Biodivers Conserv (2015) 24:2365–2381
DOI 10.1007/s10531-015-0916-6

ORIGINAL PAPER

Landscape-scale distribution and density of raptor populations wintering in anthropogenic-dominated desert landscapes

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Received: 16 December 2014 / Revised: 10 March 2015 / Accepted: 16 March 2015 /
Published online: 1 April 2015

Abstract Anthropogenic development has great potential to affect fragile desert environments. Large-scale development of renewable energy infrastructure is planned for many desert ecosystems. Development plans should account for anthropogenic effects to distributions and abundance of rare or sensitive wildlife; however, baseline data on abundance and distribution of such wildlife are often lacking. We surveyed for predatory birds in the Sonoran and Mojave Deserts of southern California, USA, in an area designated for protection under the "Desert Renewable Energy Conservation Plan", to determine how these birds are distributed across the landscape and how this distribution is affected by existing development. We developed species-specific models of resight probability to adjust estimates of abundance and density of each individual common species. Second, we developed combined-species models of resight probability for common and rare species so that we could make use of sparse data on the latter. We determined that many common species, such as red-tailed hawks, loggerhead shrikes, and especially common ravens, are associated with human development and likely subsidized by human activity. Species-specific and combined-species models of resight probability performed similarly, although the

Communicated by Dirk Sven Schmeller.

Electronic supplementary material The online version of this article (doi:10.1007/s10531-015-0916-6) contains supplementary material, which is available to authorized users.

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former model type provided higher quality information. Comparing abundance estimates with past surveys in the Mojave Desert suggests numbers of predatory birds associated with human development have increased while other sensitive species not associated with development have decreased. This approach gave us information beyond what we would have collected by focusing either on common or rare species, thus it provides a low-cost framework for others conducting surveys in similar desert environments outside of California.

Keywords Anthropogenic development · Desert Renewable Energy Conservation Plan (DRECP) · Habitat associations · Mojave Desert · Predatory birds · Raptors · Sonoran Desert · Surveys

Introduction

Deserts are globally threatened by crop and livestock production, mining, energy development, and urbanization (Lovich and Bainbridge 1999; Olson and Dinerstein 1998). This is, in part, because arid ecosystems are especially fragile and recover slowly from anthropogenic disturbances (Lovich and Bainbridge 1999). Development of deserts by humans has the potential to affect the behavior and ecology of wildlife populations by altering the size and configuration of their habitats (Averill-Murray et al. 2013; Barrows et al. 2006; Inman et al. 2013). Therefore, understanding wildlife-habitat associations is important when developing plans to manage for impending large-scale changes in land use.

Anthropogenic alterations of desert landscapes can change wildlife distributions (Inman et al. 2013), but such changes are dependent upon the scale of the alteration (Concepcion et al. 2015). As the scale of development increases, impacts to wildlife are also likely to increase (Averill-Murray et al. 2013; Inman et al. 2013). For example, at a fine scale, an isolated homestead with trees can provide otherwise unavailable nesting and perching structures for birds, thus increasing the probability of occurrence and abundance of certain bird species. As the human footprint increases from single, dispersed homesteads to large urban centers, the scope of the consequences for wildlife grow (Leu et al. 2008). For example, large-scale development could result in individuals of one species emigrating from previously established home ranges, while individuals of other species immigrate to the area. Large-scale renewable and non-renewable energy development is changing wildlife-habitat associations in desert environments. Deserts are especially suited to such development because of relatively low human population density and sometimes the high availability of energy resources. Developments, especially of renewable energy, can encompass very large areas 1400 + hectares (e.g., the 377-megawatt Ivanpah Solar Electric Generating System, CA; www.ivanpahsolar.com). Such development and associated infrastructure, including roads and transmission lines, degrades habitats (Averill-Murray et al. 2013; Inman et al. 2013), fragments landscapes (Kuvleski et al. 2007), and may affect evolutionary hotspots (Vandergast et al. 2013). Changes in the amounts and configuration of habitat brought about by large-scale development can alter predator assemblages, prey abundance, and quality of breeding sites (Esque et al. 2010; Inman et al. 2013; Kristan and Boarman 2007). These factors can have direct impacts on survival (Esque et al. 2010) and reproduction of individuals (Kristan and Boarman 2007). It is unclear how different species will respond to these changes; some species may be able to adapt by adjusting foraging or

nesting behaviors, while other more sensitive species may struggle to persist in altered habitats. To assess the influences of and to make informed decisions about development of energy production facilities, data are needed on the distribution and abundance of sensitive species and other wildlife across a gradient of human development.

In the western United States, the state of California has some of the densest human populations and correspondingly the greatest impacts to desert systems (Leu et al. 2008). The Desert Renewable Energy Conservation Plan (DRECP) is being developed to manage landscape alterations from renewable energy development (DUDEK and ICF International 2011). Such development is required to achieve renewable energy targets of the state of California and the United States of America (California Executive Order S-14-08; Department of Interior Secretarial Order 3285; Renewable Energy Action Team 2010). In deserts of southern California, wind and solar energy are the primary types of energy development (DUDEK and ICF International 2011). The DRECP is intended to identify areas of high biodiversity that are best suited for protection to enhance wildlife conservation and, in turn, identify areas best suited for disturbance through energy development (Development Focus Areas or DFAs).

