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Tolerance and avoidance of urban cover in a southern California suburban raptor community over five decades

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Abstract

We explored nest site placement and re-use relative to ornamental tree usage and urbanization level in a diurnal raptor community in southern California (USA) during three discrete time periods spanning five decades (1971–2018). Re-use of prior years' nests varied among species, with Red-tailed Hawks (*Buteo jamaicensis*) and American Kestrels (*Falco sparverius*) showing moderate re-use rates (ca. 30%), and Red-shouldered Hawks (*Buteo lineatus*), and Cooper's Hawks (*Accipiter cooperii*) showing almost none. Nearly all nests were in native and naturally-occurring trees during the 1970s, yet by 2018, most Cooper's Hawk nests, and many Red-tailed Hawk nests, were located in ornamental vegetation such as pines (*Pinus* spp.) and eucalyptus (*Eucalyptus* spp.). The amount of urban cover around nest sites increased for Red-tailed, Red-shouldered, and Cooper's hawks during the study period, but not for American Kestrels, which were confined to the least-urban areas. Cooper's Hawks appear to now be selecting urban nest sites over wildland sites, based on the increase in surrounding urban cover, even as landscape urbanization has not substantially changed in the study area during the last two time periods. Our study illustrates the utility of long-term datasets in understanding how a species' urban tolerance can change over time, and highlights species (including three extirpated taxa) that may be failing to adapt to local urbanization.

Keywords Red-tailed hawk · Red-shouldered hawk · Cooper's hawk · American kestrel · Urbanization · Urban tolerance · Change over time · Re-use

Introduction

Urban areas have been expanding in extent twice as fast as population increases (Seto et al. 2011), and understanding urban tolerance in species is crucial to conserving the Earth's biotic diversity (Vitousek et al. 1997; Marzluff 2005; Sol et al. 2014). Even as urbanization homogenizes complex ecosystems at the global scale (McKinney 2006; Devictor et al. 2007), certain species exploit urban sites, resulting in novel communities (Møller et al. 2015). Blair (1996) recognized "urban avoiders", "suburban adaptable" taxa, and "urban exploiters", which represent a gradient of tolerance from outright urban avoidance to synanthropy, a strong dependence of the built environment (Johnston 2001).

Research on urban birds must be re-assessed over time, since ecological forces (and human activity) are in constant flux (Marzluff et al. 2001; Marzluff 2016), and because cities are constantly evolving new architectural styles and landscaping palettes. Data on bird species distribution and habitat usage prior to a period of environmental change can provide an important baseline to compare with contemporary observations (e.g., Tingley and Beissinger 2009).

We examined the response of raptors (Accipitridae, Falconidae and related families) to urbanization over a nearly fifty-year period by leveraging historical data to track changes in nest location, nest re-use, and nest substrate (tree type) within the upper Malibu Creek watershed in southern California, USA. Raptors provide ideal subjects to assess tolerance of urban environments, being apex predators with readily detectable nests often re-used for years. They display a broad range of urban tolerance, with certain species such as Peregrine Falcons (*Falco peregrinus*) drawn to urban habitats

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(e.g., Cade et al. 1996), and closely related species (e.g., Prairie Falcon *Falco mexicanus*) avoiding them (Steenhof 2013). Raptor nest site choice may be related to the disposition and outcome of the prior year's nest (Jiménez-Franco et al. 2014), the availability of resources (Kreiderits et al. 2016), the presence of conspecifics and competitors (Sumasgunter et al. 2016), human disturbance (Richardson and Miller 1997), weather during nesting season (Rockweit et al. 2012), and the use of rodenticide by humans in the area (Rattner et al. 2011). In wildland areas, territory persistence has been shown to affect reproductive output (higher productivity in newly-established nests on existing territories; Jiménez-Franco et al. 2014), and nest re-use may be correlated with nest predation (higher in re-used nests; Otterbeck et al. 2019). However, data on nest re-use in urban areas are sparse, and relatively few studies have investigated the ability of birds (including raptors) to persist within urban landscapes over multiple decades (see Marzluff et al. 2001).

We asked two main questions: 1. Assuming ample nest site availability across the study area, which raptor species are using sites that are more or less urbanized than would be predicted, and has this changed over time? 2. How does nest site re-use and ornamental tree use relate to raptors' persistence in urban areas over time? Because we did not mark and track individual raptors over time, we infer the use of these strategies by analyzing historical and current land cover and nest location and re-use data, rather than by directly measuring the movements of the pairs themselves. From a conservation perspective, we suggest that urban-avoiding species – those using urbanized sites at a lower rate than would be expected – are of higher conservation concern than urban-tolerant ones, with urban-preferring species being of least conservation concern (while recognizing that certain urban-preferring species may still have specific and often unique ecological requirements, particularly when nesting). We further suggest that raptors' acceptance of artificial nest structures, and use of ornamental (vs. native/naturally-occurring) vegetation for nesting (see Bloom and McCrary 1996) may enable colonization into urban areas that did not historically support these features. Understanding changes in the pattern of nest site placement and re-use through time should provide insight into how species may respond in the future to a landscape that is less wild, and more disturbed by humans.

