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Spatial scale matters when modeling avian co-occurrence

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Abstract. The spatial scale at which competition alters the spatial distribution of a species is important to consider when evaluating competitive interactions between species. The two-species occupancy model was developed to evaluate competitive interactions between two species while accounting for imperfect detection. However, no studies have incorporated spatial scale into such models. We developed an approach to incorporate spatial scale when evaluating species co-occurrence using the two-species occupancy model and tested our approach on two wetland passerines: the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) and the Marsh Wren (*Cistothorus palustris*). We surveyed for Yellow-headed Blackbirds and Marsh Wrens using point counts at wetlands throughout Iowa in 2009 and 2010. We assigned observations to one of three distance bins: ≤20, ≤60, and ≤100 m and then created encounter histories for each distance bin for the two-species occupancy model and modeled co-occurrence as a function of habitat covariates for each distance bin. We also modeled co-occurrence using all observations regardless of distance. We found that Yellow-headed Blackbirds were less likely to co-occur with Marsh Wrens at both the ≤60 and ≤100 m scales. However, using all observations, we found that Yellow-headed Blackbirds and Marsh Wrens co-occurred independent of one another. This result illustrated that failure to incorporate spatial scale in evaluations of species co-occurrence could lead to incorrect inferences on co-occurrence of different species. The two-species co-occurrence occupancy model is a valuable tool that allows researchers to evaluate the presence of competitive interactions between species, and incorporating spatial scale into these models provides information on how species partition resources at different spatial scales within a patch. Understanding species co-occurrence patterns across multiple spatial scales provides valuable information that is useful for a better understanding of the mechanisms of competitive interactions between two species and aiding the restoration and management of habitat for multiple species.

Key words: *Cistothorus palustris*; competition; co-occurrence; interspecific interaction; Marsh Wren; occupancy; Program Mark; spatial scale; *Xanthocephalus xanthocephalus*; Yellow-headed Blackbird.

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Introduction

Competition for limited resources has long been considered a primary factor shaping ecological communities and predicting which species will occur in a given community has long been a central topic in ecology (MacArthur 1960, Diamond 1975, Grover 1997, Fox 2002). At the heart of research on competition within ecological communities is the competitive exclusion principle. This principle, also known as Gause's principle, simply states that complete competitors cannot coexist (Hardin 1960). More specifically, species that use the same resources cannot continue to use those resources indefinitely, and one species will eventually exclude the other (Den

Boer 1986). Some studies have shown evidence of direct exclusion from resources of one species by another (Slagsvold 1978, Williams and Batzli 1979, Kempenaers and Dhondt 1991, Brown and Sullivan 2005) or utilization of different habitats resulting from competitive interactions (Connell 1961, Mac Nally and Timewell 2005). To avoid competitive interactions, organisms evolve to utilize slightly different resources than competitors, allowing them to coexist. Coexistence mechanisms such as resource partitioning involve such behaviors as consuming different foods, consuming foods at different locations, or locating foods using different foraging behaviors (Cody 1974).

One condition that suggests the presence of interspecific competition is that the distribution and abundance of one species is reduced or limited by the presence of another (Dhondt 2012). The spatial scale at which the distribution of a species is altered by another species is important to consider when evaluating competitive interactions between species because the spatial scale at which species utilize habitats vary (Cody 1974). As an example, consider breeding territories of birds. These are typically areas of high resource value because adult birds need abundant resources to support their offspring and themselves. If the breeding territory of one species is larger than the breeding territory of another species, yet those two species compete for similar resources, the species with the larger breeding territory might exclude the species with the smaller breeding territory and force them to utilize areas of lower habitat quality (Dhondt 2012). However, the species with the larger breeding territory is also affected through territory size restriction, thus potentially reducing reproductive output (Orians and Willson 1964, Dhondt 2012). Spatial scale affects the space available within a particular patch, and limited space can affect individual fitness of a bird (Dhondt 2012).

In addition to affecting individual fitness, limited space can also force species to utilize different, and sometimes lower quality, habitats (Reed 1982). Dhondt (2012) lists a number of removal experiments that resulted in expanded territory, home range size, or shift in habitat preferences of species. A classic example of habitat partitioning in response to limited space is that of the Red-winged Blackbird (*Agelaius phoeniceus*) and Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) studied by Orians and Willson (1964). They found that Red-winged and Yellow-headed Blackbirds co-occur by partitioning the available habitat. Red-winged Blackbirds nested in peripheral habitat of marshes whereas Yellow-headed Blackbirds nested in the marsh interior. Each species aggressively defends territories against the other species. Similarly on winter habitat, Williams and Batzli (1979) found that removal of Red-headed Woodpeckers (*Melanerpes erythrocephalus*; the dominant species in this study system) resulted in increased habitat exploitation by Red-bellied Woodpeckers (*Melanerpes carolinus*).

