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A decision tool to identify population management strategies for common ravens and other avian predators

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Abstract: Some avian species have developed the capacity to leverage resource subsidies associated with human manipulated landscapes to increase population densities in habitats with naturally low carrying capacities. Elevated corvid densities and new territory establishment have led to an unsustainable increase in depredation pressure on sympatric native wildlife prey populations as well as in crop damage. Yet, subsidized predator removal programs aimed at reducing densities are likely most effective longer-term when conducted in tandem with subsidy control, habitat management, and robust assessment monitoring programs. We developed decision support software that leverages stage structured Lefkovitch population matrices to compare and identify treatment strategies that reduce subsidized avian predator densities most efficiently, in terms of limiting both cost and take levels. The StallPOPd (Version 4; available at https://doi.org/10.7298/sk2e-0c38.4) software enables managers to enter the area of their management stratum and the demographic properties (vital rates) of target bird population(s) of interest to evaluate strategies to decrease or curtail further population growth. Strategies explicitly include the reduction in fertility (i.e., eggs hatched) and/or the culling of hatchlings, non-breeders and/or breeders, but implicitly comprise reduction in survival or reproduction through subsidy denial. We illustrate the utilities of the software with examples using common ravens (*Corvus corax;* ravens) in the Mojave Desert of California, USA. Unfortunately, the survival and reproduction effects of each unit of a particular subsidy in that system have remained elusive, though this is the priority of current research. Because the software leverages a life history representation that is known to characterize hundreds of wildlife species in addition to ravens, the work expands the suite of tools available to wildlife managers and agricultural industry specialists to abate bird damage and impacts on sensitive wildlife in habitats with persistent human subsidies.

Key words: bird damage, common raven, *Corvus corax*, egg addling, fertility reduction, Lefkovitch matrix, population matrix model, resource management, species conflict resolution, subsidy denial

Subsidized avian populations cause tens of millions of dollars in crop damage each year (U.S. Department of Agriculture [USDA] 1999, Anderson et al. 2013) as well as measurable health and environmental harm (Alley et al. 2002, Boarman 2003, O'Neil et al. 2018, Coates et al. 2020). Public opinion and policy discourse, however, often focus only on those tangible and precisely monitored economic damages, while the impacts to sensitive wildlife and ecosystem health are comparatively ignored; those impacts from subsidized corvid populations are likely more spatially and temporally ubiquitous. Corvids are among the most damaging groups of avian species (Tobin 2002), capitalizing on subsidies ranging in variety from carefully cultivated

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Figure 1. Common ravens (*Corvus corax*; ravens) utilizing anthropogenic resources in the desert southwest, USA. From top left clockwise: ravens roosting along powerlines; ravens scavenging roadkill; ravens foraging at a dumpster; ravens perching and drinking at agricultural fields; swarm of ravens over the Mojave Desert landscape (*photos courtesy of T. Shields*).

crops and livestock to foraging in landfills and wastewater treatment facilities. Consequently, resource subsidies have promoted the (1) population expansion of corvids into previously suboptimal habitats, (2) subsequent depredation of native species in those habitats, and (3) disruption of natural predator–prey dynamics (Marzluff and Neatherlin 2006, Rodewald et al. 2011, Coates et al. 2020).

For example, common raven (*Corvus corax*; raven) densities have increased across much of this species' range as a result of expanding access to resource subsidies (i.e., water, forage, nesting substrates, nesting materials, wind protection, and shade) associated with human-manipulated landscapes (i.e., urban, suburban, exurban, and agricultural; Kristan and Boarman 2003, Bui et al. 2010, Webb et al. 2011, Delehanty 2021). These newly available resources have resulted in the expansion of raven population densities and range beyond natural carrying capacities (O'Neil et al. 2018).

