# RAPTOR FORAGING ECOLOGY AND ECOSYSTEM SERVICES IN AGRICULTURAL LANDSCAPES

By

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**ABSTRACT**

Increasing agricultural productivity while improving sustainability of agricultural landscapes are key challenges facing society. One strategy to help address these two needs is enhancing pest-regulating ecosystem services provided by organisms that reside in these landscapes. To do so, we must understand the foraging ecology of these organisms and corresponding links to ecosystem services provisioning. In some contexts, raptors provide substantial ecosystem services by reducing damage to crops through consumption and deterrence of pest species. In this review we identify measures of raptor foraging ecology that may act as ecosystem service proxies, examine predictors of these proxies (e.g., vegetation structure), and discuss how this information could be used to enhance pest regulation by raptors. Through a literature search, we identified raptors' use of cultivated land cover (use), attack rate, and successful attack rate as ecosystem service proxies for which we could analyze the effects of various potential predictors. Our results showed that increased amount of cultivated land cover, shorter vegetation, and shorter distance to the nest or roost increase use by raptors. We also found that shorter/less dense vegetation increased attack rate, although we found no effect of any predictors on successful attack rate. We suggest that growers maintain shorter vegetation immediately adjacent to crops and natural cover within the greater landscape, such as forest. We recommend future research investigate 1) additional farm management characteristics that could influence use and attack rates, 2) the spatial scales at which land cover type influences raptor foraging ecology, and 3) additional measures of raptor foraging ecology and their impact on the strength of pest regulation services.

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# INTRODUCTION

A major global challenge is ensuring food security for a rapidly growing human population while alleviating negative impacts of agriculture on biodiversity and the environment (Birch et al. 2011). Improving and increasing agricultural productivity is vital to provide for a global population that will grow to an estimated 9.1 billion people by 2050 (Godfray et al. 2010). However, increasing agricultural activity threatens ecosystems around the world through greater habitat conversion, eutrophication, and pesticide use (Tilman et al. 2001, Tilman et al. 2011). To mitigate the problems caused by agriculture, it is important to develop sustainable agricultural landscapes (Godfray et al. 2010).

One way to increase agricultural productivity and sustainability simultaneously is through enhancement of ecosystem services provided by biodiversity (or wildlife) in agricultural landscapes (Lindell et al. 2018). Ecosystem services are benefits humans gain from activities of organisms and associated natural functions of ecosystems. An important type of regulatory ecosystem service is consumption and deterrence of crop pests by predatory species (Millenium Ecosystem Assessment 2003). Pests can cost billions of dollars in crop damage and management annually. For example, the global import value of pesticides in 2018 was $35.8 billion, and insects alone are estimated to consume and damage enough food before harvest to feed 1 billion people (Birch et al. 2011, FAO 2020). Rodents are another major contributor to crop damage (Capizzi et al. 2014), estimated to consume and damage enough rice before harvest in Asia to feed 180 million people annually (Singleton 2003). Further, bird damage to five crops in five states of the U.S. was estimated to cost growers $189 million per year (Anderson et al. 2013).

Natural predators, such as raptors (birds of prey), can protect crops through pest consumption and deterrence (Hothem and DeHaven 1982, Conover 1984, Navarro-Gonzalez and

Jay-Russell 2016, Donázar et al. 2016). These pest control services can result in substantial economic benefits. For example, American Kestrels (*Falco sparverius*) reduced fruit-eating bird activity in sweet cherry orchards in Michigan, USA (Shave et al. 2018). This reduction was estimated to reduce damage to sweet cherries and save growers between $84/ha to $357/ha in lost fruit (Shave et al. 2018). In another study, New Zealand Falcons (*Falco novaeseelandiae*) reduced bird damage to vineyards, saving growers between $234/ha to $326/ha (Kross et al. 2012). Recent research shows that many growers are eager to encourage raptor activity (Kross et al. 2018, Bardenhagen et al. 2020). For example, studies suggest providing nest boxes or perches can be effective tools for growers to attract raptors to agricultural landscapes (Sheffield et al. 2001, Lindell et al. 2018).

While increased raptor use of land covers may reduce pest abundance and foraging activity, ultimately reducing damage to crops (Lima and Bednekoff 1999, Brown and Kotler 2004), little previous work has synthesized the present understanding of raptor foraging and how it could be used to enhance ecosystem services provided in agricultural landscapes. Aspects of raptor foraging ecology (e.g., use of cultivated land cover, attack rate) may impact the strength of pest regulation services and, thus, serve as useful proxies of ecosystem service provisioning. In addition, studies that quantify pest regulation services are typically focused on specific study systems and have yet to identify broadly applicable predictors of ecosystem services that may be influenced by farm management, such as vegetation structure (Table 2).

In this review we ask: What do we know about raptor foraging ecology and how can we use this knowledge to enhance pest regulation services in agricultural landscapes? We addressed this question using a systematic search of the literature and a combination of literature review and meta-analysis to 1) identify commonly studied measures of raptor foraging ecology that may act as ecosystem service proxies in agroecosystems 2) document the nature of relationships between ecosystem service proxies and commonly studied predictors (e.g., vegetation structure), 3) use results from (1 and 2) to identify best management practices for encouraging pest control services, and 4) identify the most important future research avenues. We built a dataset of 105 studies including more than 24 crops across 6 continents to identify important predictors of raptor-mediated pest control services.

## METHODS

### Literature Search

We searched the "All Databases" option in Web of Science from the years 1864 to August 3, 2020. We used the search terms "(crop or agricult*) AND (forag*) AND (hawk, eagle, falcon, owl, kite, kestrel, harrier, buzzard, or raptor)". This returned 717 articles. We subsequently searched with the term (hunt*) instead of (forag*) to expand the search domain, which added 480 articles. We screened these 1,197 articles for redundant searches, resulting in 821 papers that we examined for relevance. Our criteria for inclusion were that each paper 1) focused on at least one species of raptor, 2) included measurements of raptor foraging ecology (see next section), and 3) included a study system located in an agricultural landscape or including cultivated land cover. We defined cultivated land cover as any area used for the production of crops intended for human or livestock use, such, corn, wheat, cereal, or pasture. Studies typically met criteria (2) if they included the term "agricultural landscape" or "crop" in their title or abstract. Ultimately, 105 studies were retained for the literature review and meta-analysis.