Methods

Study area

We selected a coastal southern California study area that features human-modified (urban) land interspersed with large protected areas of open space, a history of ornithological investigation in the region dating to the nineteenth Century (e.g., Grinnell 1898), and a record of raptor nests mapped and documented since the early 1970s. We restricted our fieldwork to the Upper Malibu Creek Watershed, which covers ca. 13,000 ha in western Los Angeles County and adjacent Ventura County (Fig. 1). During this period, the study area was transformed from a mostly rural, ranching landscape of grassland with scattered oaks and small subdivisions of tract homes, to a modern one of protected open space interspersed by large expanses of homes. Since the 1970s, a vast "urban forest" has developed and matured across the Los Angeles region, featuring large ornamental trees from around the world (Gillespie et al. 2011). These trees now support a diverse avifauna year-round, including woodland species that might not have been present until a few decades ago (see Wood and Esaian 2020).

No ranching exists today in the study area, though cattle and sheep ranching was prevalent prior to the 1990s, and land ownership now includes federal, state and local park/open space agencies, and private property. A development boom occurred much later here than in the San Fernando Valley and central Los Angeles Basin to the east, with the population of Agoura Hills roughly doubling from 1980 (11,399) to 1990 (20,390), and remaining roughly constant since then (Los Angeles Almanac 2018). Elevation within the study area ranges from 185 to 730 m.a.s.l., and the climate is Mediterranean, with April temperatures with average low of 9 °C (record 3 °C) and average high of 24 °C (record 38 °C) ("Agoura Hills, CA"; www.myweather2.com). Rainfall is highly variable year-to-year, with the average since the late 1970s being ca. 43 cm/year with nearly all precipitation falling in winter.

Please refer to Supplemental Materials for historical and modern photographs of the study area, and examples of raptor nest sites.

Focal species

Nine raptor species bred regularly in the Santa Monica Mountains into the 1980s (Garrett and Dunn 1981), including several owls, which we dropped from the analysis due to the difficulty of locating nests. We also dropped three species from our urban cover analysis that have long occurred in very low densities (<5 pairs/year) in the entire Santa Monica Mountains, and that are considered extirpated within the study area such that an analysis of their urban tolerance and preferences is not possible: White-tailed Kites (*Elanus leucurus*), Golden Eagles (*Aquila chrysaetos*), and Prairie Falcons (*Falco mexicanus*) (Willet 1912, Allen et al. 2016, www.ebird.org). Thus, we focused on the four most common, widespread and extant diurnal raptor species, Red-tailed Hawks (*Buteo jamaicensis*), Red-shouldered Hawks (*Buteo lineatus*), Cooper's Hawks (*Accipiter cooperii*) and American Kestrels (*Falco sparverius*).

