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RESEARCH ARTICLE

High rates of anticoagulant rodenticide exposure in California Barred Owls are associated with the wildland–urban interface

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ABSTRACT

Pesticide use is pervasive and the exposure of non-target wildlife has been well documented over the past half-century. Among pesticides, anticoagulant rodenticides (AR) have emerged as a particularly important threat in forests of the western United States, with exposure and mortality reported for several species of conservation concern. To further quantify this threat, we collected specimens of Barred Owls (*Strix varia*) and Barred Owl x Spotted Owl hybrids from the Klamath and Cascade Mountains and Sierra Nevada in California, USA to use as indicator species for environmental contamination with AR and to infer exposure of closely related and ecologically similar Northern and California Spotted Owls (*S. occidentalis caurina,* and *S. o. occidentalis,* respectively). We tested 115 Barred Owl and 12 Barred Owl x Spotted Owl hybrid livers for 8 AR compounds and found high rates of exposure (62%) across our study area, and greater than previous studies in the Pacific Northwest. In addition, we sampled 7 ovaries from 7 females and 100% tested positive for AR. Female Barred Owls were more likely than males to be exposed (78% and 50%, respectively). Unlike previous studies, we found no clear link between illegal cannabis cultivation and AR exposure. However, Barred Owls sampled in proximity to the wildland–urban interface (WUI) were more likely to be exposed to AR. Though the exact source (e.g., cannabis cultivation or application around human dwellings) and location are unknown, the association of AR exposure with the WUI was supported from GPS data from Barred Owls, Northern and California Spotted Owls, and hybrids using the WUI for foraging. The high rate of AR exposure in Barred Owls and hybrids provides mounting evidence of an additional stressor that ARs may pose to Spotted Owls—including the first evidence for California Spotted Owls—and fauna native to western forest ecosystems.

Keywords: Barred Owl, brodifacoum, environmental contamination, pesticides, Spotted Owl, *Strix varia*, *Strix occidentalis*, wildland–urban interface

LAY SUMMARY

- Anticoagulant rodenticides have emerged as an important threat in forests of the western United States, and it is vital to understand how and where wildlife is exposed.
- As indicator species for Spotted Owl exposure, we screened 115 Barred Owls and 12 Barred Owl x Spotted Owl hybrids, collected from northern California, USA for 8 anticoagulant rodenticides.
- 62% of owl specimens (72 Barred and 7 hybrid) were exposed to anticoagulant rodenticides, in particular to the acutely toxic, second-generation class.
- Females and owls sampled close to the wildland–urban interface were more likely to be exposed to anticoagulant rodenticides.
- GPS-tagged Barred and Spotted Owls commonly foraged in the wildland–urban interface, suggesting Spotted Owls are also likely at risk of exposure.
- The high rate of AR exposure in Barred Owls and hybrids provides mounting evidence of an additional threat to Spotted Owls.

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Las altas tasas de exposición a rodenticidas anticoagulantes en *Strix occidentalis occidentalis* se asocian con la interfaz urbano-silvestre

RESUMEN

El uso de plaguicidas es generalizado y la exposición no deseada de la vida silvestre ha sido bien documentada durante el último medio siglo. Entre los pesticidas, los raticidas anticoagulantes (RA) han surgido como una amenaza particularmente importante en los bosques del oeste de los Estados Unidos, con exposición y mortalidad reportadas para varias especies de interés para la conservación. Para una cuantificación más extensa de esta amenaza, recolectamos especímenes de *Strix varia* y de híbridos de *S. varia* x *S. occidentalis* de las montañas Klamath y Cascade y de la Sierra Nevada en California, EEUU, para usarlas como especies indicadoras de contaminación ambiental con RA y para inferir la exposición de *S. o. caurina* y de *S. o. occidentalis*, dos especies estrechamente relacionados y ecológicamente similares. Evaluamos los hígados de 115 individuos de *Strix varia* y de 12 híbridos de *S. varia* x *S. occidentalis* para 8 componentes de los RA y encontramos altas tasas de exposición (62%) a lo largo del área de estudio, y mayores tasas que la de los estudios previos del noroeste del Pacífico. Además, tomamos muestras de 7 ovarios de 7 hembras y el 100% dio positivo para RA. Las hembras de *S. varia* tuvieron más probabilidad de estar expuestas que los machos (78% y 50%, respectivamente). A diferencia de estudios anteriores, no encontramos un vínculo claro entre el cultivo ilegal de cannabis y la exposición a RA. Sin embargo, los individuos de *S. varia* muestreados en las proximidades de la interfaz urbano-silvestre (IUS) tuvieron más probabilidades de estar expuestos a RA. Aunque se desconoce la fuente (e.g., el cultivo de cannabis o la aplicación alrededor de las viviendas humanas) y la ubicación exacta, la asociación entre la exposición a RA con la IUS se basó en datos de GPS de *S. varia*, *S. o. caurina*, *S. o. occidentalis* e híbridos que utilizan la IUS para buscar alimento. La alta tasa de exposición a RA en *S. varia* y en los híbridos proporciona evidencia creciente de que los RA pueden representar un factor de estrés adicional para *S. occidentalis*—incluyendo la primera evidencia para *S. o. occidentalis*—y la fauna nativa de los ecosistemas forestales del oeste.

Palabras clave: brodifacoum, cannabis, contaminación ambiental, interfaz urbano-silvestre, pesticidas, Strix occidentalis, Strix varia

INTRODUCTION

Pesticide use is pervasive with an estimated 2.5 billion kilograms applied globally each year (Alavanja 2010). The exposure of non-target wildlife to pesticides has been well documented over the past half-century (Grier 1982, Peakall and Kiff 1988), with anticoagulant rodenticide (AR) identified as a particularly widespread and important conservation issue (Stone et al. 1999, Erickson and Urban 2004). Though exposure to AR may result in direct mortality, lesser-understood sub-lethal exposure can also have subtle detrimental effects on non-target wildlife (Riley et al. 2007, Thomas et al. 2011, Serieys et al. 2018). Most accounts of wildlife exposure to AR compounds have occurred in urban or agricultural settings, where the use of rodenticides is frequently permitted for the benefit of human health and mitigation of agricultural damage (Erickson and Urban 2004). However, exposure to AR in remote forest settings is increasingly being reported in the western United States, where multiple species of conservation concern have documented cases of exposure and mortality (Gabriel et al. 2012, 2018, Thompson et al. 2014, Franklin et al. 2018, Wiens et al. 2019). Non-target avian and mammalian predators are particularly vulnerable to secondary AR exposure through the consumption of prey that has ingested rodenticide baits (Stone et al. 1999, Erickson and Urban 2004). Poisoned rodents may be easier prey, because internal hemorrhaging greatly reduces joint mobility, causes lethargy, and reduces escape responses (Brakes and Smith 2005). Mitigating the threat of ARs to non-target wildlife in these forested settings requires understanding which species are exposed, as well as where and how exposure occurs.