The consequences of competitive interactions at small spatial scales can scale up to larger spatial scales such as metacommunities and metapopulations (Kneitel and Chase 2004, Hanski 2008). At both levels, these interactions drive population dynamics, specifically patch extirpation and colonization rates, and ultimately shape ecological communities (Diamond 1975). For example, in areas of patchy, isolated habitats, species rely heavily on dispersal to persist within a network of patches even if all patches are not continuously occupied (Hanski 2008). However, interspecific interactions could cause a species to be extirpated from patches and limit colonization of other patches, thereby impacting the regional population of the species. Additionally, increased competition at preferred patches could drive species to utilize suboptimal habitats on the landscape. This could result in decreased survival and reproductive success at these suboptimal patches and ultimately affect the population at the regional level. Differential use of limited resources (Kneitel and Chase 2004) can influence the co-occurrence of species at small spatial scales (e.g., breeding territories). Therefore, species with superior competitive ability may exclude competitors from an area within a patch when competing for a single limited resource (Chase and Leibold 2003). Such exclusion and other competitive interactions at small spatial scales can reduce individual fitness (Martin 1986, 1987), thus scaling up to have potential population impacts. Understanding how species co-occur at these small spatial scales, such as breeding territories, can shed light on how competing species partition habitat characteristics and limited resources within a patch and thus potentially indicate persistence of species in a patch, given habitat characteristics.

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It is important to consider spatial scale when making inferences from co-occurrence studies because competition could be occurring at different spatial scales within a patch (Richmond et al. 2010). The objectives of our study were to outline an approach for evaluating species co-occurrence at multiple spatial scales using the two-species occupancy model established by Richmond et al. (2010) and test the approach using a case study with breeding Yellow-headed Blackbirds and Marsh Wrens (*Cistothorus palustris*). Yellow-headed Blackbirds and Marsh Wrens are marsh-nesting species whose breeding ranges overlap in North America. Both species aggressively defend breeding territories against both conspecifics and heterospecifics (Orians and Willson 1964, Twedt and Crawford 1995, Kroodsma and Verner 1997) and forage near the water surface on insects (e.g., odonate larvae and others) and other small aquatic prey (Twedt and Crawford 1995, Kroodsma and Verner 1997). Yellow-headed Blackbirds are very aggressive toward Marsh Wrens and often will exclude them from established territories (Orians and Willson 1964, Bump 1986). Leonard and Picman (1986) found that Marsh Wrens and Yellow-headed Blackbirds will segregate in marshes in which they co-occur. However, their study did not consider multiple spatial scales when establishing species segregation nor did their study evaluate how the two species partitioned available habitat. Our objective was to use co-occurring, breeding Marsh Wrens and Yellow-headed Blackbirds as a case to test for scale-dependent patterns of co-occurrence at scales that encompass the average breeding territory size for both species. With the advent of new quantitative methods for evaluating co-occurrence between species and the need to consider spatial scale, our question was, "At what spatial scale or scales does segregation between Yellow-headed Blackbirds and Marsh Wrens occur?"

Methods

Study area

We surveyed for breeding Marsh Wrens and Yellow-headed Blackbirds at wetlands across Iowa during two breeding seasons as part of a larger study of marsh birds. Approximately 74% of Iowa's landscape is in agriculture and 3.2% is in urban development. This leaves approximately 23% (approx. 3.35 million ha) of the land to natural habitats of which 13.7% (approx. 459,000 ha) is wetlands (Zohrer 2006).

We selected wetlands to be surveyed from the National Wetlands Inventory database (NWI; U.S. Fish and Wildlife Service 2009). The NWI classifies wetlands into systems, classes, and subclasses based on the type of wetland (e.g., palustrine, lacustrine, riverine) and the habitat characteristics within the wetland (Cowardin et al. 1979). We considered all wetlands within the Aquatic Bed (AB), Emergent (EM), and Unconsolidated Bottom (UB) classes of the Palustrine system (Cowardin et al. 1979) because these classes contained greater than 95% of the wetlands in Iowa and shared similar habitat characteristics suitable for our target species. These habitat characteristics included shallow water (<1 m deep), surrounded by few or no trees, and presence of both emergent and submergent vegetation. We considered both natural and constructed wetlands for selection and only considered those wetlands on public land, which constituted approximately 8% of wetlands in the NWI, to facilitate access for surveys. Mean water depth of 30 cm (± 1 cm) at wetlands supported vegetation communities consisting of cattails (*Typha* spp.), sedges (*Carex* spp.), bulrushes (*Scirpus* spp. and *Schoenoplectus* spp.), common reed (*Phragmites australis*), and reed canary grass (*Phalaris arundinacea*). Most wetlands were permanent or semi-permanent as defined by Stewart and Kantrud (1971), but some temporary and seasonal wetlands were also included in our selection.