As with most conservation planning efforts, the DRECP is based on known distributions of sensitive species and their habitats. However, in many cases the data sources used to build these distributions are incomplete (The DRECP Independent Science Panel 2012). Lack of data for some species is likely related to low densities of desert wildlife in general, lower densities of rare species, and low detection rates of these animals. Thus, adequate sample sizes required to describe wildlife-habitat relationships and distributions are difficult or expensive to collect. The result is expensive sampling schemes or few data collected for rare species, either of which may result in inadequate protection.

We surveyed the DRECP region to address the problem of lack of knowledge of high-priority sensitive avian species. We targeted raptors as they are indicators of biodiversity (Sergio et al. 2006), because abundances have been estimated for some species (Knight et al. 1999), and because they are known to show varying responses to human activities in desert environments (Boal et al. 2003; Boarman et al. 2006; Knight et al. 1999; Kristan and Boarman 2007; Rodríguez-Estrella et al. 1998). Thus, it is important to determine how avian predators were distributed throughout the region and how their distributions were influenced by habitat types and anthropocentric development. Our specific objectives were to (1) estimate abundance and density of predatory birds, (2) compare densities with previously published estimates and (3) determine how abundance was associated with cover (habitat) types and human development.

Methods

Study area

Our surveys were conducted within the DRECP or within 20 km of its boundary. The study area includes the Lower Colorado subdivision of Sonoran Desert and the Mojave Desert (Turner 1994; Turner and Brown 1994) and extended from the border with Baja California, Mexico north to Highway 190 on the west side of Death Valley, and from the Colorado River west to the foothills of the Peninsular, Traverse, and Sierra Mountain Ranges (Fig. 1).

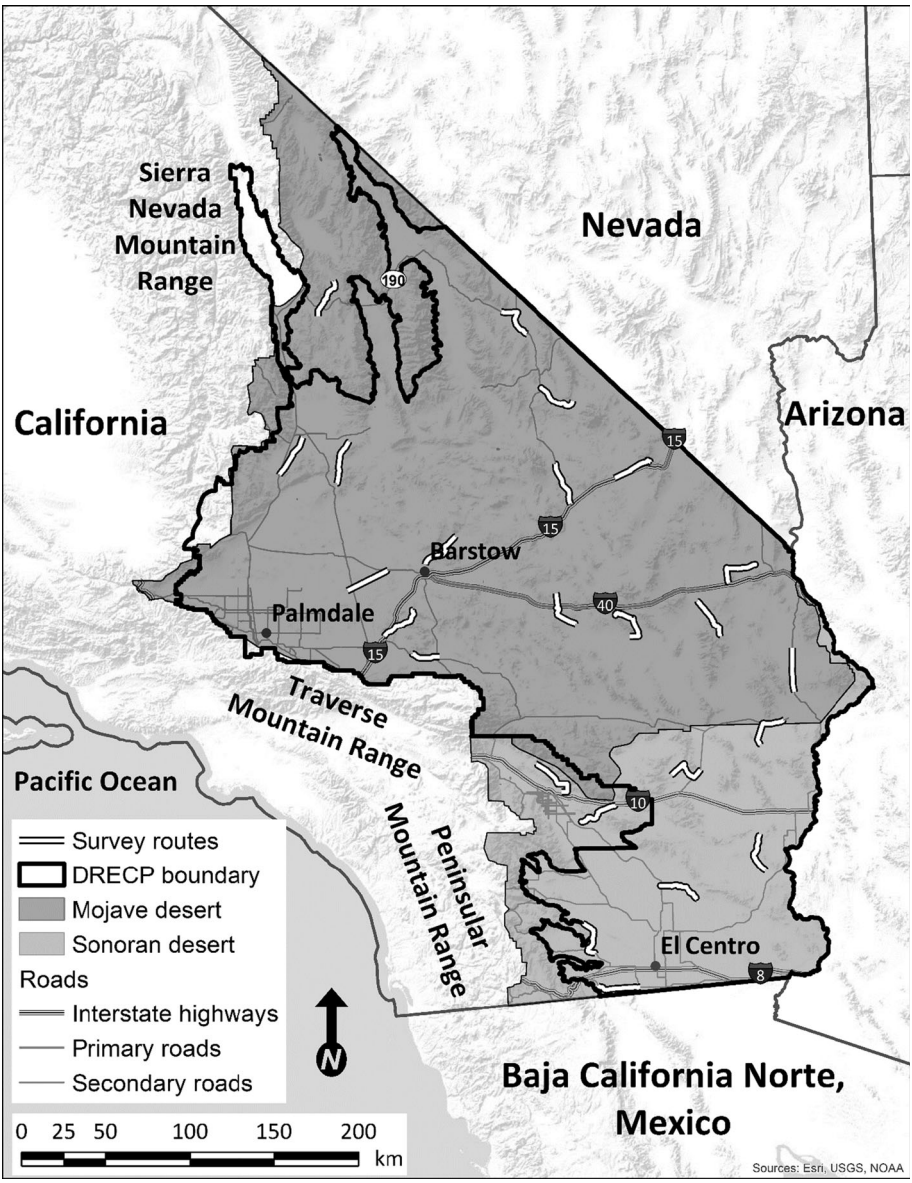

Fig. 1 The study area included the Desert Region Ecosystem Conservation Plan area and portions of Sonoran and Mojave Deserts that occurred in California. We randomly established 24 transects throughout this area. Three cities are identified with *dots*, El Centro to the south near the Mexico border, Palmdale to the West near the DRECP boundary, and Barstow at the I-15 and I-40 intersection