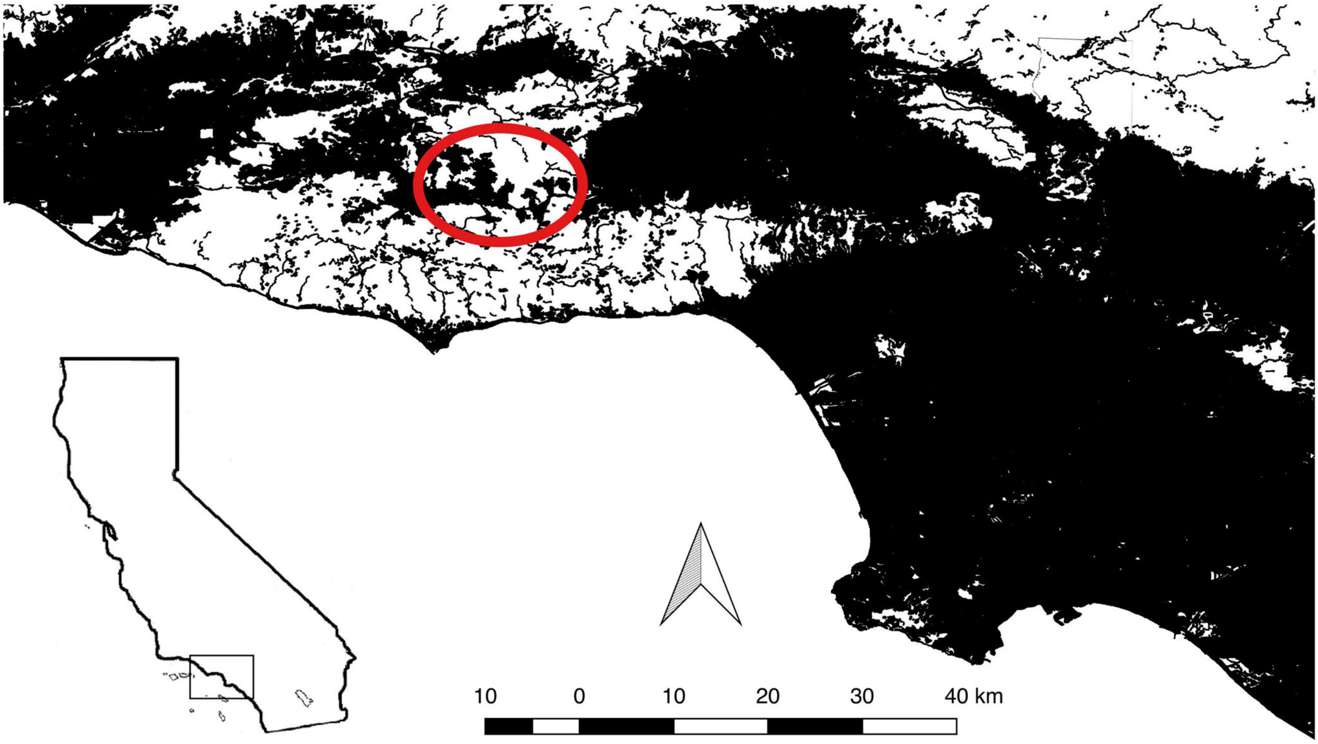

Fig. 1 Study area. The study area was established based on the historical distribution of nests monitored in prior studies (Lee 2004; NPS, unpubl. data). It is roughly bounded by: Kanan Rd. and Westlake Blvd (34.1970, −118.8228); Mulholland Hwy. and No. Kanan Dume Rd. (34.0965, −118.8123); Mulholland Hwy. and Stunt Rd. (34.1020, −118.6600), and the western terminus of Victory Blvd. (34.1850, −118.6685)

Study period

We obtained observational data from the study area from three discrete time periods, which we refer to as "eras":

1. **Early**. Opportunistic nest-mapping of raptors in the Santa Monica Mountains and Simi Hills (which includes our entire study area), beginning during the preparation of planning documents to support the Santa Monica Mountains National Recreation Area in the 1970s, and continuing as the parkland was purchased and protected in the 1980s (NPS, unpubl. data). Nest records from this era within the study era extend from 1971 to 1986 (median year = 1979).
2. **Middle**. Systematic and comprehensive mapping of raptor nesting sites (except American Kestrel) by Lee (2004) in the Simi Hills and north-central Santa Monica Mountains during 2002 and 2003, centered on and encompassing the study area;
3. **Late.** Re-surveys of prior raptor nest locations in the study area during 2017–2018, with comprehensive nest-searching throughout the study area by DSC and field assistants (this study).

No survey effort data nor methods used for nest-searching exist for the early era. Lee (2004) did not report hourly/daily effort, but reported revisiting all mapped historical nest sites, and conducting extensive field visits to both urbanized and natural open space across the study area. Her methods generally followed recommendations by Craighead and Craighead Jr. (1969), in that likely raptor nesting areas were visited on foot, and all trees/substrate scanned with binoculars.

During the spring/summer of 2017 and 2018, we attempted to replicate Lee (2004) by searching for and mapping previously-reported raptor nests in the study area, visiting each reported nest location to confirm re-use, and carefully searching the vicinity of each nest on at least two days during the breeding season, scanning in all directions from the original nest site, and as necessary, from vantage points nearby with better sight-lines to determine the current nesting status of all raptors in the area. We conducted surveys in 2017–18 only from public roads/trails (following Lee 2004). One author (DSC) lives near the center of the study area and submitted 54 eBird checklists from days afield the study area (exclusive of home) during February – July 2018 (and 15 during the same timeframe in 2017), and two interns devoted portions of 29 field days to nest-searching and monitoring here between 2 April and 1 June 2018. To augment our observations, we searched submissions of focal species within the study area in online databases (www.iNaturalist.org, www.eBird.org) throughout 2017 and 2018, and attempted to track down reports of paired birds (and nests) in the field during this time. While Lee (2004) provided fledging information for all nests, we obtained these data for a portion of nests, and do not analyze it here. We re-plotted all nest locations in 2017 and 2018 using reported coordinates or those derived from the iPhone 7 map application (OS v. 12.1.2), confirmed using satellite imagery in Google Earth Pro, and photographed each nest site in situ.

Nest assessment, including re-use

We considered a nest "active" if it appeared occupied during the nesting season, being structurally sound (fresh material used) with at least one adult bird performing nesting activity at the nest (typically nest-building, incubating, or tending young; Fuller and Mosher 1987). Lee (2004) relied on nest appearance rather than presence of birds to determine activity, and we have inconsistent data on how early-era nests were determined to be active, though many noted the number of young produced. We occasionally located nests by the presence of nearby nestlings, and counted these as active only if the young appeared not to be capable of sustained flight. We did not revisit nests to document fledgling success in 2017–18, so our late era data should be considered an analysis of "breeding events" (per Jiménez-Franco et al. 2014), rather than necessarily successful breeding.

To find new nests, we checked large stick structures on trees, transmission towers, and rock outcrops that appeared to be inactive raptor nests at least two times during the 2017–18 breeding season, but we only analyzed these further if we detected breeding activity; otherwise we dropped them from the analysis (or in the case of formerly active nests, considered them inactive). Due to the difficulty in documenting occupancy of cavity nests of American Kestrels, we assumed that a potential nest cavity was active if we observed a kestrel pair near the cavity, and at least one adult entering the cavity, during the breeding season (April–June). We pooled nest locations within each era in an effort to minimize inter-annual variation that might occur due to exceptional weather conditions in a particular year.