Prior to selection, we stratified wetlands by size (ha) into six different classes (≤5 ha, >5–10 ha, >10–20 ha, >20–30 ha, >30–40 ha, and >40 ha) to allow for equal representation of both large and small wetlands. We used Hawth's Analysis Tools (Beyer 2004) in ArcGIS (version 9.3; ESRI 2010) to randomly select wetlands within each size class. We then randomly located survey points that were >400 m apart within each wetland: we surveyed one point in wetlands ≤10 ha, two points in wetlands >10–20 ha, three points in wetlands >20–30 ha, four points in wetlands >30–40 ha, and five points in wetlands >40 ha. Survey points were located in both the wetland interior and the wetland edge, but were more frequently near the edge in smaller wetlands (<10 ha) due to sparse wetland interior.

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Habitat measurements

We measured habitat variables at each survey point within each wetland prior to conducting bird surveys. To characterize local habitat, we conducted measurements at both the survey point and within 50 m of the survey point depending on which variable we were measuring (Conway 2011). We measured water depth (cm) and maximum vegetation height (m) at the survey point. Vegetation height was measured from the surface (either the ground or surface of the water) and assigned to one of three size classes (1, 0.0–0.5 m; 2, 0.5–1.0 m; 3, ≥1.0 m) and water depth was measured from solid substrate. We visually estimated percent cover of the major vegetation types in 5% increments within a 50 m radius of the survey point including cattail, bulrush, sedge, reed canary grass, and woody vegetation. We included the sum of percent cover for all vegetation types at a single point (not to exceed 100%) as the total percent cover of vegetation for that point. We also visually estimated the percent coverage of open water. Lastly, we obtained wetland area (ha) from the NWI database (U.S. Fish and Wildlife Service 2009).

Bird surveys

We conducted unlimited-radius, 10-min point counts in conjunction with distance sampling for Yellow-headed Blackbirds and Marsh Wrens from 16 May to 15 July 2009 and from 20 April to 10 July 2010 during the early-morning (30 min before sunrise to 3 h after sunrise) and late-evening (3 h before sunset to 30 min after sunset) hours. Surveys for Yellow-headed Blackbirds and Marsh Wrens followed protocols outlined by Blondel et al. (1981). We conducted surveys at each point within each of 309 wetlands; 56 wetlands were surveyed four times in 2010 and an additional 253 wetlands were surveyed once during either 2009 or 2010. We recorded all visual and aural detections of both species during the survey period and measured the linear distance (m) to each individual using a Nikon ProStaff 550 Laser Rangefinder (Nikon Sport Optics, Inc., Melville, New York, USA). If a bird was detected visually, the distance to the bird was measured directly. If a bird was detected aurally and not visually, the approximate location of the bird was determined and the distance was measured to a landmark nearest to the bird. We measured temperature (°C) and wind speed (Beaufort scale; bft) prior to starting surveys at each point using a Weather Kestrel 4000 (Nielsen-Kellerman, Boothwyn, Pennsylvania, USA). We also visually estimated the amount of cloud cover prior to starting surveys at each point and assigned our estimate to one of four classes (0, few or no clouds; 1, partly cloudy; 2, cloudy or overcast; or 4, fog). We did not conduct surveys during periods of rain or when wind speeds exceeded 3 bft.

A priori hypotheses

We established a set of hypotheses used to develop a candidate set of models and determine the distances at which to truncate the data set. Below, we list and explain each hypothesis used to build models:

1. Distance.—Marsh Wren territories encompass an area of approximately 20–100 m in diameter and Yellow-headed Blackbird territories encompass an area of approximately 100–200 m in diameter in our study wetlands (T. M. Harms, *personal observation*). Therefore, we assigned the data set into three bins (≤20, ≤60, and ≤100 m) that spanned the approximate territory sizes of both species. We used Program Distance (version 6.2; Thomas et al. 2010) to estimate the effective detection radius (EDR; Buckland et al. 2001) for both Marsh Wrens and Yellow-headed Blackbirds given our survey data. The EDR for Marsh Wrens was 78.59 m (± 2.93 m) and the EDR for Yellow-headed Blackbirds was 175.72 m (± 4.18 m). Therefore, we did not consider distance bins >100 m as it was outside the EDR for Marsh Wrens. However, we maintained the largest distance bin as ≤100 m to allow for overlap in the territory size of both species. We hypothesized that Yellow-headed Blackbirds would be less likely to co-occur with Marsh Wrens at ≤20 m because Marsh Wrens would aggressively defend territories at this scale and potentially depredate Yellow-headed Blackbird nests within their territory. We also hypothesized that Yellow-headed Blackbirds would be more likely to co-occur with Marsh Wrens at ≥60 m because of their larger territory size. In addition, Yellow-headed Blackbirds are a colonial-nesting species, so the

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larger territory size would allow more Yellow-headed Blackbirds to better defend each territory against Marsh Wren intruders and nest depredation. Lastly, we hypothesized that the influence of habitat covariates on site occupancy of both species would not change across different spatial scales because both species are selective in regards to their microhabitat preferences (Twedt and Crawford 1995, Kroodsma and Verner 1997).