In southern California, the Sonoran and Mojave Deserts are both comprised predominantly of basin and range configurations (Commission for Environmental Cooperation 1997; Peterson 1981). Mountains are separated by long alluvial fans and wide valleys, often locations of ancient pluvial lakes that may currently contain dry lakebeds or playas at

their lowest elevations (Peterson 1981). In California, the Sonoran Desert occurs as a ~150 km band along the Mexico border. This desert is lower in elevation (−20 to 420 m) and has lower precipitation and warmer temperatures (January means, temperature 4.4 °C, 59 mm rainfall, El Centro, CA) than the more northerly Mojave Desert (−86 to 1370 m elevation; January means, temperature −0.7 °C Palmdale, CA; 105 mm rainfall, Barstow, CA; Commission for Environmental Cooperation 1997; Turner 1994; Turner and Brown 1994).

These deserts share plant communities (Lennartz et al. 2008; Turner 1994; Turner and Brown 1994). The lowest elevations or basin floors include bare playa and mixed salt desert scrub dominated by saltbush (*Atriplex* spp.). These give way to the most characteristic plant community in the study area, sparsely vegetated creosotebush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*) desert scrub. Traversing creosotebush/white bursage desert scrub are wash communities that develop where surface water drains. Washes include slightly thicker vegetation including white burrobrush (*Hymenoclea salsola*) and mesquite (*Prosopis glandulosa*). These areas within the Sonoran Desert also contain greater coverage of ironwood (*Olneya tesota*) and paloverde (*Cercidium floridum*) than washes of the Mojave Desert (Turner and Brown 1994). Above creosotebush and white bursage desert scrub occurs mid-elevation mixed desert scrub, which includes creosotebush and white-thorn acacia (*Acacia greggii*) with juniper (*Juniperus californicus*) found toward the upper limits of this community. Mid-elevation mixed desert scrub also includes characteristic Mojave Desert species such as Mojave yucca (*Yucca schidigera*) and Joshua tree (*Yucca brevifolia*; Turner 1994).

Throughout the study area there are also several communities that are nearly bare and have very low vegetative cover (Lennartz et al. 2008). Sections of desert pavement are very old surfaces of interlocked gravel with interspersed cobble and rock that have darkened over a very long time period (Peterson 1981) and that occur in relatively small flat areas, often at lower elevations. Sand dunes occur in several areas of the Sonoran and Mojave Deserts where wind has blown sand to the leeward side of pluvial lakes. Along piedmont slopes, within alluvial fans are areas of badlands that are fairly devoid of vegetation and range widely in size (Lennartz et al. 2008; Peterson 1981). Cliffs and rock outcrops or rock pediments occur within mountain valley fans, above piedmont (Peterson 1981) and volcanic rocklands occur throughout the study area (Lennartz et al. 2008).

Human activities throughout the study area vary widely and vary with land ownership. Private land is held throughout the area, with public land predominantly managed by the Bureau of Land Management (BLM), Department of Defense, and National Park Service. Agricultural production includes growing crops on private lands, which, although concentrated in the eastern portion of the Sonoran Desert, also occurs throughout the study area, and livestock grazing on public and private land (Lennartz et al. 2008). There is heavy use of off highway vehicles and other associated recreational activities (e.g., camping), predominantly on state owned and BLM land (Commission for Environmental Cooperation 1997). Other land uses include wind and solar energy production with corridors for electrical transmission. Military training occurs on land owned by the Department of Defense. Urban areas are also distributed throughout the study area, with large cities including Blythe, Barstow, El Centro, Indio, Lancaster, and Palmdale (Commission for Environmental Cooperation 1997). Cities and recreational areas are interconnected with extensive road systems that include interstate highways, major roads, and many secondary (paved and dirt) roads.

Estimating raptor abundance and density (Objective 1)

Raptor surveys

We randomly placed a series of 24 transects, each along 25.6 km (16 miles) of paved and dirt roads throughout the study area. We used a geographic information system (GIS, ArcMap 10.2, ESRI, Redland, CA) to first locate random points and then establish the start of each transect along the closest drivable road. We used several criteria to determine the direction and roads that transects followed. First, we attempted to place the majority of each transect through lands managed by the Department of Interior BLM (the origin of the funding for this project). Second, we limited transects so that the entire transect could follow drivable roads. Third, we constrained transects so that they did not include turns that caused two parts of the same transect to run parallel or close to one another, to limit double counting of birds. Fourth, transects were placed at least 15 km apart. Survey crews determined final transect routes based upon road and field conditions; therefore, some transect routes changed slightly over the 2 years of the study.