Within the past decade, exposure of non-target wildlife to AR has been documented via an unexpected route: illegal cannabis cultivation in remote forests in the western U.S. (hereafter "western forests"; Gabriel et al. 2012, Wengert et al. 2018). Growers use ARs, in addition to other pesticides, to prevent rodent damage to cannabis plants, grow-site infrastructure, and food caches (Gabriel et al. 2012, Thompson et al. 2017). Hundreds of illegal cannabis cultivation sites have been found and eradicated in the foothills and mid-elevation slopes of the southern Sierra Nevada and the Klamath/Cascade Mountains, and an average of 4.5 kg (enough to kill ~22,000 rats from an LD_{50} of 0.27 mg kg^{-1}; Erickson and Urban 2004) of AR are found per site (Wengert et al. 2018). These sites are often located far from other human developments and roads in remote parts of the forests where detection is unlikely (Thompson et al. 2017). However, another source of AR exposure in non-target forest wildlife is from more expected applications around human structures and dwellings located in or near forested settings in what is known as the wildland–urban interface (WUI; Radeloff et al. 2005), defined as where houses meet or are intermixed with undeveloped wildland vegetation. In addition to habitat conversion, exposure of non-target wildlife to ARs is an emerging conservation challenge for wildlife living in close proximity to the WUI (Riley et al. 2007, Serieys et al. 2018).

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Whether the exposure is occurring via cannabis cultivation or human communities, exposure to AR in western forests appears to threaten multiple species of conservation concern. For example, high rates of AR exposure have been reported in dead or dying Pacific Fishers (*Pekania pennanti*) in coastal California and the southern Sierra Nevada (85%, *n* = 101; Gabriel et al. 2012, 2015, Thompson et al. 2014) and in Northern Spotted Owls (*Strix occidentalis caurina*) found dead in coastal California (70%, *n* = 10; Gabriel et al. 2018). Given the lethal and potential sub-lethal effects of AR, exposure to these pesticides may exacerbate, or even be among the causes of, long-term population declines of both Northern Spotted Owls (Dugger et al. 2016) and California Spotted Owls (*S. o. occidentalis*; Tempel et al. 2013, 2014, Conner et al. 2016) when combined with other key stressors including megafires (Jones et al. 2016), historic habitat loss (Dugger et al. 2016), and competition with invasive species (Long and Wolfe 2019, Wood et al. 2020a). However, given the status of species of conservation concern for both Spotted Owl subspecies, testing Spotted Owls for AR exposure with large sample sizes of liver or blood sampling is difficult and not practical (e.g., obtaining permits).

To characterize Spotted Owls' risk of AR exposure, we used Barred Owls (*S. varia*) as indicator species (Caro and O'doherty 1999) for the presence of AR within the southern Klamath and Cascade Mountains and the Sierra Nevada in northern California. Barred Owls are a closely related and ecologically similar relative of Spotted Owls (Gutiérrez et al. 2007, Wiens et al. 2014) and were first documented within the range of the Northern Spotted Owl in the 1960s (Livezey 2009) and the core range of the California Spotted Owl in the early 2000s (Dark et al. 1998). Barred Owls compete with congeneric Spotted Owls where they occur sympatrically, and there is strong evidence they are one of the causes of declines in Spotted Owl populations (Wiens et al. 2014, Long and Wolfe 2019). Previous work has reported high rates of AR exposure in Barred Owls in Oregon and Washington (48%, *n* = 40; Wiens et al. 2019), and in coastal California (40%, *n* = 84; Gabriel et al. 2018). Barred Owls are likely a reasonable, if not conservative, indicator species for AR exposure in Spotted Owls due to a complete overlap in diet and habitat with Barred Owls being less focused on rodent prey than Spotted Owls (Wiens et al. 2014).

In this study, we leveraged biological samples collected as part of an experimental Barred Owl removal study in both the Klamath/Cascades and the Sierra Nevada, which offered a rare opportunity to collect a large sample size at a regional scale. This large sample size allowed us to assess AR exposure across a gradient of conditions likely to influence AR prevalence in the environment, including human density and cannabis cultivation. Furthermore, this is the first study to assess AR exposure in California Spotted Owls through the use of Barred Owls as an indicator species. Because the most useful viable method of testing AR exposure requires the recovery of intact liver tissue from a freshly dead carcass, the collected Barred Owls are a unique opportunity to understand the extent to which both Northern and California Spotted Owls are potentially exposed to ARs within the two sub-regions of our study area. We also GPS-tagged Barred Owls and both Northern and California Spotted Owls to assess the extent to which foraging activities occurred in areas characterized by elevated AR exposure in lethally removed Barred Owls. Finally, we tested the potential of in-utero transfer of AR in *Strix* owls by screening ovaries of AR-positive Barred Owls.

We hypothesized that exposure to AR in forest predators, such as Barred Owls and Barred Owl x Spotted Owl hybrids (hereafter "hybrids"), is influenced by biological factors, such as age and sex, and environmental factors, such as proximity to human communities and the intensity of cannabis cultivation. To test these hypotheses, we quantified the exposure of Barred Owls and hybrids to a suite of AR compounds and evaluated the degree to which exposure was associated with a suite of biological and environmental factors. We predicted higher exposure rates in hybrids, assuming hybrids would have similar foraging behavior to Spotted Owls, which have a dietary niche more focused on rodents than that of Barred Owls (Wiens et al. 2014). We predicted that younger and female Barred Owls would have higher rates of AR exposure as a result of larger dispersal movements (Greenwood 1980). We also predicted that owls exposed to ARs would be in worse physical condition than owls not exposed to ARs, given the potentially deleterious effects of sub-lethal exposure to AR. Among environmental factors, we predicted that Barred Owls collected in areas more likely to be used for cannabis cultivation or closer in distance to either known cultivation sites or the WUI, would have greater exposure to AR. Thus, in addition to characterizing the prevalence of AR in *Strix* owls in two new regions, we aimed to elucidate how behavior and human land use patterns influence AR exposure.