2. Water depth.—Marsh Wrens are commonly found to inhabit the perimeter of wetlands whereas Yellow-headed Blackbirds inhabit the interior of wetlands. This is likely because Yellow-headed Blackbirds prefer to build nests over areas of deepwater (Twedt and Crawford 1995). Therefore, we hypothesized that water depth would be an important covariate influencing the site occupancy of Yellow-headed Blackbirds in the presence of Marsh Wrens. In other words, Yellow-headed Blackbirds would retreat to areas of deeper water in the presence of Marsh Wrens to avoid aggressive interactions.

3. Percent cover of cattail.—Cattail is a common plant species in wetlands throughout Iowa and both Marsh Wrens and Yellow-headed Blackbirds will use cattail for nest substrate (Twedt and Crawford 1995, Kroodsma and Verner 1997). We hypothesized that site occupancy of Marsh Wrens would increase with increased percent cover of cattail. We also hypothesized that site occupancy of Yellow-headed Blackbirds would increase with increased percent cover of cattail, but only in the absence of Marsh Wrens.

4. Vegetation height.—Yellow-headed Blackbirds preferentially build nests in tall, robust stands of emergent vegetation (Twedt and Crawford 1995). Therefore, we hypothesized that vegetation height would positively influence site occupancy of Yellow-headed Blackbirds in the presence of Marsh Wrens. Marsh Wrens typically prefer taller vegetation but this preference can vary greatly (Kroodsma and Verner 1997). Therefore, we hypothesized that vegetation height would have no influence on site occupancy of Marsh Wrens.

Modeling approach

We generated co-occurrence encounter histories using 56 wetlands that received repeated visits and 253 wetlands that received single visits. Because we were interested in examining co-occurrence of species within wetlands as opposed to wetlands as a whole, we considered each point within each wetland as the sampling unit for our analysis. We considered each point independent because they were placed ≥400 m apart within each wetland (Conway 2011) and assumed that each point was closed to changes in occupancy state during the survey season because our surveys were restricted primarily to the breeding season of these species (Darrah and Krementz 2010).

To reduce the number of candidate models in the co-occurrence framework, we modeled detection probability for each species using the single-season occupancy model (MacKenzie et al. 2002) in Program MARK (White and Burnham 1999, Richmond et al. 2010). We modeled detection probability (p) for each species as a time-varying parameter to account for seasonal differences in detection probability of our target species (Harms and Dinsmore 2014) and included the covariates temperature, wind speed, cloud cover, and observer as factors potentially influencing detection probability while keeping site occupancy probability (Ψ) constant (denoted as "."). Using Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002), we compared 11 candidate models for detection probability for each species. We incorporated the covariate effect on detection probability in the top model for each species as the covariate effect on species-specific detection probability (pA and pB) in the co-occurrence model. If more than one model was considered to have strong support ($\Delta AIC_c \leq 2$; Burnham and Anderson 2002) in the single-season model set for each species, we included covariate effects of all competitive models on species-specific detection probability in the co-occurrence model.

Evaluating species co-occurrence at multiple spatial scales requires one piece of information not typically used in occupancy models, namely the distance to each individual observed. This additional information allows the data set to be truncated at different distances to evaluate co-occurrence at different spatial scales. For example, assume a data set with observed distances (m) to species A (the dominant species) as 23, 0 (no individual observed), and 81 on three individual visits to a study site and observed distances to species B (the subordinate species)

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Table 1. Candidate models considered for evaluating co-occurrence of Marsh Wren and Yellow-headed Blackbird at each of three spatial scales (≤20, ≤60, and ≤100 m) in Iowa marshes, 2010–2011.