Experienced raptor biologists surveyed for predatory birds during daylight hours in January 2012 and 2013. Biologist teams (AED, KCD, 3–11 Jan 2012; MJL, TAM, 11–18 Jan 2013) searched for and recorded all predatory birds, including raptors, loggerhead shrikes (*Lanius ludovicianus*), and common ravens (*Corvus corax*). Each transect was composed of five point-count locations each separated by 6.4 km (4 miles) driving transects. Surveyors searched areas along each transect, starting with a point count. At each point count, they recorded target taxa seen or heard during 4 consecutive 2.5-min count intervals (10-min of total observation time at each point). We also recorded predatory birds seen while driving between points at speeds up to 55 km h^{-1} (35 miles h^{-1}). Bird locations were recorded within 160-m (0.1-miles) segments as determined by odometer readings in survey vehicles (160 segments per 16-miles transect) and within three distance bands (0–250, 250–500, >500 m, estimated by sight) from the centerline of each transect or center of each point count. We also tracked individual birds as they followed each transect to prevent counting any bird twice. We conferred with one another after each count interval during point counts and after we passed birds during driving surveys to ensure that no birds were recorded twice.

Habitat characterization

We remotely characterized habitat features at each of the 160 segments of each transect. We used GIS to identify the center of each segment and buffered each center point by 500 m. We then calculated the proportion of California GAP ecological systems and developed areas (Lennartz et al. 2008) within each 500-m buffer. We placed these into categories with similar vegetation that could obstruct the view of surveyors (resight categories) and similar vegetation or land cover (habitat-type categories; Table 1). We measured distances from each segment center to primary and secondary roads (US Census Bureau 2011) and developed lands. We also recorded latitude and longitude of each segment.

Data analysis

We report here estimates of abundance, density and distribution. Although abundance and density are reported at different scales and the scale of abundance is not the same as the

Table 1 Ecological systems from California GAP analysis (Lennartz et al. 2008) that fell within transects surveyed for raptors, shrikes and ravens in southern California deserts in January 2012–2013. Ecological systems were placed into categories of similar vegetation that could obstruct the view of surveyors (resight categories) for models of resight probability and into categories of habitat types for models of habitat associations.

California GAP analysis ecological systems	Percentage of total area surveyed	Resight category	Habitat-type category
California Central Valley and Southern Coastal Grassland	0.0050	Low vegetation	Crop/grassland
California Central Valley Mixed Oak Savanna	0.0004	Tall vegetation	Other
Cultivated Cropland	0.9214	Low vegetation	Crop/grassland
Developed, Low Intensity	1.3467	Developed	Developed
Developed, Medium Intensity	0.1040	Developed	Developed
Developed, Open Space	4.1201	Developed	Developed
Great Basin Pinyon-Juniper Woodland	0.0061	Tall vegetation	Other
Inter-Mountain Basins Big Sagebrush Shrubland	0.0008	Tall vegetation	Other
Inter-Mountain Basins Greasewood Flat	0.0002	Tall vegetation	Other
Inter-Mountain Basins Shale Badland	0.6519	Very low vegetation	Nearly bare
Mojave Mid-Elevation Mixed Desert Scrub	6.6527	Tall vegetation	Mixed scrub
North American Warm Desert Active and Stabilized Dune	0.4734	Very low vegetation	Nearly bare
North American Warm Desert Bedrock Cliff and Outcrop	13.1210	Very low vegetation	Cliff/outcrop
North American Warm Desert Pavement	1.3990	Very low vegetation	Nearly bare
North American Warm Desert Playa	1.0936	Very low vegetation	Nearly bare
North American Warm Desert Riparian Mesquite Bosque	0.0537	Tall vegetation	Xeric riparian
North American Warm Desert Riparian Woodland and Shrubland	0.2098	Tall vegetation	Xeric riparian
North American Warm Desert Volcanic Rockland	2.6483	Very low vegetation	Nearly bare
North American Warm Desert Wash	11.8801	Tall vegetation	Xeric riparian
Open water	0.0232	Tall vegetation	Other
Sonora-Mojave Creosotebush-White Bursage Desert Scrub	49.0802	Tall vegetation	Creosote
Sonora-Mojave Mixed Salt Desert Scrub	5.7002	Tall vegetation	Salt scrub
Southern California Dry-Mesic Chaparral	0.0005	Tall vegetation	Other
Unclassified	0.5078	Tall vegetation	Other

scale of our habitat features, abundance is still reasonable to report and link to habitat because it is the foundation of previous work; and habitat features in human-dominated landscapes are strongly correlated between territory and landscape scales (Cornell and Donovan 2010; i.e., within 500 m and beyond 500 m of transects).

Determining abundance (Objective 1) and distribution (Objective 3) of avian predators required several steps. First, we identified common species as those for which we collected >30 observations (an observation may include >1 bird) from both years combined. Second, we conducted mark-recapture analyses to estimate probabilities of detecting birds (resight probability; the chance of seeing a bird when it is present). We completed species-

specific analyses for each of the common species and a combined-species analysis that included all predatory birds. Third, we used these resight probabilities to adjust raw bird counts from surveys to estimate abundance of each species. Fourth, abundance estimates were then used as response variables in generalized linear mixed models to determine how cover types and anthropogenic disturbances influenced distributions of common predatory birds.