### Identifying ecosystem service proxies and predictors of proxies

From each paper we tabulated information on geographic location and study species. We categorized responses into positive, neutral, or negative for each study, which included measures of raptor foraging behavior and space use. We then identified a subset of the resulting response variables as potential ecosystem service proxies to use for further statistical analysis. We identified response variables as ecosystem service proxies when they had the potential to influence rates and/or levels of consumption or deterrence of pests and occurred in 20% or more of studies to use in our statistical analyses. The proxies that met our criteria were raptor use of cultivated land cover (hereafter, use), home range size, diet, home range composition, attack rate, and successful attack rate (Table 1).

We identified explanatory variables as potential predictors of ecosystem service proxies if they met the following criteria: 1) explained variation in ecosystem service proxies, 2) were broadly applicable across systems (e.g., vegetation structure such as height can be applied across systems vs. presence or amount of a specific crop) and 3) could be reasonably altered by farmers or included within farm management practices. These included landscape characteristics, raptor characteristics, and abiotic factors. We further narrowed the list of predictors to those that occurred in 20% or more of studies to use in our statistical analyses (Table 2). Resulting predictors were amount of cultivated land cover, prey abundance, vegetation structure, and distance from a central location, such as a nest or roost. We categorized all crops broadly as cultivated land cover because of inconsistency in reporting of crop types among studies. For example, LaPointe et al. (2013) reported land cover types of corn, soybean, hay, and oat, which we recategorized as "cultivated".

**Statistical Analyses**

*Relationships between predictors and ecosystem service proxies: Fisher's exact test*

For each study that measured an ecosystem service proxy (Table 1) and at least one predictor (Table 2), we documented whether the predictors(s) had a positive, negative, or neutral (non-significant) effect on the proxy. For each proxy, we summed the number of positive, negative, and neutral relationships with each predictor across studies (e.g. Table 6).

In some studies a predictor or proxy was broken down into finer-resolution categories. For example, Buij et al. (2012) looked at the use of land cover by Pallid Harriers (*Circus macrourus*) by sex and age and many studies listed different crop types specific to their system.

We examined the individual relationships between finer-resolution predictors or proxies, using sample size and the magnitude of the effect, to categorize an overall relationship between a predictor and proxy when this occured. For example, in Buij et al. (2012), female and juvenile (n = 200) Pallid Harriers (*Circus macrourus*) used rice more while males (n = 100) used it less. The relationship between cultivated land cover type and use was also stronger for females than for males. Thus, we categorized the relationship between cultivated land cover type and use as positive for this study. If multiple crops were included in the study and had opposing effects, the extent of each crop and the frequency of each relationship were considered. For example, if corn and cereal had opposing effects on use, but cereal was more extensive, then the effect of cereal was recorded. If the extent of the crops was similar, the effect was listed as neutral.

We then ran a Fisher's exact test in R v. 3.5.1 (R Core Team 2018) to determine if frequency of observed relationships between each proxy (use, attack rate, successful attack rate) and each predictor (cultivated land cover, prey abundance, vegetation structure, distance to a nest or roost) were different than expected. As an example, the contigency table to test the potential relationships between raptor use and the predictor variables is illustrated in Table 6 A. We were unable to perform Fisher's exact tests for the ecosystem service proxies diet, home range size, and home range composition. Diet data were typically reported as the proportion of prey types and home range composition data were reported as the proportion of each land cover within the range. Thus, these proxies could not be labeled as having a positive, negative, or neutral relationship with any predictors. We did not include home range size in analyses because only one predictor – cultivated land cover – was typically reported in studies but multiple predictors were required to calculate the expected values to perform a Fisher's exact test. Although we were unable to analyze these proxies, we considered them in our discussion. Many studies recorded multiple predictors and ecosystem service proxies but may not have systematically analyzed each relationship. Thus, our Fisher's exact analyses totals do not equal the total number of studies where both variables were included.

*Relationship between cultivated land and raptor abundance: Meta-analysis*

We conducted a meta-analysis on the relationship between cultivated land cover and use (Supplementary Methods). For studies that examined the effects of the extent of cultivated land cover on use, we collected meta-data on the proportion of cultivated land cover available within an individual's home range and the proportion of cultivated land cover used by the individual. We also recorded the raptor family for each study to account for the variation in diet among raptor families, which may affect their attraction to cultivated land cover and the pest regulation services they could provide (Kross et al. 2012, Kross et al. 2016).

The proportion of cultivated land cover used is calculated as the number of times an individual is observed in cultivated land cover out of the total number of times the individual was observed (Lele et al. 2013). The proportion of cultivated land cover available could be calculated as the area of cultivated land cover within an individual's home range out of the total area within an individual's home range or as the number of randomly generated locations in cultivated land cover within an individual's home range out of the total number of randomly generated locations within the individual's home range (Aebischer et al. 1993, Lele et al. 2013). These measures allowed us to calculate a selection ratio of cultivated land cover for our meta-analysis (Lele et al. 2013).

Studies generally reported a mean proportion of cultivated land cover used and a mean proportion of cultivated land cover available over all the individuals within the study. Some studies reported multiple mean proportions due to the use of multiple sites within a study (e.g,. Catry et al. 2013) or reported the proportions for each individual (e.g., Donázar et al. 1993, de Frutos and Olea 2008). We recorded proportion of cultivated land cover used, proportion of cultivated land cover available, and number of individuals associated with each set of proportions as the sample size. To combine proportions from multiple finer-scale cultivated land cover types, i.e. crops, we simply summed the proportions. Variation in methodologies among studies and quality of studies is expected when conducting a meta-analysis (Koricheva et al. 2013).