We did not analyze year-to-year occupancy (due to incomplete data), so cannot say with certainty what constituted a "new" nest occupancy event (per Jiménez-Franco et al. 2014). And, we did not devote enough observation time to define territorial boundaries of nesting pairs of our focal species (nor was this reported for the historical nests). Thus, our nest re-use categories include total number of active nesting sites during each era, and number of nesting sites (nest matching the reported coordinates and tree type) reoccupied from either prior era, for each species. This differentiated pairs that have re-nested in the same site from those that selected new nest sites. It did not, however, differentiate pairs that selected new nesting sites within existing territories.

We identified to genus, and if possible, species, the trees in which nests were built. In nearly all cases, planted, ornamental trees were non-native, and naturally-occurring trees native. However, two western sycamores (or hybrids between sycamore and London plane, *Platanus* x. *acerifolia*) that held nests in the late era were almost certainly planted as ornamental landscaping, located in residential tracts well away from riparian zones, and so we treated these as non-native.

Defining "urban habitat"

Informed by prior analyses (e.g., Dykstra 2018; White et al. 2018), we used percentage of urbanized land surrounding each nest as our unit of comparison, which served as a surrogate for various urban-associated features. For nests of the middle and late eras, we used publicly available shapefiles of statewide land-cover data developed in the 2000s (CALVEG 2009), because relatively little new urbanization had occurred in the study area between the middle and late eras (confirmed by Google Earth Pro). This coverage was comprised of the "Urban or Developed" category, defined as "landscapes that are dominated by urban structures, residential units, or other developed land use elements such as highways, city parks, cemeteries and the like" (https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsbdev3_045405.pdf). We combined all other land cover categories that were not "Urban and Developed" to create a map of just two categories, urban (human-modified) and wildland (largely natural). For early era nests, we drew an urban boundary for the study area from historical aerial photographs from the mid-1970s (UCSB Library 2018), using Google Earth Pro to overlay these image files atop modern imagery.

We used QGIS (QGIS Development Team 2018) to calculate percentage of urban (vs. wildland) landcover at radial distances from all nests, using two distance scales, 250-m, which was suggested by White et al. (2018) as approximating the "macrohabitat" of raptor nests in their study of a raptor community in Reno, and 670-m ("nearest nest" *per* White et al. 2018), which approximates the midpoint between two adjoining nests, recognizing that territory size among species and pairs is highly variable and difficult to estimate. Specifically, we used percent urban cover for nests in the early era using the shapefile of urban cover from the 1970s, and used the CALVEG (2009) shapefile for nests from both the middle and late eras.

Urban tolerance vs. urban preference

We recognized two main strategies used by nesting raptors, "urban tolerating" and "urban avoiding", which may be employed by individual pairs, as well as by species. An urban-tolerant pair could either remain at the same nest site in or near urban cover year after year even as urbanization expands, or it might shift its nest site to maintain a similar level of urbanization within its breeding territory. Pairs may also shift nesting sites toward more urbanized habitat, if that habitat provides them with resources they cannot find in wildland habitat. We apply the term "urban preferring" to this latter scenario, referring to species whose nest sites appear to have shifted towards urban cover over time, utilizing urban habitat (including ornamental vegetation) at a higher rate than would be expected given the background level of urbanization across the study area. An urban avoiding pair would either maintain nest sites far from urbanization over time, or would move nest sites even farther away from urbanization, and would be occurring in urban habitats at a lower rate than would be expected given unlimited nesting options.

While urban tolerance implies some level of acceptable urbanization around a nest site, "urban preference" is nuanced and more difficult to assess, and requires that we show that species selected territories at a higher rate than would be expected by chance. This is essentially impossible to determine with certainty without knowing the distribution of suitable nest sites (e.g., the number and distribution of potentially suitable nest trees and territories in the study area) and by tracking marked birds. We addressed this indirectly, in two ways. First, we used the same urban cover shapefile for the middle and late eras since urban development has been limited since 2003. Thus, any increase in urban cover around nests between these two eras would have to be from a pair moving its territory to a more urban neighborhood. We then used a random point design to compare mean urban cover around observed vs. randomly-plotted points across the study area. While some of these random points themselves might be unsuitable for nesting, we assumed the surrounding territory (at 250 and 670 m) would support at least one nest tree. Notably, because we observed local raptor nest sites in such a wide variety of locations, including backyards, freeway offramps, school parking lots, marinas, etc., we felt that 100 randomly-placed territories (at two distance calculations) would capture a range of potential nest sites.

Data analysis

We used R (ver. 1.0.153, R Core Team 2017) to perform a Kruskal-Wallis test on mean urban cover for 250-m and 670-m buffers around nests, across all three eras, for each hawk species. Because Lee (2004) did not record American Kestrel nests, we used a Wilcoxon rank sum test with continuity correction for the two samples of American Kestrel nests (early vs. late era).