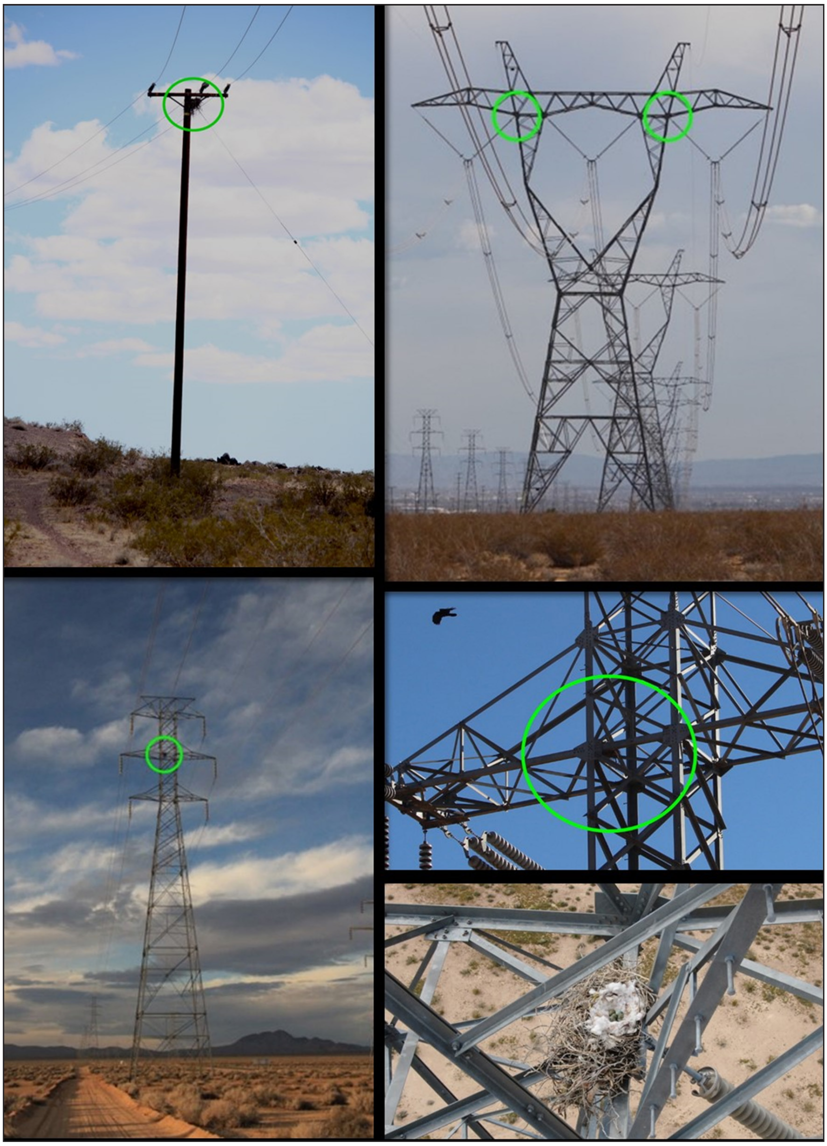

Figure 2. A small selection of anthropogenic structures (power and transmission towers) common ravens (*Corvus corax*; ravens) utilize as nesting sites (circled in green) across the Mojave Desert landscape, southwest USA. The Mojave Desert comprises sandy flats to rocky foothills and is generally dominated by low creosote (*Larrea tridentata*), burrobrush (*Hymenoclea salsola*), saltbush scrub (*Atriplex* spp.), Yucca spp., and *Opuntia* spp. (*photos courtesy of T. Shields*).

Human-associated infrastructure provides ravens access to water in the form of irrigation, ponds, and water features (Restani et al. 2001, Boarman et al. 2006, Kristan and Boarman 2007). Other point resource subsidies like landfills, dumpsters, garbage cans, agriculture sites, and roadkill of otherwise unattainable prey provide ravens with near *ad libitum* access to forage resources (Boarman et al. 2006, Kristan and Boarman 2007, Webb et al. 2011, Coates et al. 2016). Finally, and most prominently, electrical transmission towers, wood distribution poles, billboards or signs, buildings, bridges, and communication towers provide ravens alternative nesting and perching sites in previously untenable habitats such as creosote bush scrub in the desert southwest, which has theoretically relieved constraints on annual rates of recruitment (Steenhof et al. 1993, Kristan and Boarman 2007, Coates et al. 2014, Howe et al.

2014, Harju et al. 2018, Coates et al. 2020). Accordingly, once remote, scarcely provisioned environments such as the Mojave, Sonoran, and Great Basin Deserts of the United States have been transformed into the patchworks of synthetic water, forage, and nesting resources (e.g., Figure 1 and Figure 2) that characterize the Anthropocene epoch.

Like other corvids, ravens are social, intelligent, highly adaptable (Bond et al. 2003, Emery and Clayton 2004), and native to much of North America (Sauer and Link 2011), including Death Valley in the United States, arguably one of the most uninhabitable locations in the Northern Hemisphere (Jaeger 1957). Although ravens have long inhabited the U.S. desert southwest, the Mojave and Sonoran Deserts of California, USA, have historically supported only low densities due to the absence of reliable food and water sources and limited nesting substrate (Howe et al. 2014). Raven densities have increased exponentially in desert environments over the last several decades (Knight et al. 1993, Boarman and Berry 1995, Kristan et al. 2004, Sauer and Link 2011), as have species conflicts resulting from density-dependent depredation rates (Coates et al. 2020). As such, contemporary raven abundance may be partly causing the decline of Mojave Desert tortoise (*Gopherus agassizii*; tortoise) populations (K. Holcomb, U.S. Fish and Wildlife Service [USFWS], personal communication), which have been reduced by approximately 33% between 2004 and 2014 (Allison and McLuckie 2018). Decline of the desert tortoise throughout much of California's Mojave Desert could portend broader ecosystem changes if this important ecosystem engineer of the desert southwest United States continues to decline (e.g., Griffiths et al. 2011, Kinlaw and Grasmueck 2012, Gibbs et al. 2014, Walde and Currylow 2015, Lovich et al. 2018). Indeed, overabundant raven populations are known to disrupt ecosystem function (Coates and Delehanty 2004) by altering the abundances of innumerable animals and plants, including invertebrates, reptiles, mammals, songbirds, seeds, and grains (Boarman 2003). This subsidized generalist avian mesopredator has been directly implicated in the decline of the greater sage-grouse (*Centrocercus urophasianus*; sage-grouse; Bui et al. 2010, Coates and Delehanty 2010), sharp-tailed grouse (*Tympanuchus phasianellus*; Manzer and Hannon 2005), least tern (*Sterna antillarum*; Avery et al. 1995), marbled murrelet (*Brachyramphus marmoratus*; Peery et al. 2004), Mojave Desert tortoise (Boarman and Berry 1995, Boarman 2002, Berry et al. 2013), and snowy plover (*Charadrius nivosus*; Burrell and Colwell 2012) and is likely causing a broader undetected decline of unmonitored or cryptic species (Xiong 2020, Coates et al. 2021).

Ravens are known to range widely when searching for prey, but they localize their efforts to the immediate area while rearing young in the nest (Kristan and Boarman 2003, Harju et al. 2018). This focused predation pressure can heavily impact any sensitive species near raven nesting sites. Of particular concern in the desert southwest is the impact that raven depredation is having on the tortoise (K. Holcomb, USFWS, personal communication). Already threatened with extinction by a host of issues that include habitat degradation and loss, vehicle strikes, disease, poaching, and climate change, tortoises are also known to be killed by ravens (Berry et al. 2013). Young tortoises are especially vulnerable to raven mortality as their relatively soft, developing shells are susceptible to beak punctures and they lack the developed musculature to keep their limbs tucked, protecting areas of softer flesh (Boarman 2002, 2003). In fact, raven depredation has been shown to account for the majority (up to 100%) of young desert tortoise predation mortalities in some areas (Nagy et al. 2015*a*, *b*; Segura et al. 2020). Data collected between 2013 and 2019 by the California Desert Common Raven Monitoring and Management Program indicated that most raven-depredated tortoise carcasses are within the size class of 0–9 years old (i.e., midline plastron length <124 mm), consistent with Medica et al. (2012). Localized depredation during rearing coupled with the explosion of raven populations in the Mojave Desert on the heels of human development highlights the need to manage ravens at a regional scale to protect the legacy of sympatric vulnerable prey species.