METHODS

Study Area

We collected Barred Owls and hybrids from the southern Klamath and Cascade Mountains and from the Sierra Nevada in northern California (Figure 1) on National Forest lands, national park lands, and private commercial timberlands primarily owned by Sierra Pacific Industries. There was considerable variation in climate, elevation, topography, and vegetation, though both sub-regions were

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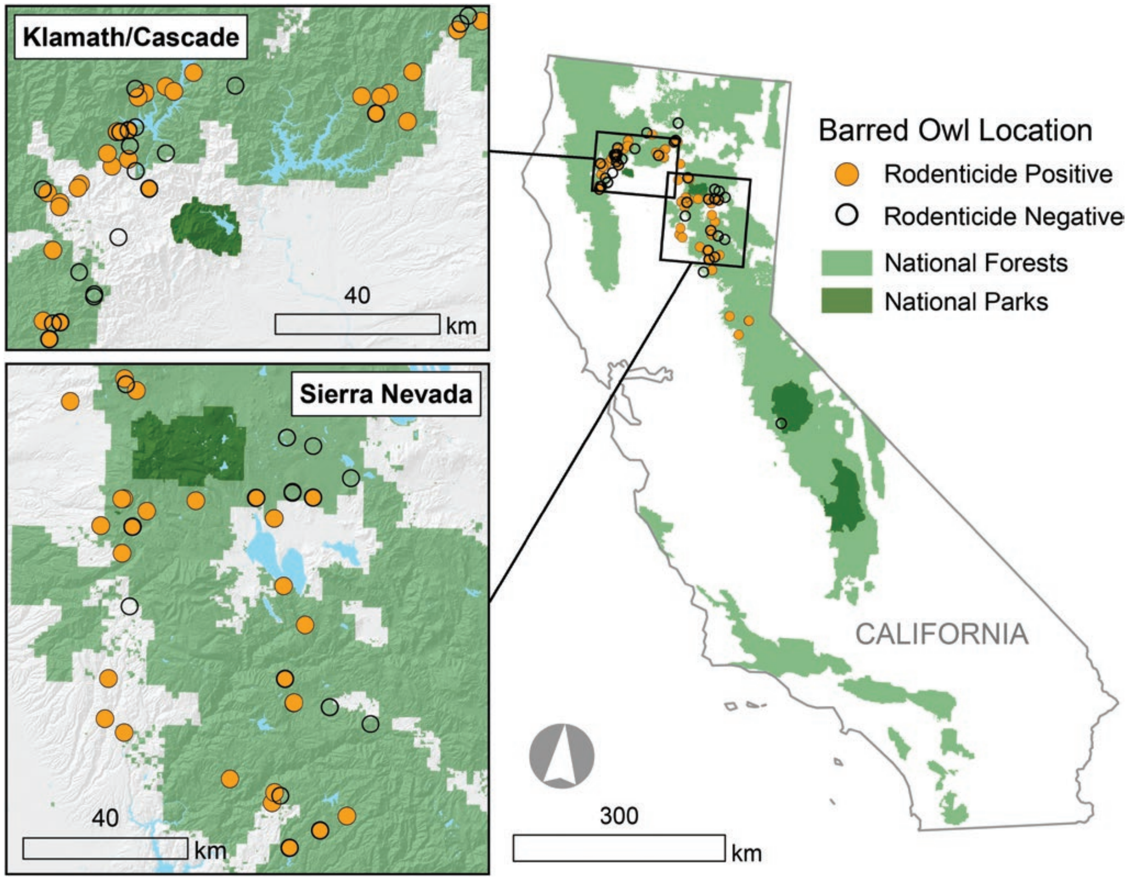

FIGURE 1. Locations of Barred Owls and Barred Owl x Spotted Owl hybrids collected from 2018 and 2019 and screened for anticoagulant rodenticides. Insets at the left show both the Klamath/Cascade and Sierra Nevada sub-regions in California, USA.

predominantly composed of mixed coniferous forest, dominated by ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), incense cedar (*Calocedrus decurrens*), Douglas fir (*Pseudotsuga menziesii*), and white fir (*Abies concolor*). Neither the U.S. Forest Service (S.C. Sawyer, personal communication) nor Sierra Pacific Industries (B.P. Dotters, personal communication) use ARs on lands they manage within our study area. However, there are houses in WUIs adjacent to lands where owls were collected, and it is not known whether ARs are used in these areas.

Tissue Collection and AR Screening

We lured territorial Barred Owls and hybrids by broadcasting digitally recorded Barred Owl vocalizations and collected them with a 12-gauge shotgun following methods described by Diller et al. (2014). We collected Barred Owls and hybrids under federal and state Scientific Collecting Permits (United States Fish and Wildlife Service permits MB24592D-0, MB53229B-0 and California Department of Fish and Wildlife permits SC-002114, SC-11963). We froze owls immediately after collecting them and stored the specimens in a –20°C freezer until we delivered them to the Museum of Vertebrate Zoology (University of California, Berkeley), where we extracted livers and ovaries. We were careful to avoid contamination between the two organs by separating them immediately after they were removed from the abdominal cavity and placing them in separate containers. We thawed all specimens for a similar amount of time to extract tissues, and we left no specimen thawed for over 24 hours. We shipped tissue samples to the California Animal Health and Food Safety Laboratory System (CAHFS; University of California, Davis) where they were screened for 8 commonly used ARs: warfarin, diphacinone, chlorophacinone, coumachlor, brodifacoum, bromadiolone, difethialone, and difenacoum. The first 4 belong within less-acutely toxic first-generation ARs (FGAR); the latter 4 are more acutely toxic second-generation ARs (SGAR) that were created in the 1970s due to rodents developing resistance to first-generation ARs (FGARs; Buckle et al. 1994). High-performance liquid chromatography-tandem mass spectrometry was used to screen tissue samples for AR exposure (whether or not any ARs were detected) and to quantify the concentration of ARs detected (Marek and Koskinen 2007). We classified AR exposure in livers and ovaries using the limit of detection (LOD), which allowed us to detect the presence of

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AR in any sample with a concentration above 0.005 μg g^{-1} wet weight (ww). We quantified AR concentrations in liver and ovary samples using the limit of quantification (LOQ), which was 0.050 μg g^{-1} ww for brodifacoum and 0.020 μg g^{-1} ww for all other ARs in owl livers, and 0.200 μg g^{-1} ww for all ARs in owl ovaries (Riley et al. 2007). Any sample above these LOQs could have concentrations quantified. These concentrations all fall below the 0.1 μg g^{-1} ww threshold for mortality rate of 10% of individuals previously reported in Barred Owls (Thomas et al. 2011). When samples had concentrations greater than the LOD and below the LOQ, we designated those individuals as having "trace" exposure.