To test for "preference" in nest site choice, we used 100 randomly plotted points within the study area (using the random point generator in QGIS), and compared these to our observed nests, for each era. For this comparison, we again calculated percent urban cover, but instead used these random points with 250-m and 670-m buffer distances, resulting in two sets of means (observed vs. random) for each species, for each of the three eras. We then used Wilcoxon rank sum tests to test for significance in the differences of mean urban cover between observed vs. random points. As with the observed nests, we calculated percent urban cover for nests in the early era using a separate shapefile of urban cover from the 1970s, and used the CALVEG (2009) shapefile for tests on data from the middle and late eras.

We evaluated whether the proportion of native vs. non-native nest trees changed over time for each species using a chi-squared test for all three eras.

Results

Nest re-use

Nest re-use within the study area over time varied greatly among species (Table 1). While Red-tailed Hawk nest re-use appears to have been low between the early and middle era (3.3%), it jumped to 25.7% by the late era (9 of 35 late-era nests were re-used from at least one prior era). Of 21 Red-shouldered Hawk nest sites, we found none active in more than one prior era. Of 25 Cooper's Hawk nest sites monitored, we found just two active in prior eras, and no late-era Cooper's Hawk nests had been active in a prior era. We found three of 11 late-era American Kestrel territories active in both the early and late eras.

Table 1 Patterns of nest site re-use, by era. We considered late-era nest sites re-used if active in *either* the early or the middle eras. We pooled data from multiple years within each era to determine the total nest sites

Species	Total Active Early	Total Active Middle	Re-used (Middle)	Total Active Late	Re-used (Late)
Red-tailed Hawk	30	39	1	35	9
Red-shouldered Hawk	4	8	0	9	0
Cooper's Hawk	10	11	2	6	0
American Kestrel	7	N/A	N/A	11	3
White-tailed Kite	2	4	0	0	0
Golden Eagle	3	0	0	0	0
Prairie Falcon	1	0	0	0	0

Native vs. non-native tree use

Nearly all raptor nests within the Upper Malibu Creek Watershed since the 1970s have been in trees, though the tree type (where known) has changed markedly in recent decades, and among the four focal species (Table 2). Red-tailed Hawk nests were overwhelmingly in (native) oaks during the early era (coast live oak *Quercus agrifolia* and valley oak *Q. lobata*). Significantly more nests were in planted/non-native trees (especially eucalyptus *Eucalyptus* and related species, and pines *Pinus* spp.) by the middle era ($X^2 = 4.75$, df = 1, $p = 0.029$), and by the late era, more than half of all Red-tailed Hawk nests were placed in non-native trees, providing an even greater contrast with the early era ($X^2 = 17.37$, df = 1, $p < 0.001$). A handful of early and middle-era Red-tailed Hawk nests were located in cliffs and transmission towers, though we documented no active nests in either of these substrates during the late era.

Every Cooper's Hawk nest during the early era was found in a native coast live oak, and native willows (*Salix* spp.) were used along with native oaks by this species during the middle era. However, by the most recent era, five of six Cooper's Hawk nest trees were non-native species. Nest substrate choice by Red-shouldered Hawks appears to be skewed toward natives, particularly sycamores. All American Kestrel nesting sites during both the early and late era were in native trees, including oaks and sycamore.

Among the extirpated species, two White-tailed Kite nests active in the early era were both in native oaks (presumably coast live oak), and all four White-tailed Kite nests active in the middle era were also in the native coast live oak. Up to three Golden Eagle territories were noted (to 1993), two in remote cliffs and one on a transmission tower within extensive oak savannah (NPS data, unpubl.). The single Prairie Falcon territory was high on a rocky outcrop along the northern edge of the study area, active only in the early era.

Table 2 Nest sites of focal raptor species, by era (where known). Asterisks indicate non-native tree species. Note that we considered certain sycamores (*Platanus* sp.), alder (*Alnus* sp.) and cottonwoods (*Populus* sp.) non-native if they were obviously planted as part of urban landscaping, or were not clearly native forms

Red-tailed Hawk	Early	Middle	Late
Cliff	1	0	0
Tower	2	3	0
Oak (*Quercus*) sp.	23	26	15
Sycamore (*Platanus racemosa*)	1	1	1
Cottonwood (*Populus fremontii*)*	0	0	1
Eucalyptus (*Eucalyptus*) sp.*	1	6	11
Pine (*Pinus*) sp.*	0	3	7
Alder (*Alnus*) sp.*	0	0	1
Native/Non-native	24/1	27/9	16/20
Red-shouldered Hawk			
Oak (*Quercus*) sp.	1	4	0
Sycamore (*Platanus racemosa*)	1	0	8
Cottonwood (*Populus fremontii*)	0	1	0
Eucalyptus (*Eucalyptus*) sp.*	1	2	1
Native/Non-native	2/1	5/2	6/3
Cooper's Hawk			
Coast live oak (*Quercus agrifolia*)	10	7	1
Sycamore (*Platanus racemosa*)	0	0	2
Cottonwood (*Populus fremontii*)	0	0	1
Willow (*Salix*) sp.	0	4	0
Shamel ash (*Fraxinus udhei*)*	0	0	1
Pine (*Pinus*) sp.*	0	0	1
Native/Non-native	10/0	11/0	1/5
American Kestrel			
Oak (*Quercus* sp.)	5	n/a	9
Sycamore (*Platanus racemosa*)	2	n/a	2
Native/Non-native	7/0	n/a	11/0
White-tailed Kite			
Coast live oak (*Quercus agrifolia*)	2	4	0
Native/Non-native	2/0	4/0	0/0