Model	*K*
{ΨA(Cattail)ΨBA(.)ΨBa(.)*p*A(Year + T)*p*B(T)*r*A(.)*r*BA(.)*r*Ba(.)}	12
{ΨA(WetSize)ΨBA(.)ΨBa(.)*p*A(Year + T)*p*B(T)*r*A(.)*r*BA(.)*r*Ba(.)}	12
{ΨA(Sedge)ΨBA(.)ΨBa(.)*p*A(Year + T)*p*B(T)*r*A(.)*r*BA(.)*r*Ba(.)}	12
{ΨA(VegSize)ΨBA(.)ΨBa(.)*p*A(Year + T)*p*B(T)*r*A(.)*r*BA(.)*r*Ba(.)}	12
{ΨA(Bulrush)ΨBA(.)ΨBa(.)*p*A(Year + T)*p*B(T)*r*A(.)*r*BA(.)*r*Ba(.)}	12
{ΨA(ReedCan)ΨBA(.)ΨBa(.)*p*A(Year + T)*p*B(T)*r*A(.)*r*BA(.)*r*Ba(.)}	12
{ΨA(WaterDep)ΨBA(.)ΨBa(.)*p*A(Year + T)*p*B(T)*r*A(.)*r*BA(.)*r*Ba(.)}	12
{ΨA(Cattail)ΨBA(WaterDep)ΨBa(.)*p*A(Year + T)*p*B(T)*r*A(.)*r*BA(.)*r*Ba(.)}	13
{ΨA(Cattail)ΨBA(WetSize)ΨBa(.)*p*A(Year + T)*p*B(T)*r*A(.)*r*BA(.)*r*Ba(.)}	13
{ΨA(Cattail)ΨBA(Water)ΨBa(.)*p*A(Year + T)*p*B(T)*r*A(.)*r*BA(.)*r*Ba(.)}	13
{ΨA(Cattail)ΨBA(Bulrush)ΨBa(.)*p*A(Year + T)*p*B(T)*r*A(.)*r*BA(.)*r*Ba(.)}	13
{ΨA(Cattail)ΨBA(VegSize)ΨBa(.)*p*A(Year + T)*p*B(T)*r*A(.)*r*BA(.)*r*Ba(.)}	13
{ΨA(Cattail)ΨBA(WaterDep)ΨBa(Cattail)*p*A(Year + T)*p*B(T)*r*A(.)*r*BA(.)*r*Ba(.)}	14
{ΨA(Cattail)ΨBA(WaterDep)ΨBa(Bulrush)*p*A(Year + T)*p*B(T)*r*A(.)*r*BA(.)*r*Ba(.)}	14
{ΨA(Cattail)ΨBA(WaterDep)ΨBa(VegSize)*p*A(Year + T)*p*B(T)*r*A(.)*r*BA(.)*r*Ba(.)}	14
{ΨA(Cattail)ΨBA(WaterDep)ΨBa(WetSize)*p*A(Year + T)*p*B(T)*r*A(.)*r*BA(.)*r*Ba(.)}	14
{ΨA(Cattail)ΨBA(WaterDep)ΨBa(Sedge)*p*A(Year + T)*p*B(T)*r*A(.)*r*BA(.)*r*Ba(.)}	14
{ΨA(WaterDep)ΨBA(WaterDep)ΨBa(Bulrush)*p*A(Year + T)*p*B(T)*r*A(.)*r*BA(.)*r*Ba(.)}	14

Notes: "ΨA" represents site occupancy of Marsh Wren; "ΨBA" represents site occupancy of Yellow-headed Blackbird in the presence of Marsh Wren; "ΨBa" represents site occupancy of Yellow-headed Blackbird in the absence of Marsh Wren; "*p*A" represents detection probability of Marsh Wren; "*p*B" represents detection probability of Yellow-headed Blackbird; "*r*A" represents detection probability of Marsh Wren given both species are present; "*r*BA" represents detection probability of Yellow-headed Blackbird given both species are present and Marsh Wren is detected; and "*r*Ba" represents detection probability of Yellow-headed Blackbird given both species are present and Marsh Wren is not detected. "Cattail" represents percent cover of cattails (*Typha* spp.); "Bulrush" represents percent cover of bulrushes (*Scirpus* spp. and *Schoenoplectus* spp.); "Sedge" represents percent cover of sedges (*Carex* spp.); "ReedCan" represents percent cover of reed canary grass (*Phalarus arundinacea*); "WaterDep" represents water depth (cm); "VegSize" represents vegetation height (categorical as 1 [<0.5 m], 2 [≥0.5 m and <1 m], and 3 [≥1 m]); "WetSize" represents wetland size (ha); "Year" represents a year effect; "T" represents a linear time trend; and "." represents no covariate effect on the parameter.

as 17, 62, and 33 on the same three visits to the study site. The encounter history using the full data set would be constructed as follows: 11 01 11. The encounter history states that both species A and species B were present and detected on the first visit, species A was not detected but species B was present and detected on the second visit, and both species A and species B were present and detected on the third visit.

Examples of encounter histories with the above data set truncated at 30 m and 60 m, respectively, are as follows: (1) 11 00 00; and (2) 11 00 01. These examples illustrate how the encounter history changes by truncating the data set at specified distances. The distance can vary depending on what is reasonable and biologically relevant to the species of interest, for example, distances that relate to mean territory size. We utilized the conditional two-species occupancy model (Richmond et al. 2010) in Program MARK (White and Burnham 1999) to evaluate species co-occurrence. The conditional two-species occupancy model estimates seven parameters, five of which were meaningful for our analysis: site occupancy probability of the dominant species (ΨA), site occupancy probability of the subordinate species given presence of the dominant species (ΨBA), site occupancy probability of the subordinate species given absence of the dominant species (ΨBa), detection probability of the dominant species (*p*A), and detection probability of the subordinate species (*p*B; Richmond et al. 2010). We modeled site occupancy probabilities (ΨA, ΨBA, and ΨBa) in the co-occurrence model framework as a function of spatial scale by developing an initial model set (Table 1) based on our hypotheses and applied that model set to each of the truncated data sets (≤20, ≤60, and ≤100 m). Keeping the model structure the same for each spatial scale eased the comparison of parameters among the different scales while allowing for evaluation of scale-dependent co-occurrence based on habitat characteristics.