We focused on use because it was the only variable for which studies provided a large enough sample size of quantitative data allowing for calculation of a selection ratio (*n* = 24) and because it has direct applications to management of agroecosystems. For each study, we calculated a standardized selectio ratio using the natural log of proportion of cultivated land cover used divided by the proportion of cultivated land cover available (Aebischer et al. 1993):

$$\ln\left(\frac{proportion\ used}{proportion\ available}\right)$$

This selection ratio tells us whether raptors are using cultivated landcover type to a greater extent than expected given its availability. A natural log ratio greater than 0 indicates that cultivated land cover type was used more than expected given availability, a natural log ratio less than 0 indicates that cultivated land cover type was used less than expected, and a natural log ratio of 0 indicates that cultivated land cover type was used as expected.

We used the sample size, or number of individuals observed for each ratio, to calculate the variance, which we used to weight each calculated ratio (Aebischer et al. 1993, Koricheva et al. 2013). We then conducted a mixed effects meta-analysis on use in cultivated land cover type using the package '*metafor*' in R v. 3.5.1 (R Core Team 2022 Viechtbauer 2010). We used raptor family as a fixed effect and study as a random effect in our model.

ln(used/available) ~ Raptor Family + 1 | Study ID

## RESULTS

The studies included in our review provided data on 4 families comprising 46 species in 32 countries (Tables 3 and 4). Accipitridae was the most frequently studied family (45), followed by Falconidae (30). However, the Lesser Kestrel (*Falco naumanni*) was the most frequently studied species, occurring in 17 studies. Studies were conducted most frequently in Europe (64) followed by North America (25). The fewest studies occurred in Australia (1).

Most studies (40) did not list a specific crop type when they examined the effects of cultivated land cover on raptor foraging (Table 5). The most frequently listed crop types were cereal (21) and alfalfa (21) followed by corn (19). A large variety of other crop types were listed infrequently including things like sugarcane (2), beets (3), legumes (8), chile (1), tobacco (1), tomato (3), onion (3), and fruit (9).

We identified 13 response variables that could potentially serve as ecosystem service proxies and 16 explanatory variables that could act as predictors of ecosystem service proxies. Of the 13 response variables, only six were found in ≥20% of studies and could be linked to potential ecosystem service provisioning through existing literature: use, home range size, diet, home range composition, attack rate, and successful attack rate (Table 1). These served as our ecosystem service proxies. Of the 16 explanatory variables, seven appeared in 20% or more of studies but only four were manageable by farmers in some way: land cover, distance to a nest or roost, vegetation structure, and prey abundance (Table 2).

Measures of vegetation structure focused on height (91%, n = 23) and density (43%, n = 23) and were reported in different ways. Some studies used qualitative or numerical categories, for example, one study used “ankle”, “knee”, “waist”, “shoulder”, “head”, and “above head” to categorize vegetation height (Rodriguez et al. 2014). Other studies simply used continuous measures for height and percent cover for density. In this paper, we're referring to taller or denser vegetation when we say "increased", "more", or "greater" vegetation structure.

Raptor use of cultivated land cover was not independent of the extent of cultivated land cover, vegetation structure, or distance to nests or roosts ($p < 0.001$, Figure 1, Table 6 A). Non-independence appears to be driven by more positive relationships between use and cultivated land cover and more negative relationships between use and increased vegetation structure and distance to a central location (Figure 1). According to our meta-analysis, falcons (Falconidae) (response ratio = -0.067 ± 0.22, $p = 0.76$, $n = 9$ studies) and owls (Strigidae) (response ratio = -0.33 ± 0.57, $p = 0.57$, $n = 2$ studies) used cultivated land cover types as expected, while hawks, eagles, and other members of Accipitridae used cultivated land cover less than expected (response ratio = -1.15 ± 0.22, $p = 0.001$, $n = 12$ studies).

We found that attack rate was not independent of the extent of cultivated land cover, increased vegetation structure, and distance to the nest or roost $p = 0.025$, Figure 2, Table 6 B). The non-independence appears to be driven by more positive relationship between attack rate and extent of cultivated land cover and more negative relationships between attack rate and vegetation structure (Figure 2). Successful attack rate was independent of the predictors examined ($p = 1$, Table 6 C). Although we did not detect an effect of any predictors examined on success rate, we do believe success rate may have an impact on pest regulation services and discuss it in conjunction with attack rate below.

While we were unable to statistically analyze links between predictors, home range size, and home range composition, we did observe that 50% of studies (n = 10) found a positive relationship between home range size and cultivated land cover, 30% of studies found a negative relationship, and 20% found that cultivated land cover had no effect on home range size.

## DISCUSSION

Based on our results, cultivated land cover and shorter, less dense vegetation are key components of raptor foraging. Across the literature, land cover type and vegetation structure played a strong role in the use, activity, and success of raptors while foraging. Based on our results,  increasing or maintaining some open non-crop habitat in and around crops may attract raptors and increase attack and success rates. While crop height and density are not something growers can necessarily manage with the aim of attracting raptors, growers could manage the height and density of surrounding vegetation, such as grass margins and hedgerows. For example, taller grassy margins may offer food and refuge for pest species and inhibit raptor access to pests (Buij et al. 2012).

### Identifying measures of raptor foraging ecology that may act as ecosystem service proxies (Objective 1)

Our literature search revealed measures of raptor foraging that could act as ecosystem service proxies including use of land cover by raptors, home range size, diet, home range compostion, and individual attack rates and successful attack rates (Table 1).