Change in urban cover over time

The mean percent urban cover surrounding each raptor nest was significantly higher by the late era for the three hawk species (Red-tailed Hawks, Red-shouldered Hawks, and Cooper's Hawks) at both the 250 and the 670 buffer distance. American Kestrels, had lower mean urban cover values during the late era than in the early era, though we did not find these values to be significantly different (Table 3).

Comparing mean urban cover around observed nests vs. those of randomly-plotted points, we found no significant difference between observed and random nest sites for Red-tailed Hawks at either the 250 m or 670 m buffer distance, across each era examined (Fig. 2a). Urban cover around Red-shouldered Hawks, Cooper's Hawks and American Kestrels nest sites differed significantly across eras (at both buffer distances), though in different directions. Late era Red-shouldered and Cooper's hawks were more urban than would be predicted by random points (Fig. 2b and Fig. 2c). American Kestrels showed a change in the opposite direction, nesting in less urbanized sites that would be expected by random points (Fig. 2d).

Discussion

Our focal species had contrasting responses in nest site placement as the study area urbanized over time, with territories of Red-tailed Hawks, Red-shouldered Hawks, and Cooper's Hawks increasing their urban cover, and American Kestrels

Table 3 Changes in mean percent urban cover surrounding each species' nest, by era. "N" refers to the total number of active nests (see text) observed in the study area during that era. Note that data for American Kestrels during the middle era were not collected. Wilcoxon rank sum test used for American Kestrel (two samples; data from middle era not collected), and Kruskal-Wallis test used for the other raptor species (df = 2 for each)

			250 m		670 m	
Species	Era	N	mean	sd	mean	sd
Red-tailed Hawk	**Early**	30	2.90	8.37	5.85	8.63
	Middle	39	19.82	30.46	28.45	26.47
	Late	35	27.93	27.72	23.36	26.90
	3-era comparison		$X^2 = 23.31$	$P < 0.001$	$X^2 = 18.80$	$P < 0.001$
Red- shouldered Hawk	**Early**	4	28.08	28.92	11.44	10.02
	Middle	8	6.56	13.02	9.89	12.95
	Late	9	66.77	32.11	69.68	20.14
	3-era comparison		$X^2 = 11.56$	$P = 0.003$	$X^2 = 14.28$	$P < 0.001$
Cooper's Hawk	**Early**	10	0.33	1.05	1.32	4.03
	Middle	11	29.59	39.93	22.51	26.01
	Late	6	79.02	13.71	58.33	15.43
	3-era comparison		$X^2 = 15.13$	$P < 0.001$	$X^2 = 19.01$	$P < 0.001$
American Kestrel	**Early**	7	11.30	27.57	10.23	19.48
	Late	9	3.16	4.49	8.52	10.66
	2-era comparison		W = 28.5	$P = 0.761$	W = 25	$P = 0.519$

showing no significant change over time. By analyzing nest placement as urbanization remained similar (i.e., middle vs. late era), we found that Cooper's and Red-shouldered hawk nests were much more urban, a bias that was confirmed by comparing randomly-placed points to observed nests (such a bias was not found for Red-tailed Hawks). We found the opposite pattern with American Kestrels, which are now selecting significantly less-urban territories than would be expected. This suggests that a species' urban tolerance can change over time, either as the landscape becomes dramatically more urbanized (i.e., early vs. middle eras), or if it remains roughly the same (middle vs. late eras).

Though data are sparse on their level of nest re-use, Cooper's Hawk pairs studied in Albuquerque, New Mexico, frequently moved in and out of nesting territories from year to year, with fewer than half the territories active for all five years (Millsap 2017). This tendency of Cooper's Hawks to rotate nest sites annually (also noted locally by McCammon and Cooper 2018), combined with the strong increase in urban cover around Cooper's Hawk nests between the middle and late eras (when urbanization across the study area did not substantially increase), suggests this species may be shifting its nesting sites toward urban areas. Though we did not confirm this using marked birds, it appears to be a recent change in strategy, as an urban bias was not apparent in the prior eras (Fig. 2c). Indeed, Bloom and McCrary (1996) reported fewer than 5% of Cooper's Hawk territories in "urban environments" in Orange and San Diego counties (California) from 1970 to 1995.

Local Red-shouldered Hawks showed even less nest site fidelity sites than Cooper's Hawks, and may be responding to factors not associated with our simple urban/wildland dichotomy, such as the presence of riparian corridors; of 29 nests in Orange County, Wiley (1975:136) found that this species "nested close to permanent or seasonal water, with no nest trees found farther than 23 m from a creek bed." Thus, Red-shouldered Hawks may use a wide range of urbanization provided these features (and suitable nest trees) are present.