Estimating resight probability

We used a multi-strata framework (Brownie et al. 1993; Lebreton et al. 2003) within Program MARK (White and Burnham 1999) to estimate resight probabilities for each common species (species-specific) and for all predatory birds (combined). Multi-strata models are especially relevant to our approach because they include an unobserved stratum (Fujiwara and Caswell 2002) which analytically "allow" birds to move between the transect and unobservable locations during surveys.

We created a capture history for each individual bird that we observed. Capture histories included seven observation occasions. The first was a positive dummy observation. Thus, all birds were recorded as present and observable first, and then each individual could have either remained within the observable stratum and were seen or unseen, or they could have moved immediately to the unobservable stratum.

The next six observation occasions corresponded to potential sightings of predatory birds. One occasion was for an observation that occurred while driving and before we reached a point. Four were for observations at each 2.5-min count interval at a survey point. The last one was for an observation while driving that occurred after we left a survey point. For each of the last six observation occasions in the capture histories, resight probability could have differed for the transect stratum and birds could have moved between the transect and the unobservable stratum.

We considered birds were recaptured or resighted if they were observed by either team member during a point count and during any one of the other 5 observation periods (driving or point count). Thus, there were three possible situations where a bird could have been recaptured: (1) a bird could have been observed first along a driving segment (within 800 m [0.5 miles] of a point) and again at a point, (2) a bird could have been observed at a point, and then again during the following driving segment (within 800 m of a point), or (3) it could have been observed at more than one time period at a point. We did not record multiple observations of birds encountered only when driving.

We structured model sets for estimating resight probability to determine the factors that were associated with resight probability. We included two effects in all models. The first was a year effect that accounted for observer differences between survey teams or annual differences in prey abundance or other measures of habitat quality. The second was an effect of survey type to differentiate resight probabilities between driving and point-count surveys.

We considered three additional factors that could have influenced resight probabilities in species-specific and combined-species models. We allowed resight probability to be either the same or different among the four 2.5-min count intervals at point counts. We also included models with and without resight probabilities differing by resight categories (Table 1) and by distance band in which we observed birds. The model sets for species-specific models included all combinations of these 3 factors (8 models).

Our combined model sets included models with and without a species factor for resight probabilities. For models with the species factor, we allowed resight probability to differ

for the common species, but held it the same for the remaining species. For models without the species factor, we constrained resight probability to be the same for all species. We included a total of 16 models in the combined-species model set.

For all models, we added constraints to survival and movement probabilities. We set survival equal to 1.0 as no birds were expected to die or permanently emigrate from the study area during the course of a 16-mile survey. We also allowed movement rates to differ between driving and point segments of each survey, because we expected the probability that birds move to or from an observable area (stratum) to change with the duration of time spent searching (i.e., different movement rates as a vehicle passed a bird than during a 2.5-min count). We also expected each bird species to behave differently and allowed movement rates to vary among common species.

The best estimates of resight probabilities are obtained after model averaging (Buckland et al. 1997; Burnham and Anderson 2002). When model averaging, we included all models from each model set that had support in the data and whose AICc weight was >0.001. Thus, we estimated resight probabilities for each species-specific model set for common species and for all species from the combined-species model set.

Calculating abundance and density

We estimated abundance and density of predatory birds at every transect segment from bird counts at each segment and model-averaged estimates of resight probabilities. We adjusted counts by dividing them by resight probabilities for all predatory birds observed. To estimate density, we used adjusted bird counts from a fixed area that included distances up to 500 m from the transect centerline (i.e., the first two distance bands). We used results from species-specific models to correct abundance and density estimates of common species and combined-species models to correct estimates of all other species.

Comparison of past and present density estimates (Objective 2)

We converted relative abundance estimates from a prior study to density estimates to facilitate comparison of survey results over time. Knight et al. (1999) surveyed for predatory birds within the central portion of our study area and reported numbers of predatory birds within 365 m of road survey transects. They reported abundances of birds observed per 100 km driven. We converted abundance estimates from Knight et al. (1999) to density estimates. For each 100 km driven, they surveyed an area 0.73 × 100 km or 7300 ha. We then compared densities by dividing our density estimates before correcting for imperfect detection by their estimates converted to density. This ratio provides an estimate of how populations of certain predatory birds may have changed from 1992–1993 to 2012–2013.

Estimating habitat associations for birds of prey (Objective 3)

We assembled model sets for each of the common species to determine how abundance was influenced by environmental characteristics (i.e., habitat features). Environmental characteristics included habitat-type categories, location (latitude and longitude), and distances to major roads and human development. We included models with and without habitat types and location to determine how distribution of predatory birds changed throughout the study area. We also included models with and without distance to major

roads and distance to development to determine how anthropocentric development influenced predatory birds. Thus, each model set included 16 models.