One-time disturbances or relocations do not reduce raven numbers over the long term, and even successful curtailment of further raven growth may simply plateau abundances at undesirable levels (Coates et al. 2007, Marchand et al. 2018). In the absence of continued management, long-lived breeders can simply return to the territory the following year to renest, or replacement breeders may instead move into the prematurely vacated nesting territories (Boarman 2003, Webb et al. 2004). Further, ravens socially circulate knowledge of threats and opportunities within groups (Marzluff et al. 1996, Blum et al. 2020), rendering repeated successes in culling adult birds increasingly difficult and time-intensive to achieve (Merrell 2012). These and other complicating factors suggest that the effective, long-term management of a raven population in any given area may involve multiple techniques that change by season, available staff, and fluctuating raven density. Wildlife professionals have pondered an approach that involves a 1-time "reset" of raven populations to sage-grouse and tortoise-specific depredation-dependent density thresholds, after which long-term maintenance of those lower densities (at levels that are sustainable for sensitive sympatric prey) could ensue through a combination of continued subsidy denial, and when densities or distances to active raven nests necessitate, targeted removals (anonymous wildlife professional, personal communication, Bird Damage Management Conference, Salt Lake City, Utah, February 2020).

Management recommendations that leverage density-independent models are important in pinpointing 1-time vulnerabilities in the life history to alterations of any 1 stage. This is because the dynamics of a density-independent population do not adjust themselves according to alterations in the status of the greater population. To enable wildlife managers to calculate the 1-time reduction in reproduction needed to halt or stall raven population growth, Shields et al. (2019*a*, *b*) provided equations, supporting software, and the novel field tools. However, management recommendations that leverage density-dependent models can account for the myriad ways an alteration in the status of the greater population may manifest themselves consequent to an initial management activity. Thus, the use of dynamic density-dependent population models promotes iterative management strategies with far more tailored precision than density-independent models.

The purpose of our study is to provide a computational tool to aid wildlife managers in assessing a variety of treatment options (1-time and longer-term) for the region-scale reduction or management of undesirable bird populations. Using the Mojave Desert raven populations and impact on the tortoise as a model, we developed analytical equations and provide interactive software that enables managers to investigate whether standalone (fertility/egg reduction or culling or subsidy denial) or compound strategies (fertility/egg reduction and culling and subsidy denial) are effective short- or long-term population management at the scale they define. We have made freely available this flexible, interactive, computational decision tool that allows managers to utilize the long-standing demographic modeling techniques to strategize and combat undesirable raven densities (https://doi.org/10.7298/sk2e-0c38.4).

Methods

We used a deterministic, Lefkovitch population matrix model (Caswell 2001; Kristan and Boarman 2005; Shields et al. 2019*a*, *b*) to depict the 3 life stages (hatchlings, immature and non-breeders, and breeders) of a representative subsidized avian predator, the common raven, under both density-independent and density-dependent scenarios. A density-independent life history with a matrix model of the form (Webb et al. 2004; Kristan and Boarman 2005; Shields et al. 2019*a*, *b*):

$$\mathbf{L} = \begin{bmatrix} 0 & 0 & a_{13} \\ a_{21} & 0 & 0 \\ 0 & a_{32} & a_{33} \end{bmatrix}$$

has a characteristic equation of the form (Hanley and Dennis 2019, Shields et al. 2019*a*):

$$\lambda^3 - a_{33}\lambda^2 - a_{13}a_{21}a_{32} = 0 \qquad (1)$$

where λ represents the long-term growth rate (Marzluff and Neatherlin 2006), and the vital rates a_{13} represents fertility (i.e., viable eggs), a_{21} represents the annual survival of hatch-year birds, a_{32} represents the annual survival (and transition) of non-breeders, and a_{33} represents the annual survival of breeders. A density-dependent life history with a matrix model of the form:

$$\mathbf{L} = \begin{bmatrix} 0 & 0 & a_{13} \\ a_{21} & a_{22} & a_{23} \\ 0 & a_{32} & a_{33} \end{bmatrix}$$

has a characteristic equation of the form (Hanley and Dennis 2019, Shields et al. 2019*a*),

$$\lambda^3 - a_{22} - a_{33}\lambda^2 + (a_{22}a_{33} - a_{32}a_{23})\lambda - a_{13}a_{21}a_{32} = 0 \qquad (2)$$

where λ, a_{13}, a_{21}, a_{32}, and a_{33} are defined as above, a_{22} represents annual survival (with a lack of transition to breeding status) of non-breeders,

Table 1. All possible cases for reduction of avian populations using simultaneous strategies targeting 1, 2, or 3 life stages in a density-independent system.

Density-independence	Number of treatment strategies	Case #	Life stage targeted for reduction
	Single initial/ annual	1	Fertility
		2	Hatchling survival
		3	Non-breeder survival
		4	Breeder survival
	2-way simultaneous	5	Fertility and hatchling survival
		6	Fertility and non-breeder survival
		7	Fertility and breeder adult
		8	Hatchling survival and non-breeder survival
		9	Hatchling survival and breeder survival
		10	Non-breeder survival and breeder survival
	3-way combinatorial	11	Fertility, hatchling survival, and non-breeder survival
		12	Fertility, hatchling survival, and breeder survival
		13	Fertility, non-breeder survival, and breeder survival
		14	Hatchling survival, non-breeder survival, and breeder survival

and a_{23} represents the survival of breeders (that have returned to non-breeding status). Both matrices assume: (1) the vital rates represent population-scale averages of stage members, (2) a projection using the matrix represents 1 calendar year, (3) the demographic inventory of each projection is taken during the winter (prior to breeding season), (4) projections are deterministic (i.e., they contain no demographic or stochastic variation), (5) transition elements (i.e., all elements except a_{13}) represent compound survival and transition probabilities, and (6) the population is closed to immigration and emigration (Webb et al. 2004, Kristan and Boarman 2005).