Calculating Biological Variables

We identified owls in the field as Barred Owls or hybrids based on both plumage and territorial vocalizations. Individuals with vertical barring on the breast feathers and horizontal barring around the nape that produced distinct 2-phrase, 8-note calls (Odom and Mennill 2010) were identified as pure Barred Owls. Individuals with bars and spots on their breast feathers and that produced territorial calls that were not distinctly Spotted Owl or Barred Owl calls were identified as hybrids (Hamer et al. 1994). We classified age as either adult (≥3 yr), sub-adult (1–2 yr), or juvenile (0 yr), based on adults having wider terminal bands than sub-adults on all flight feathers, and juveniles lacking most or all body contour feathers (Mazur and James 2020, J. D. Wiens, personal communication). We determined sex by examining gonads in the lab, and we assessed body condition by characterizing the amount of subcutaneous fat content into four categorical values, with no fat being our baseline ("0"), slight fat ("1"), moderate fat ("2"), and heavy fat ("3"). Because fat reserves in owls change throughout the year (Massemin et al. 1997, DeLong 2006), we obtained a corrected fat index by calculating the residuals of a linear regression of fat against the month of the year (Supplemental Material Figure S1).

Calculating Environmental Variables

We assigned owls that were collected north of the Pit River to the Klamath/Cascade sub-region, and owls sampled south of this river to the Sierra Nevada sub-region (Figure 1). We used this designation to differentiate Barred Owls collected within the range of the Northern Spotted Owl (Klamath/Cascade) or of the California Spotted Owl (Sierra Nevada; Barrowclough et al. 2005). We calculated remaining environmental variables within 2,000 ha circular buffers around collection locations that approximated Barred Owl home range size in the region that we measured using GPS-tagged individuals in a previous study (see Wood et al. 2020a). We used a combination of law enforcement databases (IERC 2019) to calculate the number of known cannabis cultivation sites detected from 2004 to 2019 within the circular buffers. We also related AR exposure to a measure of the probability of illegal cannabis cultivation within the buffers, estimated from a maximum entropy (MaxEnt) model (G. M. Wengert personal communication) parameterized with variables indicative of the suitability of growing cannabis on California's public and private lands. The important variables in this predictive model included elevation, slope, precipitation, canopy cover, stand age, and distances to disturbance, freshwater, roads, and private lands, and used a resolution of 90 m for individual cells. From the MaxEnt model, we obtained an averaged index of cannabis cultivation suitability (ranging from 0 to 1) for each buffer to assess whether owls were more likely to be exposed in areas with more suitable conditions for cannabis cultivation.

Additionally, we calculated the distance of each Barred Owl removal location to the WUI based on 2010 census data (Radeloff et al. 2005, http://silvis.forest.wisc.edu/data/wui-change/), where owls that occurred within the WUI were assigned a distance of 0 km. Both intermix (where housing and vegetation intermingle) and interface (where housing occurs in the vicinity of contiguous wildland vegetation) components of the WUI spatial dataset were used. Four thresholds are defined in the WUI data provided by Radeloff et al. (2005) based on the level of housing density: high, moderate, low, and very low. We chose to use the low density WUI threshold requiring at least 6.17 housing units km^{-2} because of concordance we observed with this threshold and buildings visible in a building footprint spatial layer developed from Microsoft (https://www.microsoft.com/en-us/maps/building-footprints). Finally, we calculated landownership as the proportion of the circular buffers that were composed of National Forest lands. Descriptive statistics of the environmental variables is listed in Supplemental Material Table S1.

Characterizing Barred and Spotted Owl Foraging Activities

To characterize the distribution of Barred Owl foraging locations relative to environmental factors related to AR exposure (in this case WUIs, see below), we GPS-tagged 7 Barred Owls and 3 hybrids between May and August of 2017 and 2018 in the northern Sierra Nevada. We used visual and vocal lures to attract Barred Owls and hybrids and captured them with dho-gaza nets, and applied Argos-enabled GPS backpack tags (Lotek Wireless, Newmarket, Ontario, Canada). We programmed tags to record 4–6 nighttime locations per week between April and August, and then to record 1 location per week between September and March.

We also used locations from 24 GPS-tagged Northern Spotted Owls and 106 California Spotted Owls to characterize their use of areas associated with elevated AR

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exposure in Barred Owls—and thus the potential for Northern and California Spotted Owl exposure rates to mirror Barred Owl rates. Northern Spotted Owl locations were collected in the Klamath Mountains between March and August of 2017, and California Spotted Owl locations were collected in the Sierra Nevada between May and August of 2015 through 2020 as part of previous studies (Jones et al. 2016, Atuo et al. 2018, Kramer et al. 2020). We used vocal lures to locate Spotted Owls and captured them either by hand-grab, pan-trap, or snare-poles, and applied GPS backpack tags (Lotek Pinpoint VHF 120, Newmarket, Ontario, Canada). Spotted Owl tags were programmed to record 5 hourly nocturnal locations per night between March and August. From these data, we calculated the mean proportion of locations that occurred within the WUI for both Northern and California Spotted Owls, as well as the proportion of individuals of each subspecies with at least one location in the WUI. We assumed the majority of these locations were primarily foraging locations as owls are nocturnal predators, but we acknowledge that other behaviors such as territory defense, resting, and returns to roosts and nests may be included in these locations.

Additionally, we calculated the proportion of all known Northern Spotted Owl activity centers and all California Spotted Owl activity centers in the Sierra Nevada whose home ranges at least partially overlapped with the WUI to assess the risk of Spotted Owl exposure to ARs via the possibility of foraging in the WUI. We used 2.1 km radius home ranges for Northern Spotted Owls and 1.6 km radius home ranges for California Spotted Owls (Wiens et al. 2014, Blakey et al. 2019). Activity centers were defined as nest locations or geometric centers of daytime roost locations and were obtained from the California Department of Fish and Wildlife (https://www.wildlife.ca.gov/Data/CNDDB/Spotted-Owl-Info). We also used both Northern and California Spotted Owl designated ranges (USFWS 2017) to calculate the proportion of WUI within each Spotted Owl subspecies' range (only including the Sierra Nevada for California Spotted Owls).