We structured models of habitat association as generalized linear mixed models (GLMMs; proc GLIMMIX, SAS 9.3, Cary, North Carolina, USA). Response variables included both corrected abundance and corrected density of predatory birds measured at each transect segment. GLMMs also included, as explanatory variables, each environmental characteristic from each transect segment. Every model incorporated random effects of year and transect, and used an identity link, the Gaussian distribution, and restricted maximum likelihood estimation, but not an intercept term. When support was found for more than one model in the set, we model averaged linear regression coefficients to obtain the best fitting model (Buckland et al. 1997; Burnham and Anderson 2002).

Results

We conducted 48 surveys over 1230 km of transects between 3–11 January 2012 and 11–18 January 2013. In total we made 713 observations comprised of 1734 individuals and 16 species. The most abundant birds counted were common ravens followed by (in decreasing order of abundance): red-tailed hawks, turkey vultures, loggerhead shrikes, and American kestrels (Table 2; scientific names listed). Although turkey vultures were the third most abundant species, we observed only 22 groups of them and did not consider

Table 2 Number of observations and individuals of raptors, shrikes and ravens counted during surveys in southern California deserts, January 2012–2013

Species	Scientific name	No. of observations[a]	No. of individuals[b]
Turkey vulture	*Cathartes aura*	22	159
Osprey	*Pandion haleaetus*	2	2
White-tailed kite	*Elanus leucurus*	3	3
Northern harrier	*Circus cyaneus*	12	12
Cooper's hawk	*Accipiter cooperii*	5	5
Red-tailed hawk	*Buteo jamaicensis*	162	163
Ferruginous hawk	*Buteo regalis*	2	2
Golden eagle	*Aquila chryseatos*	9	9
Great-horned owl	*Bubo virginianus*	2	2
Burrowing owl	*Athene cunicularia*	1	1
American kestrel	*Falco sparverius*	45	45
Merlin	*Falco columbarius*	3	3
Peregrine falcon	*Falco peregrinus*	1	1
Prairie falcon	*Falco mexicanus*	10	10
Loggerhead shrike	*Lanius ludovicianus*	77	78
Common raven	*Corvus corax*	350	1232
Unknown hawk		7	7

[a] No. of observations is the number of groups of birds observed

[b] No. of individuals is the total number of birds observed

them a common species. We also counted 12 other raptors, for which total observations numbered 12 or fewer individuals per species during both 2012 and 2013, combined.

Estimating raptor abundance and density (Objective 1)

Factors associated with resight probabilities for species-specific models included distance to birds, time interval of point counts and resight categories (Online Resource 1). In all model sets, as distance to birds increased, resight probabilities decreased. Resight probabilities for all species (ΣAICc weights > 0.78) except loggerhead shrikes (ΣAICc weight = 0.38) varied among the four time intervals of each point count. Resight categories were important to resight of American kestrels (ΣAICc weight = 0.85), and ravens (ΣAICc weight = 1.0), but not of red-tailed hawks (ΣAICc weight = 0.51) or loggerhead shrikes (ΣAICc weight = 0.33). There was no pattern relating decreased resight probabilities to areas with taller vegetation or development. Resight probabilities were higher for point-count surveys (>0.92) than for driving surveys (American kestrels = 0.001, all other birds >0.49; Online Resource 2). Mean resight probabilities for all observations (i.e., unlimited observation distance used for abundance estimates) were generally lower than for observations within 500 m of transects (i.e., observations used for density estimates; Table 3).

Factors associated with resight probabilities for combined-species models were similar to species-specific models. Resight probability decreased as distance to birds increased, differed by resight category (without an apparent pattern), and differed among time intervals for point counts (Online Resource 1). There was less support for models that allowed resight probability to vary by species (ΣAICc weight = 0.45) than for models without this effect (ΣAICc weight = 0.56). Resight probabilities for combined-species models were higher for point counts (>0.88) than for driving surveys (0.46–0.58), and were similar to those for species-specific models (>0.92 for point counts and >0.49 for driving surveys; except driving surveys for American kestrels <0.149).

Abundance and density estimates, adjusted for resight probability, varied widely among species recorded during surveys (Table 3). Abundance was highest for American kestrels, although this estimate was unrealistically large due to an extremely small estimate of resight probability for this species for distances >500 m. The next highest abundances, in order, were for common ravens, turkey vultures, red-tailed hawks, and loggerhead shrikes. Density estimates were highest for common ravens, loggerhead shrikes, red-tailed hawks, American kestrels, and northern harriers.

Comparison of past and present density estimates (Objective 2)

We converted relative abundance estimates from Knight et al. (1999) to density estimates for 6 species (Table 3). All species showed substantial differences in density over time as shown by growth ratios (0.18–5.20). Golden eagles showed the greatest decrease (0.18) with prairie falcons also decreasing (0.53). The largest increase was for loggerheaded shrikes (5.20). Densities of red-tailed hawks, American kestrels, and common ravens also increased (2.44–3.12).