We used the characteristic equations of the matrices (i.e., Equations 1 and 2) to derive analytical expressions that represent population treatments that could be used in isolation or in combination to produce target raven densities that are operating at (no growth) or near (limited growth) a growth rate of 1. Potential initial/annual treatment strategies for a density-independent system are outlined (Table 1). The 4-way combinatorial reduction in a density-independent system is Equation 3 (below).

Population dynamics will likely adjust in response to an applied treatment. For example, the addling of eggs in a density-independent system will functionally render the adults to be non-breeders, thereby adjusting the structure of the matrix itself to take on the form of a density-dependent matrix (i.e., where a_{23} is non-zero). Maintenance of the growth rate after an initial treatment can be investigated using a density-dependent system, which unlike the density-independent dynamics, can account for all the different ways raven populations may "adjust" to the initial treatment. Potential long-term treatment strategies for a density-dependent system are also outlined (Table 2).

While we did not derive the 4- or 5-way combinatorial reduction strategies for the density dependent system, the 6-way combinatorial reduction in a density-dependent system is Equation 4 (below). Derivations for each of the 55 treatments appear in the supplemental material.

We then used the matrices to derive analytical expressions that represent the target vital rates needed to reset current densities to desired levels over the timespan of 1 calendar year. Letting 1-time (target) vital rates be denoted a_{13}', a_{21}', a_{22}', a_{23}', a_{32}', and a_{33}', and letting H_h represent the target abundances of hatchlings, S_h represent the target abundances of immature and non-breeders, and A_h represent the target abundances of breeders, then the 1-time "reset" matrix necessary to propel a density-independent raven population toward target abundance is:

$$\begin{bmatrix} 0 & 0 & \frac{H_h}{A_t} \\ \frac{S_h}{H_t} & 0 & 0 \\ 0 & \frac{A_h - a_{33}'A_t}{S_t} & \frac{A_h - a_{32}'S_t}{A_t} \end{bmatrix} \quad (3)$$

Should the raven population have complicated dynamics at the outset of treatment such that a_{22} and/or a_{23} be non-zero (e.g., if territories are already largely filled and excess fecund birds exist but cannot breed), then the 1-time "reset" matrix necessary to propel the population of ravens toward a target abundance is:

$$\begin{bmatrix} 0 & 0 & \frac{H_h}{A_t} \\ \frac{S_h - a_{22}'S_t - a_{23}'A_t}{H_t} & \frac{S_h - a_{21}'H_t - a_{23}'A_t}{S_t} & \frac{S_h - a_{21}'H_t - a_{22}'S_t}{A_t} \\ 0 & \frac{A_h - a_{33}'A_t}{S_t} & \frac{A_h - a_{32}'S_t}{A_t} \end{bmatrix} \quad (4)$$

The derivations appear in the supplemental material.

Table 2. Possible cases for reduction of avian populations using simultaneous strategies targeting 1, 2, or 3 life stages in a density-dependent system.

Density-dependence	Number of treatment strategies	Case #	Life stage targeted for reduction
	Single initial/ annual	1	Fertility
		2	Hatchling survival
		3	Non-breeder survival (without transition)
		4	Breeder survival (with demotion to non-breeder status)
		5	Non-breeder survival (with transition to breeder status)
		6	Breeder survival
	2-way simultaneous	7	Fertility and hatchling survival
		8	Fertility and non-breeder survival (without transition)
		9	Fertility and breeder survival (with demotion)
		10	Fertility and non-breeder survival (with transition)
		11	Fertility and breeder survival
		12	Hatchling survival and non-breeder survival (without transition)
		13	Hatchling survival and breeder survival (with demotion)
		14	Hatchling survival and non-breeder survival (with transition)
		15	Hatchling survival and breeder survival
		16	Non-breeder survival (without transition) and breeder survival (with demotion)
		17	Non-breeder survival (without transition) and non-breeder survival (with transition)
		18	Non-breeder survival (without transition) and breeder survival
		19	Breeder survival (with demotion) and non-breeder survival (with transition)
		20	Breeder survival (with demotion) and breeder survival
		21	Non-breeder survival (with transition) and breeder survival

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	3-way combinatorial	22	Fertility, hatchling survival, and non-breeder survival (without transition)
		23	Fertility, hatchling survival, and breeder survival (with demotion)
		24	Fertility, hatchling survival, and non-breeder survival (with transition)
		25	Fertility, hatchling survival, and breeder survival
		26	Fertility, non-breeder survival (without transition), and breeder survival (with demotion)
		27	Fertility, non-breeder survival (without transition), and non-breeder survival (with transition)
		28	Fertility, non-breeder survival (without transition), and breeder survival
		29	Fertility, breeder survival (with demotion), and non-breeder survival (with transition)
		30	Fertility, breeder survival (with demotion), and breeder survival
		31	Fertility, non-breeder survival (with transition), and breeder survival
		32	Hatchling survival, non-breeder survival (without transition), and breeder survival (with demotion)
		33	Hatchling survival, non-breeder survival (without transition), and non-breeder survival (with transition)
		34	Hatchling survival, non-breeder survival (without transition), and breeder survival
		35	Hatchling survival, breeder survival (with demotion), and non-breeder survival (with transition)
		36	Hatchling survival, breeder survival (with demotion), and breeder survival
		37	Hatchling survival, non-breeder survival (with transition), and breeder survival
		38	Non-breeder survival (without transition), breeder survival (with demotion), and non-breeder survival (with transition)
		39	Non-breeder survival (without transition), breeder survival (with demotion), and breeder survival
		40	Non-breeder survival (without transition), non-breeder survival (with transition), and breeder survival
		41	Breeder survival (with demotion), non-breeder survival (with transition), and breeder survival

Table 3. A density-independent (DI) example of a raven (*Corvus corax*) population's vital rates and size prior to treatment in Superior-Cronese Critical Habitat Unit, Mojave Desert region, USA. The purported geographic size of this area is 2,215 km^2 with a density of 1.56 ravens per km^2. The target density is assumed to be 0.40 per km^2 (see text).