Statistical Analysis

We used a set of generalized linear models (McCullagh and Nelder 1989) within an information-theoretic framework (Burnham and Anderson 2002) to test for associations between AR exposure and biological and environmental factors. Because most exposures were at the trace level, we modeled exposure as a binomial response (exposed = 1 and not exposed = 0). Biological factors consisted of species (pure Barred Owl versus hybrid), age, sex, and the index of body condition. Juvenile and un-aged owls were omitted from the generalized linear model because of small sample sizes. Environmental factors consisted of sub-region, proximity to the WUI, number of known cannabis cultivation sites within home ranges, the average index of predictive cultivation for each Barred Owl home range from the MaxEnt model, and landownership.

We used a multi-stage secondary candidate strategy to select top-ranked models (Morin et al. 2020). First, we ran all combinations of biological models and all combinations of environmental models separately. We then identified supported models as those within 5 AIC_c (second-order Akaike Information Criterion corrected for small sample sizes) of the most supported model for each set of models. Second, we combined and evaluated support for variables in the top models from both the biological and environmental sets. In both model-selecting stages, models with uninformative variables (e.g., confidence intervals of variables overlap with zero) were not considered (Leroux 2019). We used the package *MuMIn* in R Studio 1.3.1073 (R Core Development Team 2017) for these analyses.

We also conducted a general Getis Ord-General G high/low cluster analysis (Getis and Ord 1992) to assess the degree to which AR exposure was more clustered than expected at random, less clustered than expected at random, or randomly distributed. We ran separate analyses for owls collected in the Klamath/Cascade sub-region and those collected in the northern Sierra Nevada (where the majority of Sierra Nevada removals were conducted), and only used locations for where owls were exposed, realizing that mates could be non-exposed. To reduce potential biases associated with sampling multiple owls from the same territory, owls collected within 2.52 km (the radius of a 2,000 ha Barred Owl home range in the region; Wood et al. 2020a) of other owls were combined to single points based on the geometric centers of the points. We also conducted a Moran's I spatial autocorrelation analysis with the same condensed points to assess the degree of concordance between different clustering procedures. All spatial analyses were conducted using ArcMap 10.6.1 (ESRI Inc., Redlands, California, USA).

RESULTS

Barred Owl Collections and Liver Analysis

We screened 127 livers (115 Barred Owls and 12 hybrids) for ARs (Figure 1), of which 62% (79 of 127, 72 Barred Owls, and 7 hybrids) tested positive for at least one AR. Brodifacoum and bromadiolone were the only two ARs detected, with 97% (77 of 79) of exposed individuals having exposure to brodifacoum, 15% (12 of 79) to bromadiolone, and 13% (10 of 79) to both. Eighty-seven percent of the AR exposures were at the "trace" level (below quantification limits), with 13% (seven females, and two males) having quantifiable concentrations of AR. Seven of those samples had quantifiable concentrations of brodifacoum

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TABLE 1. Generalized linear modeling results from our final stage of model selection used to examine variability in Barred Owls and Barred Owl x Spotted Owl hybrids exposure to anticoagulant rodenticides in northern California in 2018 and 2019. Model covariates include sex and proximity to the wildland–urban interface (WUI). *k* is the number of parameters, and w_i is Akaike's weight. Results for initial modeling steps are provided in Supplemental Material Tables S2 and S3

Model	*k*	ΔAIC_c [a]	w_i
Sex + WUI	3	0.00	0.869
Sex	2	3.95	0.121
WUI	2	9.28	0.008
Intercept only	1	11.94	0.002

[a]Akaike's information criterion corrected for sample size (AIC_c) of top model was 139.5.

(median = 0.084 μg g^{-1} ww, SD = 0.033, min = 0.050, max = 0.150) and three had quantifiable concentrations of bromadiolone (median = 0.150 μg g^{-1} ww, SD = 0.102, min = 0.120, max = 0.310). A total of 7 ovaries were tested for AR contamination and 100% were positive at trace levels (6 contained brodifacoum, 3 contained bromadiolone, and 2 contained both), and all ovaries were from females whose livers also tested positive for the same ARs.

Factors Associated with AR Exposure

After excluding 4 juveniles (because of small sample sizes), 5 un-aged owls, and 2 owls lacking fat scores, 116 individuals (107 Barred Owls and 9 hybrids) were used to conduct the generalized linear model to predict AR exposure. No pairwise combination of variables were highly correlated (all Pearson's *r*'s < 0.6), although distance to WUI and cannabis cultivation suitability were moderately and negatively correlated ($r = -0.42$, $P < 0.01$) – suggesting that cannabis cultivation was more likely to occur near the WUI. The highest ranked model in the biological-only modeling step contained only sex; all other biological variables occurred in models within 5 AIC_c but they were considered uninformative as the 95% confidence intervals overlapped zero and not considered further (Supplemental Material Table S2). The highest ranked model in the environmental-only modeling step contained only distance to WUI; all other environmental variables occurred in models within 5 AIC_c of the top model but they were considered uninformative as the 95% confidence intervals (95% CI) overlapped zero and not considered further (Supplemental Material Table S3). In our second (i.e. combined) modeling step, the top model contained sex and distance to WUI (w_i = 0.869; Table 1). Based on this model, females (78%) were more likely to be exposed to ARs than males (50%; β = –1.448, 95% CI: –2.391 to –0.590; Figure 2). In addition, the probability of AR exposure declined with distance from the WUI (β = –0.146, 95% CI: –0.271 to –0.029) – in other words, Barred Owls sampled near the WUI were more likely to be exposed (Figure 2). Based on this modeling process,

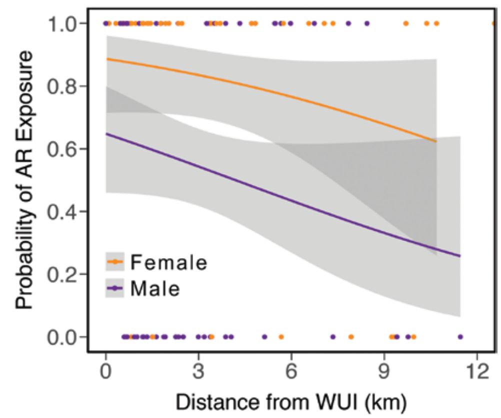

FIGURE 2. Predicted probability of Barred Owls and Barred Owl x Spotted Owl hybrids being exposed to anticoagulant rodenticides (AR) in northern California in 2018 and 2019 plotted against the distance from the wildland–urban interface (WUI; Radeloff et al. 2005). The predicted probability of AR exposure is shown as the solid lines, whereas the 95% confidence intervals are shaded in gray. Colored dots at the top and bottom of the figure represent the raw data of individual owls that were exposed to AR (top) and not exposed to AR (bottom).

there was little support for an association between AR exposure and known grow sites, the predictive index for the suitability of cannabis cultivation, age, species (purebred versus hybrid), body condition, or landownership.