Estimating habitat associations for birds of prey (Objective 3)

Predatory birds showed wide variation in abundance and density patterns throughout the Sonoran and Mojave Deserts of southern California (Online resources 3 and 4). Density of

Table 3 Abundance (number per 16-miles transect) and density (number per ha) estimates before (raw) and after adjusting for resight probability (p) from surveys of raptors, shrikes and ravens in southern California deserts, January 2012–2013. Abundance was calculated from unlimited observation distances and density estimates were calculated from observations within 500 m of transects. Abundance estimates (number per 100 km of survey transects) from surveys conducted in December 1992 (golden eagles) and January 1993 (other species) from Knight et al. (1999) are converted to density estimates for comparison. Growth ratios are the proportion change from 1992–1993 to 2012–2013 based on raw density estimates. Growth ratios >1 indicate an increase in density, those <1 suggest a decrease in density.

Species	Abundance (no/transect)			Density (no/ha)			Knight et al. (1999)		
	Raw	Adjusted	Mean p	Raw	Adjusted	Mean p	No/100 km	Converted density	Growth ratio
Turkey vulture	3.31	5.70	0.58	0.000024	0.000026	0.93			
Osprey	0.04	0.10	0.40	0.000008	0.000026	0.31			
White-tailed kite	0.08	0.11	0.73	0.000016	0.000016	0.99			
Northern harrier	0.25	0.33	0.76	0.000049	0.000073	0.66			
Cooper's hawk	0.10	0.13	0.78	0.000032	0.000035	0.93			
Red-tailed hawk[a]	3.40	5.52	0.62	0.000744	0.000996	0.75	1.74	0.000238	3.1
Ferruginous hawk	0.04	0.05	0.89	0.000008	0.000008	0.95			
Golden eagle	0.19	0.23	0.82	0.000016	0.000022	0.74	0.67	0.000092	0.2
Great-horned owl	0.04	0.07	0.63	0.000016	0.000026	0.63			
Burrowing owl	0.02	0.02	1.00	0	0				
American kestrel[a]	0.94	1.9×10^{30}	<0.01	0.000251	0.000432	0.58	0.75	0.000103	2.4
Merlin	0.06	0.11	0.59	0.000024	0.000041	0.59			
Peregrine falcon	0.02	0.04	0.57	0	0				
Prairie falcon	0.21	0.27	0.79	0.000032	0.000035	0.93	0.45	0.000062	0.5
Loggerheaded shrike[a]	1.63	2.93	0.55	0.000599	0.001042	0.57	0.84	0.000115	5.2
Common raven[a]	25.67	33.37	0.77	0.003795	0.004265	0.89	11.04	0.001512	2.5
Unknown hawk	0.15	0.15	0.99	0.000016	0.000017	0.97			

[a] Adjusted abundance and density estimates were based on species-specific models of p. All others were based on combined-species models of p

red-tailed hawks and abundance and density of American kestrels were not associated with habitat types, location, or distances to major roads and human development. Abundance of red-tailed hawks and loggerhead shrikes and abundance and density of common ravens showed unique and habitat-specific distribution patterns.

Abundance of red-tailed hawks was associated with habitat types (ΣAICc weight = 0.87) and latitude and longitude (ΣAICc weight = 0.59), but density was constant throughout the study area (Online Resources 3 and 4). Red-tails appeared most abundant in crop/grassland areas and developments, although neither relationship was strong (i.e., coefficients were large but 95 % CI included 0). Abundance appeared to decrease as one moved north and east through the study area (ΣAICc weight = 0.59).

Abundance of loggerhead shrikes was highest in crop/grassland (95 % CI included 0) and showed increasing trends toward the south and east (Online Resource 4). Loggerheaded shrike density appeared to increase slightly away from major roads and decreased toward the north and east, although neither pattern was strongly supported in the data (ΣAICc weight < 0.10).

Raven abundance and density were related to habitat types (ΣAICc weight = 1.0; Online Resources 3 and 4). Raven abundance was positively associated with development (2.4 ± 1.1; Beta ± SE) and density was positively associated with development (0.11 ± 0.02) and crop/grassland areas (0.06 ± 0.01).

Discussion

Understanding distributions of desert organisms is essential to their conservation management. This is especially important in areas with accelerated increases in human population density and development, such as in southern California. Human population growth in such areas has great potential to affect wildlife populations through habitat destruction (Lovich and Bainbridge 1999; Olson and Dinerstein 1998) and by subsidizing predator populations (Boarman et al. 2006; Esque et al. 2010; Knight and Kawashima 1993; Kristan and Boarman 2007). Our surveys provided important insight at low cost and, as such, show the value of data which are easy to collect and inexpensive for management of desert ecosystems.

We found overlap in habitat use among three of the four most common predatory birds, red-tailed hawks, loggerhead shrikes, and ravens. These birds showed preferences for areas with agricultural crops (shrikes) or areas of human development and crops (red-tailed hawks and ravens). These patterns highlight the ability of these avian predators to persist in association with humans in a desert system. Human production of crops in the desert often requires irrigation (Lovich and Bainbridge 1999), which dramatically increases primary productivity relative to adjacent natural areas and provides water for predatory birds (Boal et al. 2003). Human food becomes available to wildlife, often in the form of refuse, at developments in the desert which increases scavenging opportunities and benefits predators or their prey (Boarman et al. 2006; Esque et al. 2010).