### Identifying Predictors of Ecosystem Service Proxies and Defining their Relationships (Objective 2)

*Quantitative relationships from the analyses*

We found that more studies than expected found a positive relationship between cultivated land cover and use. However, our meta-analysis revealed that members of the family Accipitridae (hawks, eagles, and kites) used cultivated land covers less than expected given their availability. Cultivated land covers may provide all the necessary resources for some species, such as Lesser Kestrels and Barn Owls, and deter other species, such as Hen Harriers, because they are often extensive monocultures and because agricultural landscapes lack important complementary land covers that provide suitable nesting sites and sources of prey (Robinson and Sutherland 2002, Kovács-Hostyánszki et al. 2017). It is possible this explains our finding that members of Accipitridae (hawks, eagles, and kites) use cultivated land cover less; complementary habitat could be of greater importance to them because they are often perch hunters and nest in trees. Meanwhile members of Strigidae and Falconidate may use cultivated land cover in proportion to its availability because some species of owls and falcons are cavity nesters which allow them to nest in man-made structures such as barns or nest boxes and, thus, do not require complementary land covers (Orta and Kirwan 2020, Smallwood and Bird 2020). Additionally, falcons are often pursuit-style hunters that chase prey in more open land covers, which may facilitate their use of open cultivated land covers such as crops (Mosto et al. 2022). Pesticide use and other pest management activites may also reduce prey abundance in crops, further discouraging raptors from foraging in cultivated land cover. Another possibility is that the species that were included in our meta-analysis were not representative of general family characteristics. For example, Vali et al. (2017) studied Lesser-spotted Eagles (Accipitridae) that used cultivated land covers significantly less than expected relative to its availability and Dwyer et al. (2013) studied Creasted Caracaras (Falconidae) that used cultivated land cover significantly more than expected. However, two studies of Swainson's Hawks (Accipitridae), a species known to use cultivated land cover more, had to be omitted because a sample size was not reported. Thus, our meta-analyses excluded important species in Accipitridae that select for cultivated land covers and may have provided results that are not representative of the whole family.

Reduced distance to a nest or roost increased raptor use of an area. The effect of distance to a central location was shown to better predict the use than amount of cultivated land cover in some studies (e.g. Rosenberg and Haley 2004, Arroyo et al. 2009). Raptors likely try to remain closer to their nests because they endure a lower energetic cost to capture prey items when they travel shorter distances (Orians and Pearson 1979, Buij et al. 2015).

Areas with tall and dense vegetation structures were generally used less by raptors hunting in cultivated land cover while short and less dense structures were used more (Figure 1), likely due to the ability to see and capture prey (Arlettaz et al. 2010, Rodríguez et al. 2014, Valdez-Gómez et al. 2018). Raptors may be unable to locate or capture prey in tall or dense vegetation, although prey are abundant (Casagrande et al. 2008). For example, Buij et al. (2012) found that small mammals were associated with denser, woody vegetation, which likely made it more difficult for harriers (*Circus* spp.) to access them. However, more open vegetation structures may allow prey to detect predators at great distances (Whittingham and Evans 2004). In contrast to the first two points, which would benefit prey, taller or more dense vegetation may provide cover to predators while searching for prey (Cresswell 1996, Cresswell and Quinn 2013).

Attack rate increased in cultivated land cover, with shorter and less dense vegetation, and closer to the nest or roost. It's likely that vegetation structure contributed most to the non-independence of increasing attack rate, followed by cultivated land cover. Distance from a nest or roost likely contributed the least, due to its very small sample size (2). Attack rate and success rate were often highest for land cover types such as grasslands, fields, or pastures (e.g. Wakeley 1978, Casagrande et al. 2008, Garratt et al. 2011, Rodríguez et al. 2014, Väli et al. 2017). Increased vegetation height or density decreased attack rate and success rate (Buij et al. 2015). Again, taller or more dense vegetation likely reduced prey accessibility, which may deter raptors from attacking or affect their ability to catch and handle prey items (Casagrande et al. 2008).

*Qualitative patterns from the literature search*

Studies that have examined raptor diet within agricultural landscapes have typically found that the vast majority of their diet is pests (Kross et al. 2012, Kross et al. 2016). The majority of studies that investigated diet did not analyze relationships between landscape characteristics or other predictors and diet, but rather, described the content of a species' diet. While predictors, such as amount of cultivated land cover and vegetation structure, often had an effect on diet, it is difficult to identify any general patterns because of the species-specific nature of this variable (e.g. Amar and Redpath 2005, Šálek et al. 2010, Buij et al. 2012).

Raptors select a home range composition that incorporates more of the land cover types that they use more, relative to those that are available within the region (e.g. Marzluff et al. 1997, de Frutos and Olea 2008, Pande and Dahanukar 2011, Vali et al. 2017). If land covers that raptors use more are less available, home range size typically increases (Peery 2000). This may mean that raptors spend more time traveling to those land cover types and less time in cultivated land cover if they use it less , which may result in lower pest deterrence and consumption. Some studies found that raptors used each land cover type, including cultivated land cover, in proportion to availability within the home range, but selected for a home range that incorporated more or less of a specific land cover given what was available within the region. For example, Cinerous Vultures (*Aegypius monachus*) selected home ranges that included more "open lands" and less agriculture than was available in the study area over over 2 million hectares but used all land covers proportional to availability within their home ranges (Carrete and Donázar 2005). Creating complex agricultural landscapes by providing and maintaining complementary land covers is likely important to attracting raptors to the landscape and increasing their use of cultivated land cover.

**Potential Ways to Enhance Ecosystem Services Provided by Raptors Identify Best Management Practices to Harness Pest Control Services (Objective 3)**

**Managing landscape structure and agricultural practices**

We suggest that growers work to increase and maintain open non-crop habitat in and around crops to attract raptors and increase attack and successful attack rates (Garratt et al. 2011, Rodríguez et al. 2014). In addition, we suggest growers manage surrounding vegetation, by reducing the height and density of grass margins and hedgerows immediately surrounding crops. However, while many studies reported raptors hunting in and striking at prey in shorter, less dense vegetation, many also noted that raptors typically did so from a perch provided by woody edge habitat (Kadowaki et al. 2007, Burgess et al. 2009, Bader and Bednarz 2010, Horikoshi et al. 2017, Denac et al. 2019). For example, Eurasian Sparrowhawks (*Accipiter nisus*) may use forest edge for cover, Dark-chanting Goshawks use trees for perch hunting, and American Kestrels perch in trees at blueberry crop edges while hunting (Cresswell 1996, Cresswell and Quinn 2013, Buij et al. 2015, Personal obs). Growers may be able to support sit-and-pursue predators in and around crops by leaving or restoring forest edge near, but not directly adjacent to, crops (Preisser et al. 2005, Preisser et al. 2007). However, forest edge may also increase crop damage in some systems (Lindell et al. 2016, Tscharntke et al. 2016). If maintaining forest edge is not an option, artificial perches may encourage raptors to hunt in and around crops (Sheffield et al. 2001, Lindell et al. 2018, Wong and Kross 2018).