Starting proportion	Hatchlings	Non-breeders	Breeders
Fertility (viable eggs)	0.00	0.00	0.78
Survival and transition	0.40	0.00	0.00
Survival and transition	0.00	0.64	0.96
DI resulting # of ravens in life stage:	*n* = 1,237	*n* = 442	*n* = 1,384 eggs / 1,775 adults

Table 4. A density-independent (DI) example of a raven (*Corvus corax*) population's vital rates and size after treatment in Superior-Cronese Critical Habitat Unit, Mojave Desert region, USA. The geographic size of this area is 2,215 km^2 with a post-reset density of 0.40 ravens per km^2. The target density is assumed to remain at 0.40 per km^2 (see text).

Starting proportion	Hatchlings	Non-breeders	Breeders
Fertility (viable eggs)	0.00	0.00	0.78
Survival and transition	0.40	0.00	0.00
Survival and transition	0.00	0.64	0.96
DI resulting # of ravens in life stage:	*n* = 317	*n* = 113	*n* = 355 eggs / 455 adults

Table 5. A density-dependent (DD) example of a raven (*Corvus corax*) population's vital rates and size prior to treatment in Superior-Cronese Critical Habitat Unit, Mojave Desert region, USA. The purported geographic size of this area is 2,215 km^2 with a density of 1.56 ravens per km^2. The target density is assumed to be 0.40 per km^2 (see text).

Starting proportion	Hatchlings	Non-breeders	Breeders
Fertility (viable eggs)	0.00	0.00	0.78
Survival and transition	0.40	0.10	0.10
Survival and transition	0.00	0.54	0.86
DD resulting # of ravens in life stage:	*n* = 1,179	*n* = 649	*n* = 1,268 eggs / 1,626 adults

Table 6. A density-dependent (DD) example of a raven (*Corvus corax*) population's vital rates after treatment in Superior-Cronese Critical Habitat Unit, Mojave Desert region, USA. The purported geographic size of this area is 2,215 km^2 with a post-reset density of 0.40 ravens per km^2. The target density is assumed to remain at 0.40 per km^2 (see text).

Starting proportion	Hatchlings	Non-breeders	Breeders
Fertility (viable eggs)	0.00	0.00	0.78
Survival and transition	0.40	0.10	0.10
Survival and transition	0.00	0.54	0.86
DD resulting # of ravens in life stage:	*n* = 302	*n* = 166	*n* = 325 eggs / 417 adults

At the time of writing, it is unclear how many ravens can reside in the Mojave Desert region without causing harm to sympatric species such as the tortoise. However, Coates et al. (2020) reported that raven densities >0.40 ravens per km^2 lead to deleterious impact to sympatric wildlife species such as greater sage-grouse. A similar density value was approximated given the values reported in Coates and Delehanty (2010). Therefore, in the absence of a threshold density that neutralizes conflict among ravens and sympatric species within a monitoring and management strata (i.e., area of conservation interest) in the Mojave Desert region, the proxy threshold of 0.40 ravens per km^2 may be used.

Given the rapid tool to calculate density (Brussee et al. 2021), we derived expressions to convert target densities to target abundances using the spatial area of the monitoring or management strata of interest. We programmed the matrix structures, their characteristic equations (Equations 1 and 2), the expressions for the 1-time "reset" treatment (Equations 3 and 4), and the analytical equations representing the mathematics of the 55 treatment options into a free interactive software (StallPOPd Version 4 [StallPOPdV4]; Hanley et al. 2021). StallPOPdV4 allows the user to enter for the monitoring or management strata of interest: (1) the current vital rates of the target species, (2) the current density of target species, and (3) the geographical area (in km^2), from which the software generates the reduction in vital rates required to achieve the 1-time population reset and the subsequent long-term maintenance of the population. Beyond prescribing strategies to reset and constrain the growth rate to 1, StallPOPdV4 additionally allows the user to identify the deterministic consequences of any level of treatment, such as those that suppress growth while not necessarily halting it.

Density-independent system: a 1-time reset

We illustrated the use of the StallPOPd software for a 1-time "reset" of raven population size using an example from the Superior-Cronese Critical Habitat Unit (SC CHU; Table 3). The SC CHU is a 2,215-km^2 area of the Mojave Desert of California and is home to historical populations of both ravens and tortoises. In recent years, the population of ravens in the SC CHU has increased to an estimated 1.56 total ravens per km^2 (K. Holcomb, USFWS, personal communication). While the raven population in the SC SCH is likely to contain complications such that the density-dependent model is more appropriate (even for an initial reset), not all demographic rates of ravens in the SC CHU are known, so for this example we used proxy rates from the density-independent "Urban" scenario in Table 1 of Kristan and Boarman (2005). Further unknown is the desired target density of ravens (under which deleterious impacts to tortoises would not occur), so we assume the proxy threshold of 0.40 ravens per km^2 from estimations of damage by ravens to sage-grouse (Coates et al. 2020). Finally, we do not know the demographic structure (proportions) of the current nor desired raven population, so we use a proxy structure that follows the stable stage distribution (Caswell 2001), as calculated from the Urban scenario.