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We modeled eight habitat covariates on site occupancy probabilities (ΨA, ΨBA, and ΨBa) in the co-occurrence model: percent cover of cattail, percent cover of bulrush, percent cover of sedge, percent cover of reed canary grass, percent cover of woody vegetation, percent cover of open water, water depth (cm), vegetation height (categorical as 1 (<0.5 m), 2 (≥0.5 m and <1 m), and 3 (≥1 m)), and wetland size (ha). Prior to building candidate models, we assessed correlation among our habitat covariates using a correlation matrix and considered covariates with $r \geq 0.80$ as highly correlated (Lor and Malecki 2006). We did not include highly correlated covariates as effects on the same parameter in the same model. Because we did not hypothesize an annual difference in co-occurrence at different spatial scales, we combined data from both years for this analysis.

Using a hierarchical modeling approach similar to that used by Olson et al. (2005), we first modeled all covariate effects on ΨA while including covariate effects on *p*A and *p*B from the single-season models and keeping all other parameters constant ("."). Using the best model from this exercise, we then modeled all covariate effects on ΨBA. We repeated this approach for ΨBa for a total of 18 candidate models evaluated to obtain a single best model or competitive models with covariate effects on ΨA, ΨBA, ΨBa, *p*A, and *p*B. Again, we compared models using AIC_c and considered models with $\Delta AIC_c \leq 2$ to have strong support (Burnham and Anderson 2002). We repeated this process for each of the four data sets to obtain parameter estimates for each spatial scale.

We evaluated species co-occurrence using the species interaction factor (SIF), a derived parameter that is the ratio of how likely the two species are to co-occur compared to independent occurrence (Richmond et al. 2010). If the SIF is equal to one or if the 95% confidence interval of the SIF includes 1, the two species occur independently. An SIF <1 indicates that the subordinate species is less likely to co-occur with the dominant species and an SIF >1 indicates that the subordinate species is more likely to co-occur with the dominant species (Richmond et al. 2010).

Results

We detected 573 Marsh Wrens and 278 Yellow-headed Blackbirds in 2009 and 342 Marsh Wrens and 194 Yellow-headed Blackbirds in 2010. We detected Marsh Wrens at 393 points (51%) in 184 wetlands (60%) and detected Yellow-headed Blackbirds at 248 points (32%) in 132 wetlands (43%) during both 2009 and 2010.

Scale-dependent co-occurrence

Yellow-headed Blackbirds and Marsh Wrens co-occurred independently at the ≤20 m (Table 2). Water depth was the primary habitat covariate allowing the two species to co-occur at these scales; Yellow-headed Blackbird site occupancy increased as water depth increased in the presence of Marsh Wrens (β = 0.05, 95% CI = 0.007, 0.09 and β = 0.03, 95% CI = 0.01, 0.04, respectively).

At both the ≤60 and ≤100 m scales, Yellow-headed Blackbirds were less likely to co-occur with Marsh Wrens according to the SIF (Table 2). However, confidence intervals for the SIFs estimated in the competitive model ($\Delta AIC_c \leq 2$) at both spatial scales did overlap one, suggesting the effect is weak at each spatial scale (Table 2). Again, Yellow-headed Blackbird site occupancy increased with increasing water depth in the presence of Marsh Wrens at the ≤60 and ≤100 m scales (β = 0.03, 95% CI = 0.01, 0.04 and β = 0.03, 95% CI = 0.01, 0.04, respectively). Yellow-headed Blackbird site occupancy was associated with percent cover of bulrush in the absence of Marsh Wrens at the ≤60 and ≤100 m spatial scales although this effect was not significant at both scales nor was it estimated well (β = −5.37, 95% CI = −47.2, 36.5 and β = −4.72, 95% CI = −18.3, 8.89, respectively). Percent cover of cattail was associated with Yellow-headed Blackbird site occupancy in the absence of Marsh Wren at the ≤60 and ≤100 m spatial scales (ΔAIC_c = 1.39 and ΔAIC_c = 0.10, respectively); the association was not significant at the ≤60 m spatial scale (β = 0.11, 95% CI = −0.05, 0.27) but was weakly positive at the ≤100 m spatial scale (β = 0.11, 95% CI = −0.01, 0.22). Marsh Wren site occupancy increased with increased percent cover of cattail at all scales except ≥100 m (β = 0.06–0.10, 95% CI = 0.02, 0.18, averaged from best models for all three scales).