**Maintaining complementary nesting habitat and providing artificial structures close to crops**

Reduced distance from nests or roosts plays a key role in increasing use in cultivated land covers. Higher distances traveled increase the cost of foraging, thus keeping nests or roosts close to cultivated land cover may reduce the cost and encourage foraging. Farms can maintain some complementary land covers close to crops (see above) to provide suitable nesting habitat nearby. In addition, if a farmer is providing artificial nesting sites such as nest boxes to attract raptors, placing these structures closer to crops may facilitate use of crops for hunting (Lindell et al. 2018).

**Questions for Future Research to Address (Objective 4)**

**Limitations of our study: linking ecosystem service proxies to realized pest regulation**

Our study assumes that measures of raptor foraging ecology we label as ecosystem service proxies may reduce damage in and increase productivity of crops. Theoretical and field studies of predator effects on prey behavior suggest that individuals reduce foraging activity in the presence of predators and this may have effects on lower trophic levels (Lima and Bednekoff 1999, Brown and Kotler 2004, Billings et al. 2017). Many studies have documented reduced pest activity and reduced damage due to the presence of raptors (e.g. Shave et al. 2018, Kross et al. 2012, Luna et al. 2020). In addition, other studies have examined the diets of raptors that reside in agricultural landscapes and found that it primarily consists of crop pests (Kross et al. 2016). Yet, it is important to investigate links between these ecosystem service proxies and realized crop damage and productivity in specific systems in order to provide well-supported recommendations to farmers.

In addition, use was the most commonly reported measure, however it may be the least informative proxy. While the presence of a predator, due to their use of a land cover, may deter pests and reduce their foraging activity, this proxy assumes pests are aware of the predator's presence in the area and respond to it no matter what the predator is doing (Moll et al. 2017). However, many studies have shown that predator behavior while present is an important component of reduced foraging activity by prey (Moll et al. 2017, Creel et al. 2019). A number of other potential ecosystem service proxies have yet to be explored. Measures that did not meet the 20% criteria but may be more informative included hunting strategy, savage selectivity index (a measure of habitat selection), prey size, and provisioning rate. For example, we found only 16 studies that examined effects of predictors on variation in hunting strategy; however, in a meta-analysis of 193 studies, sit-and-pursuit hunting had a stronger negative effect on the growth, fecundity, and density of prey than active hunting (Preisser et al. 2005). This suggests that managing predictors like landscape, can increase sit-and-pursuit hunting and may enhance pest regulation services by raptors. Investigation of different proxies may improve our understanding of how raptor species, crop type, landscape context, and other variables impact the strength of pest regulation services and how to increase pest regulation services at larger scales, across systems.

**What are other possible predictors of pest regulation services?**

Shorter vegetation and closer distances to the nest may enhance raptor pest regulation services in crops across systems. However, further investigations of how landscape characteristics influence raptor use of agricultural landscapes may provide more specific recommendations to enhance services. For example, while raptors including American Kestrels, Great-horned Owls (*Bubo virginianus*), Golden Eagles (*Aquila chrysaetos*), Barn Owls, and Red-tailed Hawks (*Buteo jamaicensis*) perched on hilltop and hill bottom perches equally frequently in vineyards in a California study, they spent more time on perches on hill tops (Wong and Kross 2018). Thus, growers may benefit from providing supplementary perches on hilltops so that raptors spend more time in and around vineyards.

Researchers should also consider how landscape composition affects use of land covers. A small number of studies in our review found that land cover type selection may be influenced by the heterogeneity of the landscape (e.g. Sunde and Redpath 2006, Alves et al. 2014, Emin et al. 2018, Väli et al. 2020). For example, Tawny Owls (*Strix aluco*) used woodlands more intensively in more fragmented landscapes (Sunde and Redpath 2006). Thus it's possible that reducing fragmentation in landscapes in this system may increase owl use of cultivated land cover and pest regulation services. In addition, the importance of edge habitat for providing cover and perches for raptors was often discussed anecdotally, but not explored systematically.

**At what spatial and temporal scales do we detect variation in raptor use of land covers and other measures of foraging ecology?**

Considering multiple spatial and temporal scales in future studies will provide more information about contexts in which raptors provide pest regulation services and how to increase services across systems. Use of a land cover is affected both by land cover type at the landscape scale (when selecting a home range) and at the local scale (within a home range). For example, Little Owls (*Athene noctua*) in the Czech Republic were positively associated with arable land at the landscape scale and negatively associated with it at the local scale (Šálek et al. 2016). In addition, the resolution at which researchers considered land cover types varied considerably. For example, many studies investigating the effects of land cover type on use by raptors used broader categories such as "urban" and "agricultural" (e.g. de Frutos and Olea 2008) while other studies used more narrow categories such as "alfalfa", "cereal", and "maize" (e.g. Cardador and Mañosa 2011). We recommend investigators report land cover types to as narrow a category as possible to improve recommendations for crop and landscape management. Cooperative management strategies may need to develop among growers and target crop, local, and landscape scales in order to optimize pest regulation services.

# CONCLUSION

## Final Key Recommendations

Our findings suggest the following specific recommendations for growers.

