen occasionally traveling across our study area after the nesting season, but most do not become local residents in the fall, instead migrating to other areas in the Mojave Desert where both adults and juveniles gather at human-made subsidies to forage (Boarman et al., 2006, pers. obs.).

Neither the size of replicas nor their distance from powerlines significantly influenced risk of raven attack in our study. However, attack rates did decrease slightly as replica size increased. Previous research has shown that tortoise size is a driving factor in post-release mortality, and that desert tortoises < 90 mm in carapace length are most vulnerable to raven predation (McGovern et al., 2020, Nagy et al., 2015b). Although size was not a significant predictor of raven attacks on replicas in our study, half of the attacks were on the smallest replicas (75 mm) compared to just 25 % on each of the larger sized replicas (100 and 125 mm). Thus, the size of the replicas that experienced greatest risk of raven attack was the only replica smaller than the 90 mm threshold reported for raven predation on wild juvenile desert tortoises. The distance at which the replica was located from powerlines was also not significantly correlated with attack rates on replicas by ravens, at least over the range of distances we tested. While most of the raven attacks on replicas occurred at 250 m (10 of 26 attacks) and 750 m (12 of 26 attacks), we observed raven attacks on replicas placed as far as 1250 m from the powerline (4 of 26 attacks). Daly et al. (2019) reported predation risk by ravens on released head-started tortoises as extending out as far as 1600 m from raven nesting sites. In the current study, we intentionally selected station locations <1600 m from

the powerline to refine the distance at which raven predation risk extends from the powerline towers where they often nest. Although we observed a low attack rate on replicas, our results suggest that predation risk by ravens extends beyond 1250 m and may indeed extend as far as the 1600 m estimated by [Daly et al. \(2019\)](#).

Over the course of this study, we observed only 26 attacks on our replicas from ravens. The low attack rates by ravens may have been driven by two factors. First, though curious and intelligent ([Merrell, 2012](#)), ravens are visual predators ([Conover et al., 2010](#)). Because the replicas did not move, ravens may not have been enticed to visit the replicas or did not return after learning the replicas were not actual prey. Second, while raven numbers are increasing across the Mojave Desert, the eastern region of Mojave Desert where our study was conducted has not experienced the dramatic increases in raven density and abundance like that seen in the western Mojave Desert ([Boarman and Kristan, 2006](#), [Holcomb et al., 2021](#)). The western region has been subject to more human development than the eastern Mojave and has experienced earlier colonization and growth of raven populations ([Boarman, 2003](#), [Boarman and Kristan, 2006](#)). Additionally, the eastern Mojave does not have the same anthropogenic subsidies to support high densities of ravens year-round, which may have contributed to the low attack rates by ravens in our study. Camera trials conducted in areas of greater raven abundance might reveal a clearer understanding of the patterns of predation risk by ravens to juvenile Mojave desert tortoises.

Attack rates on replicas by coyotes were not associated with replica size, distance from powerline, or season. We did, however, see slightly higher attack rates by coyotes in the fall compared to spring. Coyotes have been shown to exhibit temporal variation in landscape occupancy, with pup dispersal in fall potentially altering predation risk across the landscape ([McClure, 1993](#)), and perhaps accounting for some temporal variation in coyote predation risk in our study. Additionally, although tortoise size can influence survival of juvenile desert tortoises ([McGovern et al., 2020](#), [Nagy et al., 2015b](#)), even the largest of the replicas we tested (125 mm) was within the size of tortoises vulnerable to coyote predation ([Candal, 2021](#), [McGovern et al., 2020](#), [Woodbury and Hardy, 1948](#)). Distance from the powerline was also not significantly correlated with attack rates by coyotes. Intuitively, the powerline towers do not offer coyotes the same nesting and perching resource they offer ravens; however, coyotes do use service roads located near or underneath powerline towers for travel efficiency ([Grubbs and Krausman, 2009](#)), and if the road along the powerline towers at our study site was more heavily trafficked by vehicles, there may be roadkill that could serve as a food subsidy. Coyotes are highly mobile, can have extensive territories up to  $>100 \text{ km}^2$  in the Southwest United States, and are able to cover  $>6 \text{ km}$  in one night ([Grinder and Krausman, 2001](#)). Though coyotes frequently use roads or other linear pathways for travel or to forage on roadkill ([Esque et al., 2010](#), [Grubbs and Krausman, 2009](#)), our replicas were placed  $\geq 250 \text{ m}$  from the road; the absence of olfactory cues to lure coyotes off the pathway and toward replicas likely led to the lack of evidence supporting an effect of distance from the powerlines on attack rate by coyotes.