Scale-independent co-occurrence

Using the full data set (no spatial truncation), Marsh Wren and Yellow-headed Blackbird co-occurred independently at Iowa marshes

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Table 2. Best-supported models ($\Delta AIC_c \leq 2$) for site occupancy and detection probability using the co-occurrence model framework at different spatial scales in Iowa marshes, 2009–2010.

Scale	Model	ΔAIC_c	K	ω_i	Dev	SIF
≤20 m	ΨA(Cattail)ΨBA(WaterDep)ΨBa(Bulrush) pA(Year + T)pB(T)rA(.)rBA(.)rBa(.)	0.00†	13	0.66	1645.44	1.23 (0.978–1.49)
≤60 m	ΨA(Cattail)ΨBA(WaterDep)ΨBa(Bulrush) pA(Year + T)pB(T)rA(.)rBA(.)rBa(.)	0.00‡	12	0.54	2203.77	0.862 (0.742–0.983)
≤60 m	ΨA(Cattail)ΨBA(WaterDep)ΨBa(Cattail) pA(Year + T)pB(T)rA(.)rBA(.)rBa(.)	1.39	14	0.27	2201.01	0.852 (0.698–1.01)
≤100 m	ΨA(Cattail)ΨBA(WaterDep)ΨBa(Bulrush) pA(Year + T)pB(T)rA(.)rBA(.)rBa(.)	0.00§	12	0.42	2374.96	0.912 (0.836–0.989)
≤100 m	ΨA(Cattail)ΨBA(WaterDep)ΨBa(Cattail) pA(Year + T)pB(T)rA(.)rBA(.)rBa(.)	0.10	14	0.40	2370.92	0.903 (0.798–1.01)

Notes: "ΨA" represents site occupancy of Marsh Wren; "ΨBA" represents site occupancy of Yellow-headed Blackbird in the presence of Marsh Wren; "ΨBa" represents site occupancy of Yellow-headed Blackbird in the absence of Marsh Wren; "pA" represents detection probability of Marsh Wren; "pB" represents detection probability of Yellow-headed Blackbird; "rA" represents detection probability of Marsh Wren given both species are present; "rBA" represents detection probability of Yellow-headed Blackbird given both species are present and Marsh Wren is detected; and "rBa" represents detection probability of Yellow-headed Blackbird given both species are present and Marsh Wren is not detected. "Cattail" represents percent cover of cattails (*Typha* spp.); "Bulrush" represents percent cover of bulrushes (*Scirpus* spp. and *Schoenoplectus* spp.); "Sedge" represents percent cover of sedges (*Carex* spp.); "ReedCan" represents percent cover of reed canary grass (*Phalarus arundinacea*); "WaterDep" represents water depth (cm); "VegSize" represents vegetation height (categorical as 1 [<0.5 m], 2 [≥0.5 m and <1 m], and 3 [≥1 m]); "WetSize" represents wetland size (ha); "Year" represents a year effect; "T" represents a linear time trend; and "." represents no covariate effect on the parameter. "ΔAIC_c" is the difference in Akaike's Information Criterion adjusted for small sample sizes (AIC_c) relative to the smallest value; "K" is the number of parameters estimated in the model; "ω_i" is the AIC_c weight; and "Dev" is the model deviance. "SIF" is the derived species interaction factor, or the ratio of how likely the two species are to co-occur compared to independent occurrence. If SIF is equal to one, the two species occur independently. An SIF <1 indicates the subordinate species is less likely to co-occur with the dominant species and an SIF >1 indicates the subordinate species is more likely to co-occur with the dominant species.

† $AIC_c = 1671.92$.

‡ $AIC_c = 2228.18$.

§ $AIC_c = 2399.37$.

(SIF = 1.00, SE = 0.05 for both years). Percent cover of cattail was positively associated with site occupancy of Marsh Wren (β = 0.08, 95% CI = 0.05, 0.11) as indicated by the best supported scale-independent co-occurrence model. Site occupancy of Yellow-headed Blackbird in the presence of Marsh Wren increased with increasing water depth (β = 0.02, 95% CI = 0.01, 0.04). In the absence of Marsh Wren, percent cover of bulrush was associated with site occupancy of Yellow-headed Blackbird but the association was not significant (β = 0.16, 95% CI = −0.07, 0.39). A competitive model (ΔAIC_c = 0.46) included the covariate effect percent cover of cattail on site occupancy of Marsh Wren, water depth on site occupancy of Yellow-headed Blackbird in the presence of Marsh Wren, and vegetation height on site occupancy of Yellow-headed Blackbird in the absence of Marsh Wren. Vegetation size did not significantly affect site occupancy of Yellow-headed Blackbird in the absence of Marsh Wren (β = 0.81, 95% CI = −0.03, 1.65). Site occupancy of Marsh Wren for both years was 0.91 (SE = 0.06) whereas site occupancy of Yellow-headed Blackbird (ΨB) was 0.58 (SE = 0.04). Site occupancy of Yellow-headed Blackbird in the presence of Marsh Wren was 0.59 (SE = 0.03) and site occupancy of Yellow-headed Blackbird in the absence of Marsh Wren was 0.56 (SE = 0.28).