1. Provide hedgerows and maintain forest edges that may offer nest sites, cover, and perches for sit-and-pursue raptors (Fig. 3 A). Farmers may adjust the distance between these features and the crops depending on the use of these features by species that damage crops.
2. Reduce the amount of tall, dense herbaceous vegetation around crops by mowing grass margins (Fig. 3 B)
3. Maintain complementary land cover and provide artificial nesting structures close to crops (Fig 3 C)

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## APPENDIX: FIGURES AND TABLES

**Table 1** Raptor-based response variables occurring in ≥20% of published studies (n=105) with potential to act as proxies for ecosystem serives. We defined categories broadly to account for differences among studies in units and scale of measurements. We did not distinguish between MCP and Kernel estimators for home range size, because we felt this was beyond the scope of our review (Objective 1).

| Response Variable Categories | Description | Inclusion | Percent of studies that measured response (n = 105) | Rationale for inclusion |
|---|---|---|---|---|
| Use of a land cover (use) | Presence/absence or abundance of raptors in space or time | Yes | 74.29% | Raptors reduce pests directly through consumption and indirectly through fear and anti-predatory responses (Werner and Peacor 2003, Preisser et al. 2005, Cresswell 2008). Pests may spend less time in land cover types where raptors are present or reduce their rate of foraging, which may reduce the amount of damage done to crops (Lima and Bednekoff 1999, Brown and Kotler 2004). |

**Table 1 (cont'd)**

| | | | | |
|---|---|---|---|---|
| Home range size | Area of space used by an individual or pair of raptors. | Yes (discussion only) | 45.71% | Home range size provides information on the extent of land cover over which a raptor is expected to hunt and on the intensity with which a raptor is expected to hunt in an area. As the home range expands, an individual may spend less time on average in any given area. |
| Diet | Types of prey consumed. | Yes (discussion only) | 36% | The diet of a raptor can indicate whether a particular species may be helpful in reducing pests in specific crops (e.g. Kross et al. 2013, Kross et al. 2016). |
| Home range composition | Amount of each land cover type within the home range. | No | 29.50% | |
| Attack rate | Number of attempts to capture prey by an individual raptor. May be presented as a rate or proportion. | Yes | 20% | Higher attack and success rates may induce increased antipredator behaviors in pests, thus reducing crop damage (Brown and Kotler 2004, Creel et al. 2019). |
| Succesful attack rate | Number of food items captured by an individual raptor. May be presented as a rate or proportion. | Yes | 19% | Higher attack and success rates may induce increased antipredator behaviors in pests, thus reducing crop damage (Brown and Kotler 2004, Creel et al. 2019). |

**Table 2** Variables occurred in ≥20% of studies (n=105) that can be managed by farmers in some capacity, and have the potential to predict ecosystem service proxies. Different studies may have used different units for the same variable; for example, a study may have provided a numerical measurement for vegetation height (e.g. 0-10cm) or a categorical height (e.g. "below the knee"). In addition, different studies may have categorized variables at different resolutions; for example, land cover type may be recorded as "agriculture" or as "corn, cereal, and beets". We defined categories broadly to account for differences in units and scale of measurements (Objective 1).

| **Explanatory Variable Categories** | **Definitions** | **Percent of studies that measured effect (n = 105)** | **Rationale for inclusion** |
|---|---|---|---|
| Distance | Distance from a central location (e.g. nest) | 26.67% | Distance was included in many studies of ecosystem service proxies, interacted with other predictors of proxies, and could feasibly be managed by growers when managing vegetation structure or providing artificial structures for raptors (e.g. Rosenberg and Haley 2004, Arroyo et al. 2009). |
| Cultivated land cover | Categorization of land covers at any scale. | 90.48% | Land cover was included in most studies of ecosystem service proxies and is a key factor of agricultural management (Lindell et al. 2018). |
| Prey abundance | Number of prey available in the study landscape. | 22.86% | Prey abundance was included in many studies of ecosystem service proxies and may be of concern to growers. |

**Table 2 (cont'd)**

| | | | |
|---|---|---|---|
| Vegetation structure | The height or density of vegetation. | 22.86% | Vegetation structure was included in many studies of ecosystem service proxies, may be broadly applicable across systems, and could be feasibly managed by growers. |

**Table 3** Most studies were conducted in Europe, followed by North America.

| Continent | Frequency |
|---|---|
| Africa | 4 |
| Asia | 4 |
| Australia | 1 |
| Europe | 64 |
| North America | 25 |
| Oceania | 2 |
| South America | 5 |

**Table 4** The Lesser Kestrel (*Falco naumanni*) was the most frequently studied species.

| Raptor species | Frequency |
|---|---|
| *Accipiter cooperii, Accipiter striatus* | 1 |
| *Aegypius monachus* | 1 |
| *Aquila chrysaetos* | 2 |
| *Asio flammeus* | 2 |
| *Asio otus* | 3 |
| *Athene cunicularia* | 5 |
| *Athene noctua* | 6 |
| *Bubo bengalensis* | 1 |
| *Bubo bubo* | 1 |
| *Bubo scandiacus* | 1 |
| *Butastur indicus* | 3 |
| *Buteo buteo* | 1 |
| *Buteo buteo, Buteo lagopus, Milvus milvus* | 1 |
| *Buteo buteo, Circus aeruginosus, Circus cyaneus, Milvus migrans* | 1 |
| *Buteo regalis* | 2 |
| *Buteo swainsoni* | 4 |
| *Caracara cheriway* | 1 |
| *Circus aeruginosus* | 5 |
| *Circus aeruginosus, Circus macrourus, Circus pygargus* | 1 |
| *Circus cinereus* | 1 |
| *Circus cyaneus* | 2 |
| *Circus cyaneus, Circus aeruginosus, Circus pygargus* | 1 |
| *Circus hudsonius* | 2 |
| *Circus pygargus* | 2 |