We detected little evidence for clustering among locations where Barred Owls were exposed to AR in either the Klamath/Cascade Mountains or the Sierra Nevada. This was the case based on both the Getis Ord-General G high/low cluster analysis (Klamath/Cascade P = 0.27, Sierra Nevada P = 0.83), and the Moran's I analysis (Klamath/Cascade P = 0.39, Sierra Nevada P = 0.58), which indicates that AR was randomly distributed across space in both sub-regions (without considering other environmental variables).

Distribution of GPS-Tagged Owl Locations Relative to the WUI

We tracked the 7 GPS-tagged Barred Owls and 3 hybrids for an average of 229 days (range: 52–392), obtaining an average of 40 foraging locations (range: 15–72) per individual. An average of 2% of Barred Owl and hybrid GPS locations (range: 0–18) occurred within the WUI, and 50% of tagged individuals had at least 1 foraging location within the WUI (Figure 3). We tracked the 24 GPS-tagged Northern Spotted Owls for an average of 65 days (range: 29–79) and obtained an average of 228 foraging locations per individual (range: 94–276). Among Northern Spotted Owls, an average of 2% of GPS locations occurred within the WUI (range: 0–43) and 33% had at least one foraging location within the WUI (Figure 3). We tracked the 106 GPS-tagged California Spotted Owls for an average of 58 days (range: 4–161) and obtained an average of 132 foraging

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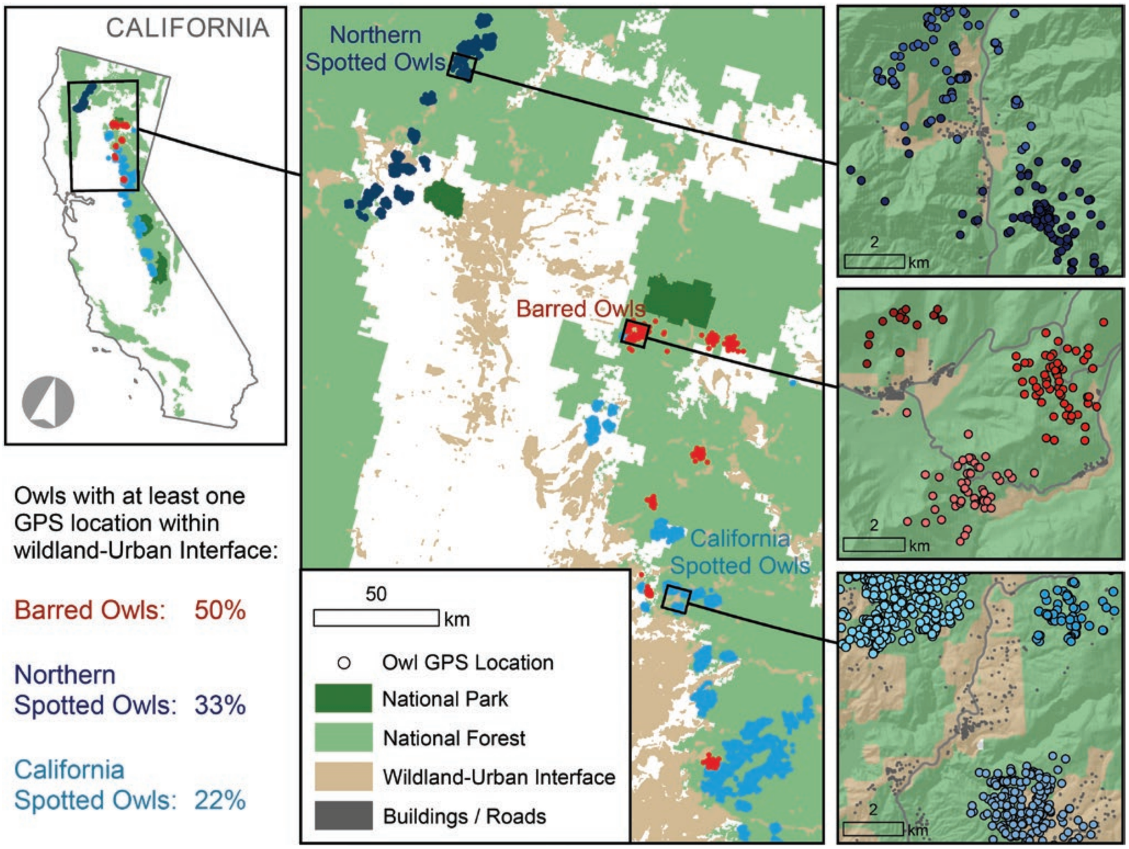

FIGURE 3. Locations and summary statistics of GPS-tagged Barred Owls (*n* = 10), Northern Spotted Owls (*n* = 24), and California Spotted Owls (*n* = 106) in relation to the wildland–urban interface (WUI) in the Klamath/Cascade Mountains and Sierra Nevada in northern California, USA. Dark blue dots on the California map represent GPS-tagged Northern Spotted Owls, red dots represent Barred Owls and hybrids, and light blue dots represent California Spotted Owls. Different color shades in the inset maps represent the GPS locations of individual owls.

locations per individual (range: 9–348). Among California Spotted Owls, an average of 2% of GPS locations occurred within the WUI (range: 0–219) and 22% of tagged individuals had at least one foraging location within the WUI (Figure 3). Based on all known Northern and California Spotted Owl activity centers in the Sierra Nevada, 35% (range: 0.001–1363 ha) and 28% (range: 0.003–751 ha) of individual home ranges overlapped at least partially with the WUI, respectively. However, only 4.3% and 11.9% of Northern and California Spotted Owl ranges overlapped with the WUI, respectively.

DISCUSSION

A high proportion of Barred Owls and hybrids were exposed to AR in both the Klamath/Cascade Mountains and the Sierra Nevada, with exposure being widespread and no evidence for spatial clustering among AR-positive individuals (Figure 1). Females were more likely to be exposed than males and tended to have higher quantifiable concentrations of AR. This is of conservation concern, because we documented, for the first time, AR-positive ovaries and a potential for in-utero transfer of AR in *Strix* owls. AR exposure was not clearly linked to illegal cannabis cultivation, but Barred Owls sampled in proximity to the WUI were more likely to be exposed to ARs. The exposure of such a high proportion of Barred Owls, an apex forest predator, signifies that AR is a pervasive toxicant in western forest ecosystems and contributes to mounting evidence of potential AR exposure in Northern Spotted Owls—and the first potential evidence in California Spotted Owls. Although our sample of hybrids was small, we found similar rates of AR exposure between pure Barred Owls and hybrids, suggesting that Barred Owls may serve as reasonable indicator species for AR environmental contamination and to infer exposure in Spotted Owls. Further support of Barred Owls as reasonable indicator species for Spotted Owl exposure to ARs is provided by the similar use of WUIs by GPS-tagged Barred Owls and Northern and California Spotted Owls. Thus, our study supports previous work showing widespread AR exposure in predators inhabiting remote western forests (Gabriel et al. 2012, 2018, Thompson et al.