Though our replicas were not scented to provide olfactory cues to mammalian predators like coyotes, we still observed more attacks on replicas by coyotes than ravens (35 vs. 26 attacks). The results of our camera trials largely mirror findings from concurrent radio-telemetry monitoring of head-started desert tortoises released in the same general area, with greater predation by coyotes than ravens during the study period ([Candal, 2021](#), [McGovern et al., 2020](#), [Richter et al., 2024](#), [Glass et al., 2024](#)). Coyotes, like ravens, are primarily visual predators but also depend on their keen sense of smell while foraging ([Wells, 1978](#)). Future studies that include tortoise-scented replicas may lead to increased visitation and attack frequency, helping elucidate the factors that influence risk of predation to juvenile desert tortoises by coyotes.

Several studies have used 3D-printed replicas to examine predator behavior or to estimate risk of predation to live counterparts. For example, [Tetzlaff et al. \(2020\)](#) examined risk of predation in eastern box turtles (*Terrapene carolina*) using 3D replicas, finding that raccoons (*Procyon lotor*) were the primary predator and that predation risk was most influenced by habitat type. Recently, 3D replicas of animals have been employed to train potential predators to avoid focal species of interest to aid in conservation efforts. Prior to the reintroduction of the endangered Southern Corroboree frog (*Pseudophryne corroboree*), for example, [Umbers et al. \(2020\)](#) conducted serial deployments of 3D clay frog replicas and found that the number of attacks between replica deployments decreased, thereby teaching predators that the 3D replicas, and potentially the live frogs, are not a viable food source. Additionally, replicas like those used in our study are being used in combination with avian irritants to deter raven predators (Hardshell Labs, Inc. Joshua Tree, CA; [Peebles and Spencer, 2020](#)). Thus, the use of tortoise replicas is a potentially useful conservation tool in both their utility in examining factors that influence predation risk and their role in actively reducing landscape-scale predation risk to juvenile desert tortoises through aversive training of subsidized predators like ravens or coyotes.

## 5. Conclusions

Subsidized predators such as common ravens and coyotes represent a growing challenge for desert tortoise conservation ([USFWS, 2011](#)) and can hamper recovery efforts of other threatened species ([Boarman, 2003](#), [Loehr and Keswick, 2021](#), [O'Neil et al., 2018](#), [Smith and Quin, 1996](#)). Predation risk to juvenile desert tortoises is increasing due to elevated densities of predators that have capitalized on human-made subsidies, which can lead to further reductions in juvenile recruitment of desert tortoises ([Boarman, 2003](#)). Our data support previous findings that predation risk from common ravens, while not statistically significant in the current study, was highest within 750 m of the powerlines yet still occurred as far away as 1250 m from the powerlines. We continue to recommend that head-started and translocated juvenile tortoises are released  $>1600 \text{ m}$  from powerline structures ([Daly et al., 2019](#)). Our data also support previous findings that predation risk from common ravens decreases in the fall ([Daly et al., 2019](#), [Stiehl, 1985](#)), and we continue to recommend fall releases for head-started or translocated juvenile tortoises to reduce their initial mortality after release. Future research should continue to examine how predation risk varies over spatial scales and the influence of human subsidies on predation of juvenile tortoises. The 3D-printed tortoise replicas could be implemented as a tool for quantifying predation risk at a candidate release site to assess site suitability prior to the introduction of head-started tortoises. Additionally, 3D-printed tortoise



replicas could be used as a potential tool for predator aversion conditioning. Implementation of 3D replicas for predator studies can inform best practices for reducing predator access to juvenile head-started or translocated tortoises during targeted releases, thereby effectively reducing predation on juvenile desert tortoises and other similarly at-risk species.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data Availability

Data will be made available on request.

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### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e03220](https://doi.org/10.1016/j.gecco.2024.e03220).

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