**Table 4 (cont'd)**

| | |
|---|---|
| *Clanga pomarine* | 6 |
| *Elanus axillaris* | 1 |
| *Elanus leucurus* | 1 |
| *Elanus leucurus, Asio flammeus, Circus hudsonius, Buteo lineatus, Buteo jamaicensis, Falco peregrinus* | 1 |
| *Falco naumanni* | 17 |
| *Falco novaeseelandiae* | 2 |
| *Falco peregrinus* | 1 |
| *Falco punctatus* | 1 |
| *Falco Sparverius* | 2 |
| *Falco tinnunculus* | 4 |
| *Falco vespertinus* | 2 |
| *Haliaeetus leucogaster* | 1 |
| *Hieraaetus pennatus* | 2 |
| *Ictinia mississippiensis* | 1 |
| *Melierax metabates* | 1 |
| *Milvus migrans* | 3 |
| *Otus scops* | 1 |
| *Strix aluco* | 2 |
| *Tyto alba* | 5 |
| *Tyto alba, Asio flammeus* | 1 |

**Table 5** Studies did not list a specific crop type most frequently when studying cultivated land cover (40). When studies did list a crop, cereal was the most frequently listed (21).

| Crop type | Frequency |
|---|---|
| alfalfa | 21 |
| barley | 3 |
| bean | 2 |
| beet | 3 |
| beetroot | 1 |
| berry | 1 |
| canola | 1 |
| celery | 1 |
| cereal | 21 |
| chile | 1 |
| citrus | 2 |
| corn | 19 |
| cotton | 8 |
| dry cereals | 2 |
| drylands | 1 |
| fodder | 1 |
| fruit | 9 |
| Fruit trees | 1 |
| grain | 2 |
| greenbean | 1 |
| hay | 6 |
| legume | 8 |
| maize | 9 |
| milo | 2 |
| none | 40 |
| oat | 4 |
| oilseed rape | 2 |
| olive | 5 |
| olive groves | 2 |
| onion | 3 |
| parsley | 1 |
| pasture | 15 |
| pea | 3 |
| pecan | 1 |
| pepper | 1 |
| ploughed fields | 2 |

**Table 5 (cont'd)**

| | |
|---|---|
| potato | 3 |
| rape | 3 |
| rice | 6 |
| roots | 1 |
| rowcrops | 1 |
| rye | 2 |
| safflower | 1 |
| silage | 1 |
| sorghum | 3 |
| soybean | 4 |
| spinach | 1 |
| squash | 1 |
| sugarbeet | 4 |
| sugarcane | 2 |
| sunflower | 11 |
| tobacco | 1 |
| tomato | 3 |
| vegetable | 2 |
| vineyard | 8 |
| wheat | 13 |

**Table 6** The table used for a Fisher's exact test for use (A), attack rate (B), and successful attack rate (C). Each column corresponds to a predictor of use and each row corresponds to a possible relationship the predictor had with use. Each cell contains the total number of studies that documented the corresponding relationship between the corresponding predictor and use.

| A | **Cultivated land cover** | **Prey abundance** | **Vegetation structure** | **Distance from a nest or roost** |
|---|---|---|---|---|
| **Negative** | 22 | 3 | 9 | 18 |
| **Neutral** | 15 | 4 | 0 | 2 |
| **Positive** | 29 | 4 | 3 | 0 |

B

| | **Cultivated land cover** | **Vegetation structure** | **Distance from a nest or roost** |
|---|---|---|---|
| **Negative** | 1 | 5 | 1 |
| **Neutral** | 4 | 1 | 1 |
| **Positive** | 7 | 1 | 0 |

C

| | **Cultivated land cover** | **Vegetation structure** | **Distance from a nest or roost** |
|---|---|---|---|
| **Negative** | 4 | 3 | 1 |
| **Neutral** | 3 | 2 | 1 |
| **Positive** | 2 | 1 | 1 |

**Figure 1** Cultivated land cover and prey abundance had positive effect on raptor use/abundance in more studies than expected, while vegetation structure and distance from nest or roost had a negative effect in more studies than expected. Symbols below bars indicate the different kinds of relationships between predictors: - negative, o neutral, and + positive.