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2014, Franklin et al. 2018, Wiens et al. 2019), but also suggests that exposure is higher within and around WUIs.

Barred Owl Exposure to AR

Barred Owls collected in our study area were exposed to brodifacoum and bromadiolone. This has important conservation implications because both of these compounds are SGARs and due to the threat they pose to non-target wildlife, their use in California was prohibited in 2014 without a licensed professional, as was their application more than 15 m from human structures (California Code of Regulations Title 3, Section 6471). Indeed, it is unlikely that the high percentage of Barred Owl exposure to AR in our study area comes entirely from legal applications of SGARs, because from 2015 to 2018 only 8.26 kg of brodifacoum were reported to have been sold in the entire state of California (California Department of Pesticide Regulation, https://www.cdpr.ca.gov/docs/mill/nopdsold.htm about the same mass as found at just 2 average illegal cannabis cultivation sites in California (Wengert et al. 2018). Thus, it appears that even with stricter regulations, the legal or more-likely illegal applications of dangerous SGARs and exposure of non-target wildlife remain a challenge for conservation, as does identifying the main sources of illegal applications. Additionally, the proportion of Barred Owls and hybrids exposed to SGARs in our study area (62%) was greater than proportions reported in coastal California (40%, $n = 84$; Gabriel et al. 2018) and Oregon and Washington (48%, $n = 40$; Wiens et al. 2019), suggesting that the use of SGARs could be more intense in our study area.

Similar to what has been documented in Oregon and Washington (Wiens et al. 2019), most of our AR-positive specimens had trace liver concentrations below the quantifiable level. As of yet, the sub-lethal effects of ARs and the causes and consequences of trace concentrations in Barred and Spotted Owls have not been studied, although the majority of trace concentrations could be explained by at least 3 non-exclusive possibilities. First, owls with high AR concentrations may have acutely died due to these toxicants and therefore were not available for sampling. If so, our samples may be biased toward the low end of an exposure, with the 9 owls with high concentrations of AR suggesting that concentrations greater than trace levels can occur in Barred Owls. Second, owls may have consumed prey that varied in their concentrations of AR and over different periods of time, which resulted in the majority of, but not all, exposures being at the trace level. However, due to the unknown kinetics of toxicant uptake or sequestration, or degradation mechanisms of AR in *Strix* owls, this possibility will need to be explored further. Third, given that all Barred Owl ovaries tested positive for AR, trace levels could be the result of in-utero transfer of ARs rather than or in addition to the consumption of contaminated prey—a phenomenon that has been reported in Barn Owls (*Tyto alba*; Salim et al. 2015). However, we recognize AR presence in the ovaries still does not necessarily confirm the maternal transfer and that this possibility will need to be explored further by comparing plasmatic vs. ovarian tissue exposure to AR and/or testing eggs directly.

Although the majority of our specimens had trace levels of AR, 9 owls (7 female, 2 male) had concentrations of up to 0.150 $\mu g\ g^{-1}$ ww for brodifacoum, and 0.310 $\mu g\ g^{-1}$ ww for bromadiolone. These concentrations are both higher than the 0.1 $\mu g\ g^{-1}$ ww threshold reported in Barn and Barred Owls, when clinical signs of AR toxicosis begin to show and reflected a mortality rate of 10% of individuals (Thomas et al. 2011). Though not documented in Barred Owls, sub-lethal exposure to SGARs can reduce clutch size and fledgling success in Barn Owls (Salim et al. 2014). In addition, sub-lethal internal hemorrhaging has been documented in Golden Eagles (*Aquila chrysaetos*) and Northern Spotted Owls with liver concentrations of brodifacoum as low as 0.030 and 0.050 $\mu g\ g^{-1}$ ww, respectively (Stone et al. 1999, Franklin et al. 2018), and Pacific Fishers have died with signs of AR toxicosis with liver concentrations as low as 0.040 $\mu g\ g^{-1}$ ww (Gabriel et al. 2012). More research into the effects of sub-lethal exposure on specific species of concern may be merited, especially because Barred Owl populations are expanding (Wood et al. 2020a) despite high rates of AR exposure. Indeed, no atypical behaviors were observed while collecting Barred Owls who had confirmed trace levels of AR in their tissues. However, the effects of widespread sub-lethal exposure could be more severe in Spotted Owls due to the stress of competitive interactions with more dominant Barred Owls (Wiens et al. 2014), as stress can exacerbate deleterious effects of AR, such as internal hemorrhaging (Cox and Smith 1992).

Biological and Environmental Factors influencing AR Exposure

In contrast to previous studies (Gabriel et al. 2018, Wiens et al. 2019), we found that females were more likely to be exposed to AR than males. Though information is limited for Barred Owls, this may be explained by female Spotted Owls, and female birds in general, having greater dispersal distances on average than those of males (Greenwood 1980, Jenkins et al. 2019). Thus, female Barred Owls, and likely female Spotted Owls, may encounter more sources of ARs that translate to higher rates of exposure and potentially higher concentrations of AR, which also suggests that individuals could have brought AR exposure from natal areas located far from where they were collected. This trend could additionally be explained by Barred Owl females' dependence on males delivering food to them while they are on the nest for a substantial amount of time

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every year (Mazur and James 2020). The fact that females had higher rates of exposure is cause for concern because if ovaries testing positive for ARs does indeed signify maternal transfer, it is possible that this transfer is widespread among owls in this study area. However, further research on the possibility of maternal transfer of AR is necessary through the direct testing of eggs.