Ravens are subsidized by humans in deserts. In the DRECP area, ravens that use human developments have greater access to food, water, perches and nest sites (Boarman et al. 2006; Knight and Kawashima 1993; Kristan and Boarman 2007), which results in higher nesting success (Kristan and Boarman 2007). One consequence of subsidizing populations of ravens is an increase in predation risk to other native prey, such as the desert tortoise (*Gopherus agassizii*; Kristan and Boarman 2003). In other desert and semi-desert regions,

raven populations benefit from presence of power poles, and predation of sage grouse (*Centrocercus* spp.) is a major conservation concern in those areas (Coates et al. 2008). Perch deterrents on power poles do not limit their use by ravens or other predatory birds (Prather and Messmer 2010) and wildlife managers are turning to control programs to reduce raven populations (US Department of Agriculture 2014).

A key aspect of raven ecology that contributes to their ability to apply predation pressure to rare populations is they have a generalist diet (Kristan et al. 2004). Humans directly subsidize ravens by providing food (e.g., landfills, roadkill) and indirectly by bolstering prey populations. Food sources for other predatory birds, such as red-tailed hawks and loggerhead shrikes, are most likely subsidized through anthropogenic benefits to prey populations, but also with increases in roadkill that they scavenge. Like ravens, red-tailed hawks and shrikes also benefit from human made structures that provide perch and nest sites (Boal et al. 2003; Knight and Kawashima 1993), which could also increase quality of habitats in native deserts without subsidized food sources.

Populations of red-tailed hawks, American kestrels, and loggerhead shrikes appear to have increased in the DRECP area over the last 20 years; however, these species show different patterns of associations with humans and likely are affected differently by human subsidies. Red-tailed hawks have increased during migration throughout western North America and kestrels have increased in the Goshute Mountains, NV (Hoffman and Smith 2003) thus increases of these species in the Sonoran and Mojave Deserts may be related to increasing use by migrants during winter. Red-tailed hawks were associated and likely subsidized by agricultural and other developments. Kestrels showed no associations with humans and are unlikely subsidized, and shrikes were associated with and likely subsidized by agriculture.

Increased development of renewable energy within the DRECP is likely to affect certain predatory birds but not others. Populations of ravens and red-tailed hawks are likely to increase due to human subsidies, although increases of red-tailed hawks may depend upon continued increases of migratory populations elsewhere. Renewable energy development is unlikely to affect loggerhead shrikes or American kestrels, as neither species shows association with such non-agricultural development.

Winter surveys of predatory birds provide key data on their populations in southern deserts. At this time of year, counts peak or are near peak levels for red-tailed hawks, golden eagles, American kestrels, and ravens (Knight et al. 1999). These patterns suggest there is either an influx of migrants to the Sonoran and Mojave Deserts during winter or they become more visible this time of year. For example, resident common ravens shift habitat associations from areas of native desert to human development during winter and are more readily counted (Boarman et al. 2006). Such changes in seasonal use provide valuable information when interpreting new data.

Although comparison of data collected and analyzed with different techniques is challenging, they may also be informative. Within the DRECP, populations of avian predators that were associated with humans appeared to have increased from 1992–1993 to 2012–2013. This corresponds with a 240 % increase in urban development and a 120 % increase in agriculture and developed open space (Online Resource 5) from the first GAP Analysis in California (Davis et al. 1998) to the second (Lennartz et al. 2008). Population changes of avian predators could result from multiple factors including growth of the human population in the California deserts and subsidization of these predatory birds, changes in migratory patterns and wintering locations for red-tailed hawks, and other landscape-level changes that could benefit resident ravens and shrikes. Not all species of raptors have benefited from increased anthropogenic disturbance on the landscape and

prairie falcons and golden eagles, in particular, appeared to have declined. This finding has important implications for our continued conservation of both the increasing and decreasing species.

Estimating abundance and density of animals in the desert is vital to understanding how populations change over time. The highest quality data from our surveys came from species-specific estimates of resight probability for common species. We also obtained vital information, albeit lower quality, for rare species from combined-species analyses of resight probability. In particular, we show population trends for prairie falcons and golden eagles may be in decline, and further study is warranted. Other datasets for these species, including nest monitoring, are not likely to capture population changes associated with winter use of the DRECP area. Additionally, we provide baseline data on raptor abundance and density corrected for resight probability for future comparisons. Because this approach gave us information beyond what we would have collected by focusing either on common or rare species, it provides a cost effective framework for others conducting surveys in similar desert environments outside of California.

The DRECP is a proactive plan to site renewable energy development in areas with the least possible impacts to sensitive desert species (DUDEK and ICF International 2011). In addition to effects from habitat destruction from large projects and fragmentation of native deserts, such development has great potential to change desert ecology by changing predation patterns through non-food subsidies to avian predators. Further investigation is needed to determine if populations of other avian predators are in decline and if any declines are due to competition with subsidized predators.

Acknowledgments The Bureau of Land Management, California State Office provided funding. This work is Scientific Article No. 3239 of the West Virginia Agricultural and Forestry Experiment Station, Morgantown. We thank T. Esque and two anonymous reviewers for their comments that greatly helped to improve this manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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