Density-independent system: post-reset maintenance

To illustrate the use of the StallPOPd software for the "maintenance" of the raven populations in the SC CHU, we assume that SC CHU has undergone the 1-time reset as prescribed (above) and is therefore reset to a density of 0.40 ravens per km^2 (Table 4). We again use the proxy vital rates from Kristan and Boarman (2005) and assume stable-stage distribution (Caswell 2001).

Density-dependent system: a 1-time reset

We next illustrated the use of the StallPOPd software for a 1-time "reset" of raven population size using a hypothetical density-dependent example from the identical SC CHU (Table 5). As above, we assume an estimate of 1.56 total ravens per km^2 and a slightly modified density-independent "Urban" scenario in Kristan and Boarman (2005). The arbitrary modification assumes that a portion of non-breeders did not transition into breeders and another portion of breeders did not breed. We further wish to achieve a density of 0.40 ravens per km^2 (Coates et al. 2020), and we again use a proxy structure that follows the stable-stage distribution (Caswell 2001).

Density-dependent system: post-reset maintenance

To illustrate the use of the StallPOPd software for the "maintenance" of the hypothetical density-dependent raven population in the SC CHU, we assume that the hypothetical SC CHU had undergone the 1-time reset as prescribed in the previous example and was therefore reset to a density of 0.40 ravens per km^2 (Table 6). We again use the hypothetical vital rates (above) and assume a stable stage distribution (Caswell 2001).

Results

Density-independent system

The StallPOPdV4 software computed the lowest possible proportion(s) of egg and/or birds that need to be removed each year to constrain the growth rate at 1 (Table 7). These target "reset" abundances in SC CHU were calculated to be 355 viable eggs (down from 1,384 that are estimated to exist in the untreated population), 317 surviving hatchlings (down from 1,237), 113 surviving non-breeders (down from 442), and 455 surviving breeders (down from 1,775). The target total of eggs and birds on the landscape is then 1,240 (355 eggs + 317 hatchlings + 113 non-breeders + 455 breeders). To achieve these target abundances, managers must reduce 1-time target fertility to 0.18 (down from 0.78), reduce 1-time hatchling survival to 0.09 (down from 0.40), reduce 1-time non-breeder survival to 0.47 (down from 0.64), and reduce 1-time breeder survival to 0.14 (down from 0.96). Such 1-time reductions will reduce current abundances to the target abundances of 0.40 ravens per km^2 in 1 calendar year so that subsequent annual management can begin. In Table 7, we show a comparison of all 14 possible density-independent treatment strategies that may be used on an annual basis thereafter to maintain desired densities (Table 1), with the example in Table 3.

Table 7. An example StallPOPd output comparison among the 14 possible treatments in a density-independent (DI) system that would keep the raven (*Corvus corax*) growth rate equal to 1 in the Superior-Cronese Critical Habitat Unit of the Mojave Desert, USA. The results show the lowest possible proportion(s) of eggs and/or birds that need to be removed each year in each case to constrain the growth rate at 1.

Treatment option	a_{13} proportion eggs culled	a_{21} proportion hatchlings culled	a_{32} proportion non-breeders culled	a_{33} proportion breeders culled
DI case 1	0.80	–	–	–
DI case 2	–	0.80	–	–
DI case 3	–	–	0.80	–
DI case 4	–	–	–	0.17
DI case 5	0.80	0.01	–	–
DI case 6	0.01	–	0.80	–
DI case 7	0.01	–	–	0.16
DI case 8	–	0.01	0.80	–
DI case 9	–	0.01	–	0.16
DI case 10	–	–	0.01	0.16
DI case 11	0.09	0.91	0.01	–
DI case 12	0.34	0.66	–	0.01
DI case 13	0.34	–	0.66	0.01
DI case 14	–	0.34	0.66	0.01

Density-dependent system

The StallPOPdV4 software again computed the lowest possible proportion(s) of egg and/or birds that need to be removed each year to constrain the growth rate at 1 considering density-dependence (Table 8). These target "reset" abundances in the hypothetical SC CHU were calculated to be 325 eggs (down from 1,268 that are estimated to exist in the untreated population), 302 hatchlings (down from 1,179), 166 non-breeders (down from 649), and 417 adults (down from 1,626). Totals of eggs and birds in the management unit is then 1,210 (325 eggs + 302 hatchlings + 166 non-breeders + 417 breeders). Managers must reduce 1-time target fertility to 0.19 (down from 0.78), reduce 1-time hatchling survival to 0.03 (down from 0.04), and reduce 1-time breeder survival to 0.04 (down from 0.96) to achieve these target abundances. It is interesting to note that non-breeder survival does not need treatment in this example reset. Such 1-time reductions will achieve the target abundances in the hypothetical system in 1 calendar year. Table 8 illustrates the comparison of 41 possible treatment strategies that may be used on an annual basis thereafter to maintain 0.40 ravens per km^2 in this density-dependent system.

Discussion

Damage caused by subsidized avian predators is a pressing challenge for state and federal land and wildlife management agencies who manage predators and, in many instances, recovery of its prey. Vast discrepancies between current and target raven densities in wildlife habitats such as the Mojave Desert highlight the urgent priority for managers to take aggressive action to stem further damage from subsidized predators. This is particularly true in the Mojave Desert considering the previous 8 or more years of subsidy management and offending raven removals appears to have not resulted in a sustainable predator–prey relationship.

The StallPOPdV4 is a flexible computational tool that enables managers to tailor their analysis to a study area of interest to investigate and compare many possible short- and long-term strategies for population reduction of ravens. The tool may also reveal treatment strategies that are mathematically viable and not otherwise obvious. For example, the 1-time reset in the SC CHU

Table 8. An example StallPOPd output comparison among the 41 possible treatments in a density-dependent (DD) system that would keep the raven (*Corvus corax*) growth rate equal to 1 in the Superior-Cronese Critical Habitat Unit of the Mojave Desert, USA. The results show the lowest possible proportion(s) of eggs and/or birds that need to be removed each year in each case to constrain the growth rate at 1 and maintain a density of 0.40 ravens per km^2.