Higher rates of AR exposure in Barred Owls and hybrids sampled near the WUI indicated that those owls whose home ranges were closer to human development were more likely to be exposed to AR. Indeed, 50% of Barred Owls and hybrids (and 33% of Northern Spotted Owls and 22% of California Spotted Owls) had at least one point in the WUI. Moreover, Barred Owls and hybrids with higher concentrations of AR were collected on average 2 km closer to the WUI than owls with trace AR concentrations, and 3 km closer than owls that were not exposed to AR. However, the mechanism of exposure in the WUI, and whether it is due to cannabis cultivation within the WUI or applications around homes or both, remains unknown. Furthermore, we do not necessarily know where AR-positive owls collected outside of the WUI were exposed. For instance, the half-life for brodifacoum can be as long as 350 days in rats, but predators (including owls) tend to have longer degradation times (up to three times in duration), as demonstrated with the 2–3-day half-life of diphacinone in rats and the 11.7-day half-life of diphacinone in Eastern Screech Owls (*Megascops asio*; Herring et al. 2017). Therefore, it is possible that sampled owls could have been exposed any time over the last 3–4 yr, especially given the apparently recent immigration of some sampled individuals to our study area resulting from vacancies created by removals (D.F. Hofstadter and B.P. Dotters, unpublished data). Nevertheless, we might expect that such discordance between exposure and collection sites resulting from dispersal movements might erode a true association between the WUI and AR exposure, rather than create a false association of WUI and exposure.

Contrary to predictions, AR exposure was unrelated to either of our 2 metrics of illegal cannabis cultivation—an observation that could also have several non-mutually exclusive explanations. First, after California enacted the partial ban on SGARs in 2014, this class of AR was no longer as commonly reported at illegal cannabis cultivation sites, though other toxicants (like FGARs and neurotoxins) were often reported instead (Thompson et al. 2017). Second, illegal cannabis cultivation is by nature clandestine and many grow sites go undetected every year (M. W. Gabriel and G. M. Wengert, personal communication), which could have obscured an actual association to AR exposure. Finally, AR poisoned owls may die near grow sites due to exposure to AR as well as more acutely lethal compounds like neurotoxins, and thus never get sampled. Despite these uncertainties, exposure rates were high in owls sampled several kilometers from the WUI, and particularly so for females—a pattern we consider most likely attributable to either the past or recent use of ARs for illegal cannabis cultivation given low housing densities in these areas (Figure 2).

Threats to Spotted Owls and Western Forest Ecosystems

Our study area adds two new regions to the list of western forests where a high rate of Barred Owls have been exposed to ARs in both remote forested settings and in proximity to the WUI. The 62% of Barred Owls exposed to AR demonstrates that ARs have contaminated the food webs of northern California forests and suggest that AR could pose a threat to wildlife, including Spotted Owls. Although our sample size of hybrids was small, the fact that we did not have any evidence for a difference in exposure rates between pure Barred Owls and hybrids suggests that similar rates of AR exposure could also result in Spotted Owls—a possibility further supported from our GPS foraging locations. In fact, previous work reported 40% (n = 84) of collected Barred Owls and 70% (n = 10) of Northern Spotted Owls that were found dead in coastal California had also been exposed to AR, with Spotted Owls all exposed at trace levels (Gabriel et al. 2018). Spotted Owls prey more selectively on rodents than Barred Owls (Wiens et al. 2014) such that, in regards to diet, Spotted Owls may be more at risk for exposure. However, we found that the proportion of Spotted Owls that frequent the WUI was lower than Barred Owls and also that only a small portion of the WUI overlaps with the U.S. Fish and Wildlife Service designated ranges for both subspecies. Therefore, Spotted Owl behavior and habitat selection may buffer them more from exposure than Barred Owls, which often select suburban habitat containing mature trees (Clement et al. 2019).

In addition to other threats facing Spotted Owl populations, including megafires (Jones et al. 2016), a deficit of large trees (Jones et al. 2018), habitat homogenization (Hobart et al. 2019), and competition with Barred Owls (Wiens et al. 2014, Long and Wolfe 2019), the effects of AR exposure, in comparison, could easily go undetected. Moreover, there is a likely possibility of synergistic effects with sub-lethal effects of AR and other threats faced by Spotted Owls. For example, large disturbances to habitat are correlated to increased cortisol levels in Pacific Fishers (Kordosky 2019) and California Spotted Owl energy expenditure is increased with the presence of Barred Owls in the northern Sierra Nevada (Wood et al. 2020b). Therefore, there is a possibility of environmental stressors accentuating synergistic effects of AR in owls and other forest wildlife.

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Our results provide additional evidence that AR exposure could be a more significant threat to forest species of conservation concern than previously thought, and also that it is positively associated with the WUI. This threat is augmented by the long half-life and sub-lethal effects that these toxicants can have (Herring et al. 2017) Exposure in apex predators, like Barred Owls, likely indicates that contamination by AR is pervasive in forest food chains. Indeed, the ubiquity of AR contamination has been documented in many cases, ranging from earthworms and snails being exposed through the soil (Booth and Fisher 2003), to birds eating exposed insects (Masuda et al. 2014), to exposed rodents eaten by various predators, and even to streams, where fish exposed to AR have been reported (Kotthoff et al. 2019). Furthermore, there is the biological significance of low concentrations of AR in various wildlife taxa (Stone et al. 1999, Gabriel et al. 2012, Franklin et al. 2018), suggesting the high rates of trace exposure in Barred Owls and hybrids indicate a significant threat to wildlife, including Spotted Owls.

We believe that future studies should focus on the WUI to elucidate more details on the mechanism of AR exposure, and whether tighter regulations of SGAR applications within the WUI could help to lower this exposure. In fact, as of September 2020, California regulation has recently changed to become stricter regarding the use and application of SGARs (California Assembly Bill No. 1788, Chapter 250). This provides an opportunity to further examine whether further AR exposure is a consequence of legal or illegal applications. Finally, more work is also needed to better understand potential sub-lethal effects and the in-utero transfer of ARs in *Strix* owls, as well as addressing the consequences of high rates of AR exposure in apex predators for forest food webs.

SUPPLEMENTAL MATERIAL

Supplemental material is available at *Ornithological Applications* online.

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Ethics statement: Barred Owl, Spotted Owl, and hybrid handling and tagging procedures were consistent with approved IACUC protocol A005367-R01. Barred Owl and hybrid collection procedures were consistent with approved IACUC protocol A006106-A01.

Conflict of interest statement: The authors declare no conflicts of interest.

Author contributions: MZP, CMW, and MWG conceived the study; MZP and CMW secured funding; DFH, NFK, BPD, KGK, KNR, and CMW contributed to specimen collection; DFH, NFK, and EDF extracted tissue samples; DFH, NFK, CMW, SAW, WJB, BPD, and KNR captured owls and attached GPS tags; MWG and GMW contributed to the cannabis measurements; DFH wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Data availability: Our data is deposited in Dryad. Analyses reported in this article can be reproduced using the data provided by Hofstadter et al. (2021).

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