Red-tailed Hawks showed a clear tendency to re-use prior nest sites (including those inactive in the middle era yet active in the early era). This behavior has long been noted in the species (e.g., Fitch et al. 1946), and is still frequent in the local population elsewhere in the region (McCammon and Cooper 2018). Thus, many Red-tailed Hawks in the study area may be tolerating some increased level urbanization while remaining at the same nests year after year. American Kestrels, with some territorial fidelity noted (though with a relatively low sample size), may be using a similar strategy, though at the opposite end of the urbanization spectrum, remaining in the least-urbanized habitats year after year.

The acceptance of planted/non-native trees (which were scarce historically) by all three hawk species may enable their persistence in urban areas (see discussion in Chiang et al. 2012). Red-tailed Hawks may simply select territories with trees of any type (either planted or native) at the edges of natural habitat used for daily foraging (see Chace and Walsh 2006), as long as these areas support very tall nesting trees

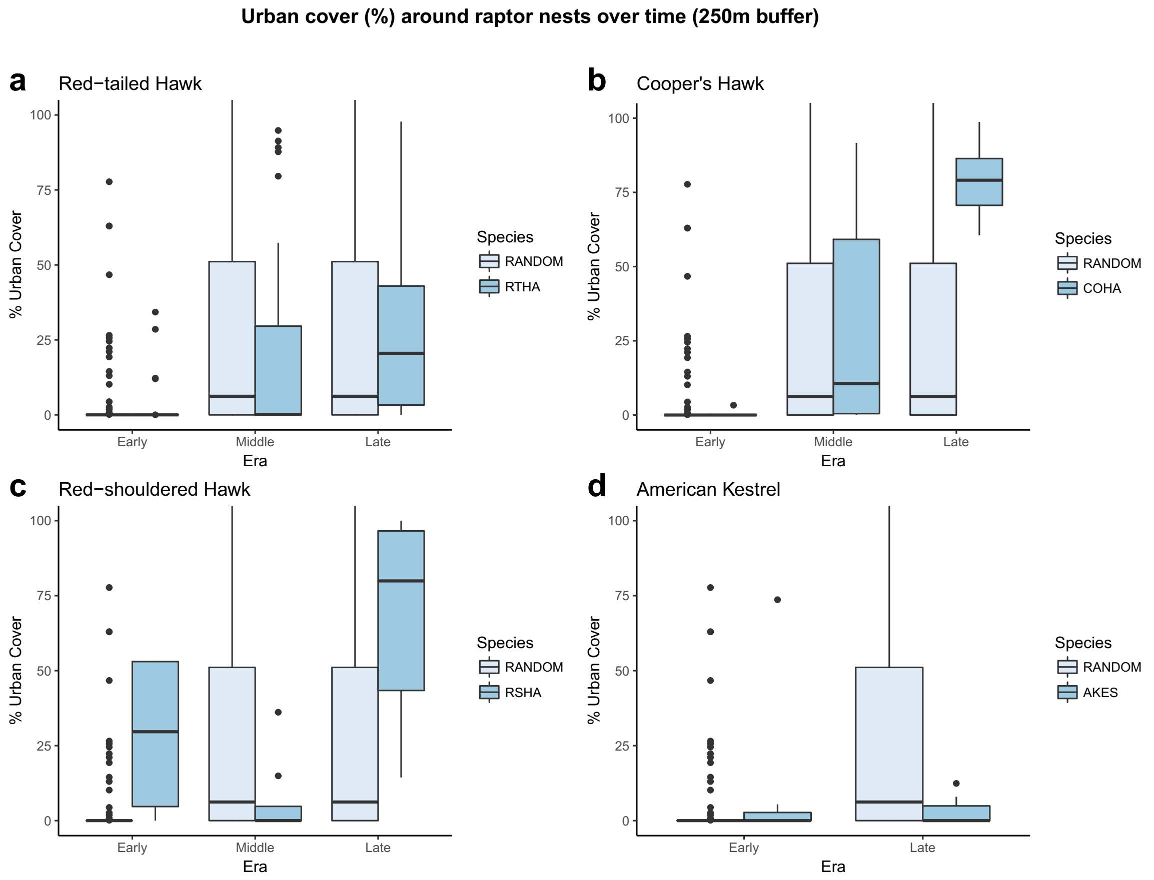

Fig. 2 a Mean urban cover of Red-tailed Hawk territories, random vs. observed, by era Fig. 2b Mean urban cover Cooper's Hawk territories, random vs. observed, by era Fig. 2c Mean urban cover of Red-shouldered Hawk territories, random vs. observed, by era Fig. 2d Mean urban cover of American Kestrel territories, random vs. observed, by era

(Fitch et al. 1946; Wiley 1975). Cooper's Hawks frequently nest in non-native street trees in wholly-urban settings in southern California, including areas with no undeveloped land for several kilometers around (D.S. Cooper, unpubl. data). Elsewhere, they have become an urban bird since the 1990s in places like Tucson, AZ (Boal and Mannan 1999), Albuquerque, NM (Millsap 2017), Reno, NV (White et al. 2018) and Milwaukee, WI (Stout and Rosenfield 2010).