Treatment option	a_{13} proportion eggs culled	a_{21} proportion hatchlings culled	a_{22} proportion non-transition non-breeders culled	a_{23} proportion transition breeders culled	a_{32} proportion transition non-breeders culled	a_{33} proportion non-transition breeders culled
DD case 1	0.82	--	--	--	--	--
DD case 2	--	0.80	--	--	--	--
DD case 3	--	--	0.80	--	--	--
DD case 4	--	--	--	1.00	--	--
DD case 5	--	--	--	--	0.81	--
DD case 6	--	--	--	--	--	0.18
DD case 7	0.01	0.80	--	--	--	--
DD case 8	0.84	--	0.29	--	--	--
DD case 9	0.84	--	--	0.05	--	--
DD case 10	--	--	--	--	0.81	--
DD case 11	0.01	--	--	--	--	0.18
DD case 12	--	0.84	0.29	--	--	--
DD case 13	--	0.84	--	0.05	--	--
DD case 14	--	0.84	--	--	0.05	--
DD case 15	--	0.01	--	--	--	0.18
DD case 16	This strategy is not capable of constraining the growth rate at 1.					
DD case 17	--	--	--	--	0.81	--
DD case 18	--	--	0.01	--	--	0.18
DD case 19	--	--	--	--	0.81	--
DD case 20	--	--	--	0.01	--	0.18
DD case 21	--	--	--	--	0.01	0.18
DD case 22	This strategy is not capable of constraining the growth rate at 1.					
DD case 23	0.20	0.80	--	0.02	--	--
DD case 24	0.21	0.79	--	--	0.01	--
DD case 25	0.25	0.75	--	--	--	0.01
DD case 26	This strategy is not capable of constraining the growth rate at 1.					
DD case 27	0.83	--	0.17	--	0.01	--
DD case 28	0.77	--	0.23	--	--	0.01
DD case 29	0.83	--	--	0.17	0.05	--
DD case 30	0.76	--	--	0.24	--	0.01
DD case 31	0.30	--	--	--	0.70	0.01
DD case 32	--	0.84	0.16	0.05	--	--
DD case 33	--	0.83	0.17	0.01	--	--
DD case 34	--	0.77	0.23	--	--	0.01
DD case 35	--	0.83	--	0.17	0.01	--

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DD case 36	--	0.76	--	0.24	--	0.01
DD case 37	--	0.30	--	--	0.70	0.01
DD case 38	This strategy is not capable of constraining the growth rate at 1.					
DD case 39	This strategy is not capable of constraining the growth rate at 1.					
DD case 40	--	--	0.21	--	0.79	0.01
DD case 41	--	--	--	0.21	0.79	0.01

requires the simultaneous reduction in fertility, the survival of young birds, and the survival of breeders; a result that was only evident when the situational conditions (and desired densities) of the SC CHU were considered in tandem. Beyond pinpointing strategies that will precisely propel current conditions to desired conditions, the StallPOPdV4 software further allows managers to visualize the full mathematical relationships between 2- and 3-way treatment strategies, which allows for the exploration of strategic compromises that may be more practical for managers to apply in myriad real-life situations.

We used ravens in the Mojave Desert as our example because human-subsidized populations are known to produce deleterious impacts to the threatened Mojave Desert tortoise. While adult tortoise shells are rigid, reinforced by calcified bone, allowing them to tuck behind their heavily armored limbs as a generally effective predator defense, juvenile tortoises have relatively soft, developing shells and lack the mature musculature in their limbs, rendering their shells vulnerable to raven beak punctures (Boarman 2002, 2003) and natural tucking behavior ineffective. In 1 study, 26.5% of 68 released juvenile tortoises were depredated by ravens after a single spring and fall active period, a conservative estimate given that another 14.7% of released juvenile tortoises were either lost or could not be unequivocally assigned to a single predator (Daly et al. 2019). If we assume this annual raven depredation rate of 1:3.8 (26.5%) for all 68 of those tortoises while ≤9 years old, we would expect only 4.8 (7.0%) to survive to a more resistant size. Provided the mortality rate of tortoises is linearly scaled to raven densities, a 1-time reset of the raven population overlapping that study would have alleviated at least 18 deaths of the original 68 released tortoises, constituting a significant improvement of the effort toward restoration goals.

Successful management of raven populations such as those in the Mojave Desert may be achieved in 3 broad ways: the denial of resource subsidies that are beneficial to survival and/or rapid population expansion (e.g., forage, water, and nesting substrates), the removal of live birds (hatchlings, non-breeders, and/or breeders), and/or the curtailment of recruitment. StallPOPdV4 computes situational growth rates of ravens that arise from reductions in recruitment and/or survival, but the resulting mathematical solutions are invariant to the manner in which the alterations are achieved in real life. Yet, not all of strategies are economical, achievable, and/or pragmatic in practice. For example, we found that managers would need to addle ~80% of eggs, cull 80% of hatchlings, cull 80% of non-breeders, or cull 17% of breeders to achieve an identical mathematical outcome in the SC CHU. After all, it is well established that the elasticity (the relative influence on the growth rate by an instantaneous change to a vital rate) for a species consisting of long-lived breeders is often dominant to alterations in breeder survival (see Doak et al. 1994, de Kroon et al. 2000, Caswell 2001, Shields et al. 2019*a*). Stripped of its real-world context, this side-by-side numerical comparison suggests that the culling of breeders is the most efficient strategy for controlling raven populations in this stratum. However, adult ravens have proven sometimes difficult to kill in the Mojave Desert, in part because they very quickly learn to avoid even distant sounds from Wildlife Services trucks, will evacuate the area before a shot can be fired, and will remain away until the threat is gone. And there is evidence that in some regions, even long-term, widescale raven removal programs may have little effect on the overall population numbers (Skarphédinsson et al. 1990). Despite these real-life complications in killing offending adult birds (i.e., those that are known to target sensitive species; e.g., Dinkins et al. 2016), there have been pointed successes through trapping and euthanasia or the use of corvicides, both becoming increasingly used as effective culling strategies (O'Neil et al. 2021).