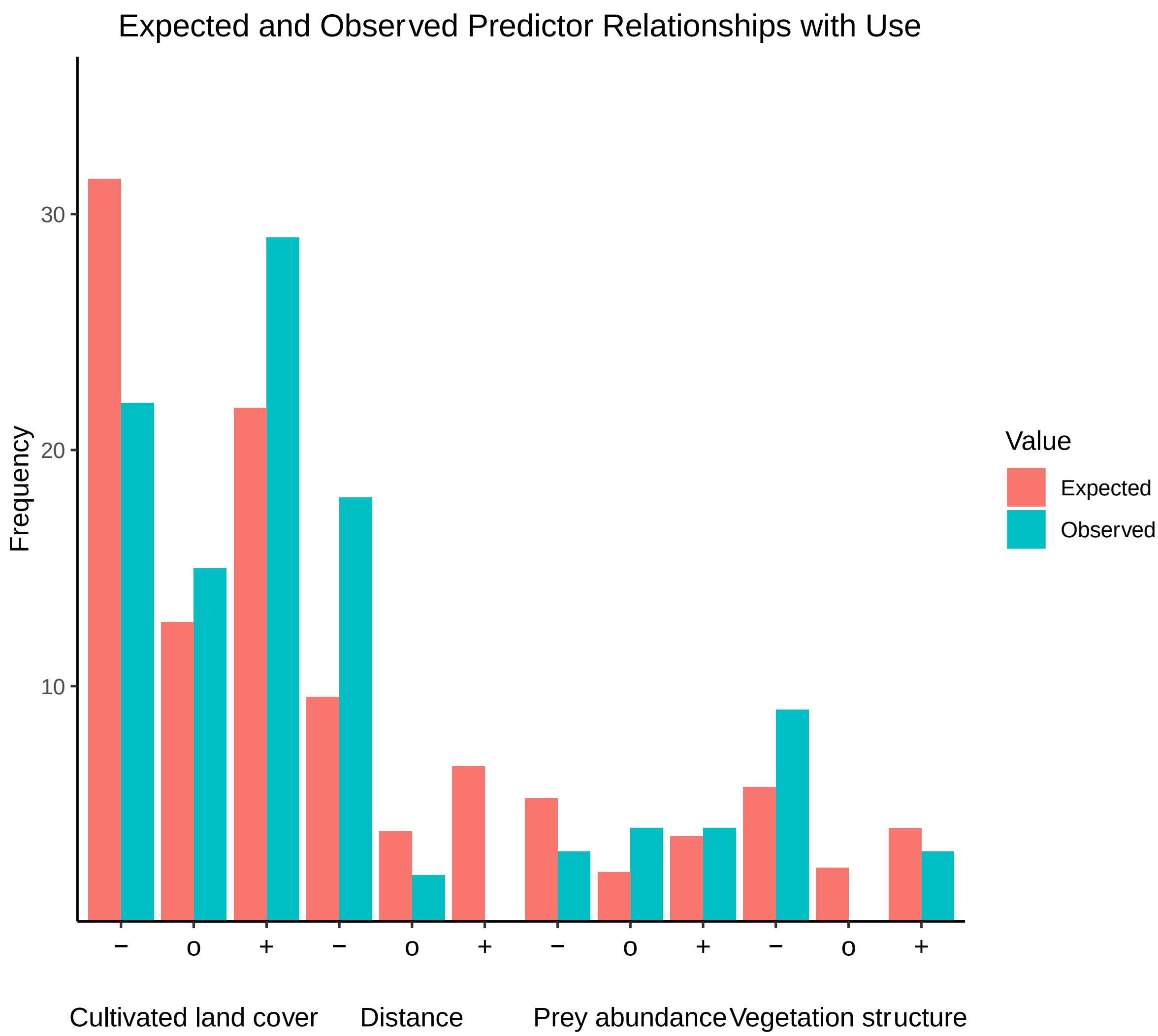

**Figure 2** Cultivated land cover had a positive effect on attack rate in more studies than expected, while vegetation structure and distance had a negative effect in more studies than expected. Symbols below bars indicate the different kinds of relationships between predictors: - negative, o neutral, and + positive.

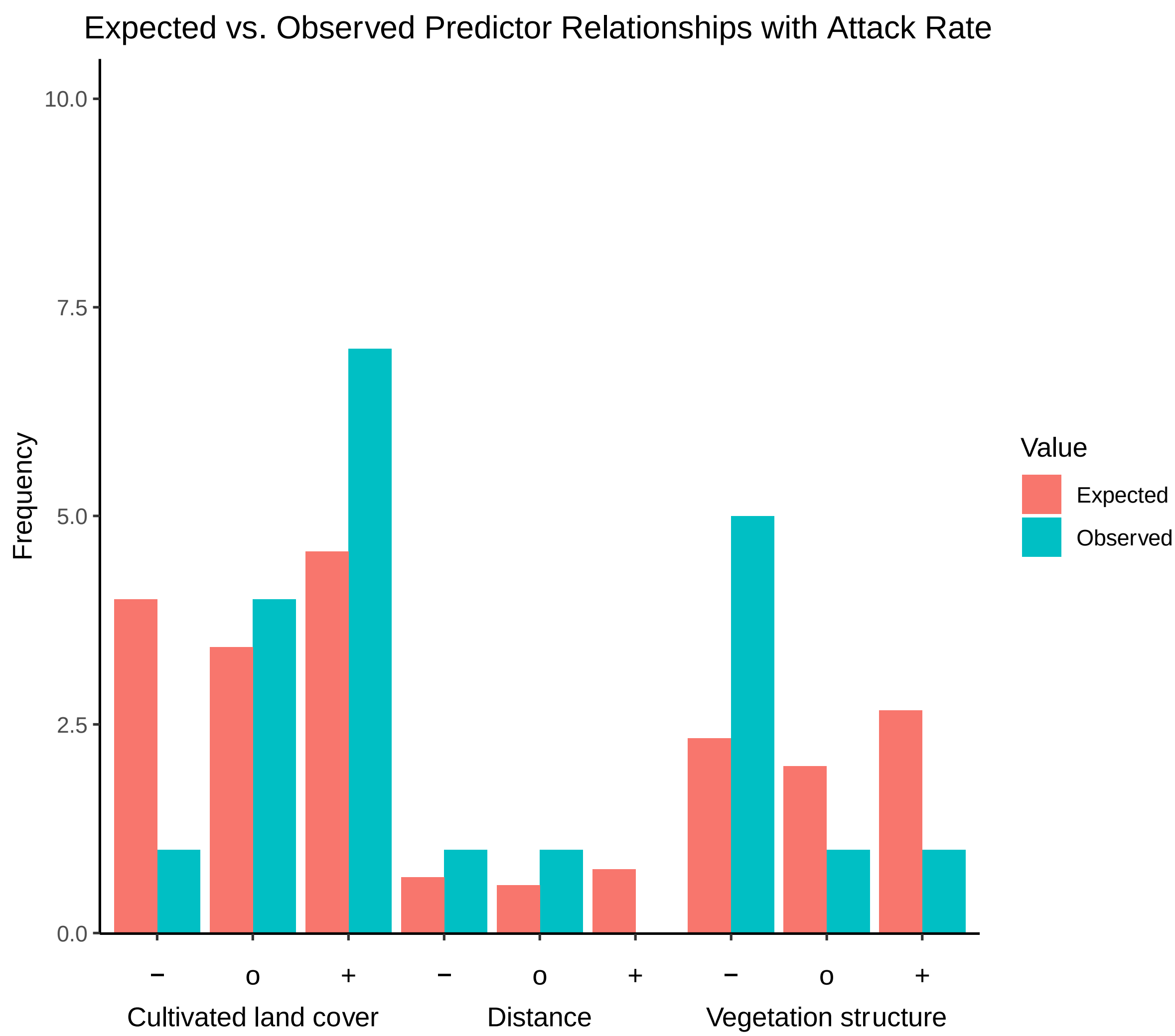

**Figure 3** A visual representation of key recommendations for growers to attract raptors and maintain their use of the landscape. Growers can maintain important complementary habitat in the landscape (A), mow margins and uncultivated vegetation around crops (B), and locate artificial structures, such as nest boxes, near crops, if they are provided (C).