Nest site choices have clear conservation implications. Local American Kestrels are now nesting in significantly less urbanized sites than would be predicted by random points, which suggests that urbanizing regions – at least with the type of urbanization found in the study area – may not support them in the long-term. The species is known to be in decline throughout North America, which some authors have correlated with loss of large habitat patches (e.g., Smallwood et al. 2009). Since kestrels have previously responded positively to nest box programs (e.g., Steenhof and Peterson 2009), these declines may be reversible. Yet, if kestrels rely on some prey type or nest feature absent from urban and urban-edge sites, they may not recover as areas become more urban. This may be happening in the region, as just a single potential territory has been noted in each year of the Griffith Park raptor survey, which examined a study area roughly the same size as ours closer to the urban core of Los Angeles (McCammon and Cooper 2018). It could be that natural nest cavities are scarce within urban areas (both Los Angeles County and Ventura County require that homeowners remove dead trees from residential properties, and dead native trees are scarce in and near urban areas; pers. obs.). Because species' ecology varies geographically, we caution against extrapolating our findings too broadly across the entire range of our focal species. For example, American Kestrels are known to nest in industrial areas elsewhere in the Los Angeles area (DSC, pers. obs.), and Red-shouldered Hawks may be both a riparian specialist and a suburban adaptor, depending on the location of the study area (Bloom et al. 1993).

Finally, the extirpated species in our study area are arguably more imperiled than any of our four focal species in the region. Golden Eagles were extirpated over most of the Los Angeles Basin, including most of the Santa Monica Mountains, by the mid-1990s (Allen et al. 2016). Prairie Falcons were probably declining even earlier (e.g., Willet 1912), and while a single breeding territory may have been present at the edge of the study area (Simi Peak) into the 1970s (NPS, unpubl. data), specific information on this pair is sparse, and the species is not considered an extant breeder today. Kites persisted very locally as breeders into the 2000s, yet have not nested in the study area since ca. 2010 (D.S. Cooper, unpubl. data; www.ebird.org), and rarely nest near urban areas in southwestern California (Unitt 2004). While we have little data on Golden Eagle, White-tailed Kite or Prairie Falcon, their absence may indicate a current level of urbanization above a particular threshold within the study area, the cumulative effect of lack of a food source, or loss of a key foraging habitat. White et al. (2018:57) found Golden Eagles to be among the most sensitive to urbanization in a survey of nesting raptors in and around Reno, NV, noting that during their study "residential development encroached within 0.5 km of nesting Golden Eagles coinciding with the nesting area being unused the following year for the first time in recent years". A larger-scale survey would be needed to adequately assess the needs of these species.

We acknowledge that many other factors, such as food availability and interspecific interactions, must also play a role in nest site selection. Common Ravens (*Corvus corax*), which harass raptors, are abundant in the study area year-round, and we noted multiple raven nests in transmission towers and tall trees, including some that had been mapped as raptor nests in earlier eras (when ravens were apparently less common, *per* Lee 2004). Regional climate may also play a role in determining nest site location. Average rainfall dropped during each of our three temporal eras examined; the total winter precipitation for the three years preceding the average year of discovery of the early nests (1976–1979) was 64 cm of rain, then 40 cm (2000–2003), and just 28 cm (2015–2018; Woodland Hills; http://www.laalmanac.com/weather/we137a.php). This drop in rainfall may have had a strong effect on local nesting raptors and prey levels by pushing raptors toward urban-edge habitats (with irrigated trees and abundant squirrels and rabbits for prey), and away from wildland habitat and oaks struggling with drought. We have no prey data for nests of any of the eras, though we recognize this would be a fruitful area of study. We also recommend examining the effect of wildfire in the study area, as several major fires have impacted the wildland habitats in the study area since the 1970s, including the Topanga Fire in 2005 which burned a large portion of the study area between the middle and late eras, and impacted many mature oaks (the devastating Woolsey Fire burned much of the study area in November 2018, just after our fieldwork ended). Finally, we note that our analysis of site fidelity is based on discrete nest sites (generally trees), rather than on the much larger territories used by our focal species. Estimates of site fidelity would be higher if we considered whether whole territories, rather than specific nest sites, were re-used, but since individual birds were not marked, it is nearly impossible to determine the boundaries of territories from our data, particularly when temporally separated by decades.

Our study provides an example of how to incorporate historical data and modern nesting observations, and how to use these data to understand how species persist in urbanizing areas. Multi-decade studies may clarify species that may be in need of continued conservation attention, such as Golden Eagles, and ones that may be at risk of future decline, such as American Kestrels. Research into the shared characteristics of urban-avoiding species would aid in their conservation in areas that have not yet been subject to the type of urban expansion of places like Los Angeles, but whose avifauna may be similarly threatened.

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Data availability We are providing our data table of historical and recent raptor nests, and the R code used to generate the plots and conduct the statistical analysis, as supplementary data

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