Managers have sought other strategies to remediate the raven issue (USFWS 2008), but short-term successes of 1-time population management options (egg addling and culling) are limited in ongoing efficacy. For example, the removal of nests does not dissuade renesting (Steenhof et al. 1993) and sometimes merely relocates the problem just a short distance away. Considering ravens' behavioral plasticity within the constraints of current technology, field methods, and permitting, a managerial goal to cull 4 times more eggs or hatchlings may be far more achievable in practice than even a small percentage of breeding adults. Further, innovations in applied technology have recently made targeting younger age classes achievable by bringing a decades-old but highly effective egg addling technique to previously inaccessibly high nests, including ravens in tortoise habitats (Shields et al. 2019*a*, Sanchez et al. 2021). In areas where depredation permits limit the number of live birds managers can kill, egg addling may be the best option. Addling the eggs without removal has been observed to "trick" the unwitting parental pair into incubating inviable eggs beyond the expected hatch date (Brussee and Coates 2018), longer into the breeding season, and rendering them less likely to relocate and/or attempt to renest that season. Similarly, the culling of breeders or removal of nests late in the breeding period will result in failed nests, eliminating the threat for that year. Both methods limit the predation pressure on sympatric species and effectively "close" the nesting territory to other potential fecund pairs for the year (Boarman 2003, Webb et al. 2004, Sanchez et al. 2021).

The StallPOPdV4 decision tool pinpoints many potential combinations of addling and culling that may be used to achieve a desired density despite real-world challenges to treatment, but we further hypothesize that population management will depend largely on subsidy denial. For example, maximum annual reproductive output is limited by the number of available breeding territories, and the number of productive breeding territories is in turn dependent on the available subsidies. A number of methods ranging from complete subsidy denial (raven proof trashcan installation, landfill capping, etc.) to hazing using novel tools (lasers, artificial intelligence, drones; W. Boarman and T. Shields, Hardshell Labs, unpublished data) are in use or under development. These tools provide iterative management strategies to suppress raven numbers in the Mojave Desert region in efforts to conserve desert tortoises. Indeed, some of the authors are preparing a full report that analyzes preliminary data regarding suppression management in the Mojave Desert region.

The StallPOPdV4 uses deterministic population matrix models to advance the exploration of alternative strategies for population management, but this computational approach should not be used in isolation. In addition to the behavioral complications of culling, StallPOPdV4 omits biological considerations that include carrying capacity, genetics, sex ratios, behavior, any type of stochasticity (demographic, environmental, temporal, sampling error), geographical considerations (weather, climate, seasonality), or competition with other species. The software further assumes the population is closed to immigration and emigration (see Kristan and Boarman 2005, Fleischer et al. 2008). Adjustments that account for those important ecological factors should be considered whenever interpreting the recommendations from StallPOPdV4 output.

Management implications

The application of StallPOPdV4 extends the breadth of tools available to managers to explore methods for population reduction of subsidized predators in the Mojave Desert and beyond. Indeed, the symbolic matrix used in the StallPOPdV4 represents the life history of not only common ravens, but an additional 510+ wildlife species (see the COMPADRE and COMADRE databases; Silvertown and Franco 1989, Salguero-Gómez 2011). By meshing theoretical tools with existing and emerging technologies, we can enhance our understanding of pest management and contribute knowledge to the development of the long-term Best Management Practices and strategies. We have made the entire StallPOPd software series a free decision tool available online at cwhl.vet.cornell.edu/tools/stallpopd or freely downloadable at doi.org/10.7298/sk2e-0c38.4.

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Supplemental material

Supplemental material can be viewed at https://digitalcommons.usu.edu/hwi/vol15/iss3/25.

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BRENDA J. HANLEY is a research associate in the Department of Public and Ecosystem Health at Cornell University. She uses mathematical and statistical techniques to adapt or invent analytical tools that enable natural resource professionals to answer emerging questions regarding wildlife populations and their system-scale health. She holds a B.A. degree in geography and land studies, B.S. degree in mathematics, M.S. degree in statistical science, and a Ph.D. degree in bioinformatics and computational biology.

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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.

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 laser-based 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.

STEPHEN BOLAND has 35 years of experience as a wildlife biologist, 29 of which have been in the Mojave and Sonoran Deserts. From 1983–1989, he conducted pelagic bird surveys in the Gulf of Mexico from Miami to Panama and from Panama to Central California along the Pacific Coast, multi-year studies on willow flycatcher and the American dipper and nesting raptor surveys in the Central Sierra, Nevada. In 1989, he conducted breeding black guillemot behavior and demographic studies in Alaska. Since 1990, he has conducted numerous nesting raptor and burrowing owl surveys in the San Joaquin Valley and the Mojave Desert. He has extensive experience conducting all aspects of desert tortoise research and monitoring. He has supervised many projects over the years and has experience in all aspects of scientific research and environmental compliance implementation. In addition to his B.S. degree in environmental biology, he holds a B.S. degree in surveying and photogrammetry, affording our team accurate and quality GIS/mapping skills. He is also a principal of Sundance Biology, Inc., an environmental consulting firm based out of Paso Robles, California.

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 predation 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.

MERCY VAUGHN is a conservation biologist who has worked for >30 years in the deserts of the southwestern United States and northwestern Mexico. She has specialized in research and conservation of tortoises and other sensitive desert species. Along with her colleagues, she discovered a new species of tortoise, Goode's thornscrub tortoise, in the tropical deciduous forest of southern Sonora and northern Sinaloa, Mexico. She is also president of Sundance Biology, Inc., an environmental consulting firm based out of Paso Robles, California.