Detection probability

The best supported single-season model for Marsh Wren included the effects of year and observer on detection probability (Table 3). Detection probability for Marsh Wren was greater in 2009 than in 2010 (β = 2.17, 95% CI = 1.60, 2.75). Detection probability for Marsh Wren varied from 0.65 (SE = 0.06) early in the season and 0.89 (SE = 0.02) late in the season in 2009 and 0.77 (SE = 0.07) early in the season and 0.94 (SE = 0.02) late in the season in 2010.

The best supported single-season model for Yellow-headed Blackbird included a linear time trend within year on detection probability (Table 3). Detection probability for Yellow-headed

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Table 3. Model selection results for single-season occupancy models for Marsh Wren and Yellow-headed Blackbird to determine covariate effects on detection probability at Iowa marshes, 2009–2010.

Model	ΔAIC_c	*K*	w_i	Dev
Marsh Wren				
{*p*(Year + T)Ψ(.)	0.00†	4	0.92	833.21
Yellow-headed Blackbird				
{*p*(T)Ψ(.)	0.00‡	3	0.75	1039.49

Notes: "*p*" denotes detection probability and "Ψ" denotes site occupancy probability. "Year" represents a year effect on the parameter; "T" represents a linear time trend on the parameter; and "." represents no covariate effect on the parameter. "ΔAIC_c" is the difference in Akaike's Information Criterion relative to the smallest value; "*K*" is the number of parameters estimated in the model; "w_i" is the AIC_c weight; and "Dev" is the model deviance.

† AIC_c = 841.30.

‡ AIC_c = 1045.54.

Blackbird declined slightly throughout the survey season (β = −0.02, 95% CI = −0.04, −0.01). Detection probability for Yellow-headed Blackbird ranged from 0.88 (SE = 0.04) early in the survey season to 0.51 (SE = 0.05) late in the survey season.

Model predictions

We obtained model-based predictions of site occupancy probabilities (ΨA, ΨBA, ΨBa) by utilizing the user-specified covariate values option in Program MARK. We used the best co-occurrence model for each scale and specified a range of values for the covariate of interest while setting values for all other covariates in the model to the mean, therefore allowing us to obtain a set of occupancy predictions for co-occurrence based on a range of values for biologically relevant covariates. We predicted site occupancy of Marsh Wren (ΨA), site occupancy of Yellow-headed Blackbird in the presence of Marsh Wren (ΨBA), and site occupancy of Yellow-headed Blackbird in the absence of Marsh Wren (ΨBa) as a function of percent cover of cattail because this covariate most influenced all site occupancy probabilities (Fig. 1). This illustrates how Yellow-headed Blackbirds respond to increased percent cover of cattail in the presence of Marsh Wrens and in the absence of Marsh Wrens at different spatial scales.

Discussion

Our study with Yellow-headed Blackbirds and Marsh Wrens in Iowa demonstrated that species co-occurrence at small spatial scales such as breeding territories within a habitat patch is different from species co-occurrence at the habitat patch as a whole. Yellow-headed Blackbirds were less likely to co-occur with Marsh Wrens at the ≤60 and ≤100 m spatial scales. However, this effect was weak at both spatial scales. Although we did not expect this result, it was not entirely surprising. There is substantial literature documenting aggressive interactions between these two species in the literature. Marsh Wrens are predators of Yellow-headed Blackbird nests as well as nests of other wetland species (Orians and Willson 1964, Picman 1977, 1980, Grieves and Forbes 2012) and the number of Yellow-headed Blackbird nests depredated by Marsh Wrens increased as distance between the active Yellow-headed Blackbird nest and an active Marsh Wren nest decreased (Leonard and Picman 1986). Therefore, two mechanisms could be occurring in our study: (1) Yellow-headed Blackbirds are increasing the distance between their nests and those of Marsh Wrens in an attempt to establish a "buffer" and avoid depredation by Marsh Wrens; or (2) Marsh Wrens could be actively excluding Yellow-headed Blackbirds from areas immediately adjacent to their territories to gain increased access to foraging areas and perhaps increase their territory size. Simply evaluating co-occurrence of these species independent of scale suggested that they always co-occur in Iowa marshes. Using the scale-dependent approach demonstrated that co-occurrence of these species is a function of spatial scale and allowed us to improve our inferences regarding co-occurrence of Yellow-headed Blackbirds and Marsh Wrens at Iowa marshes.

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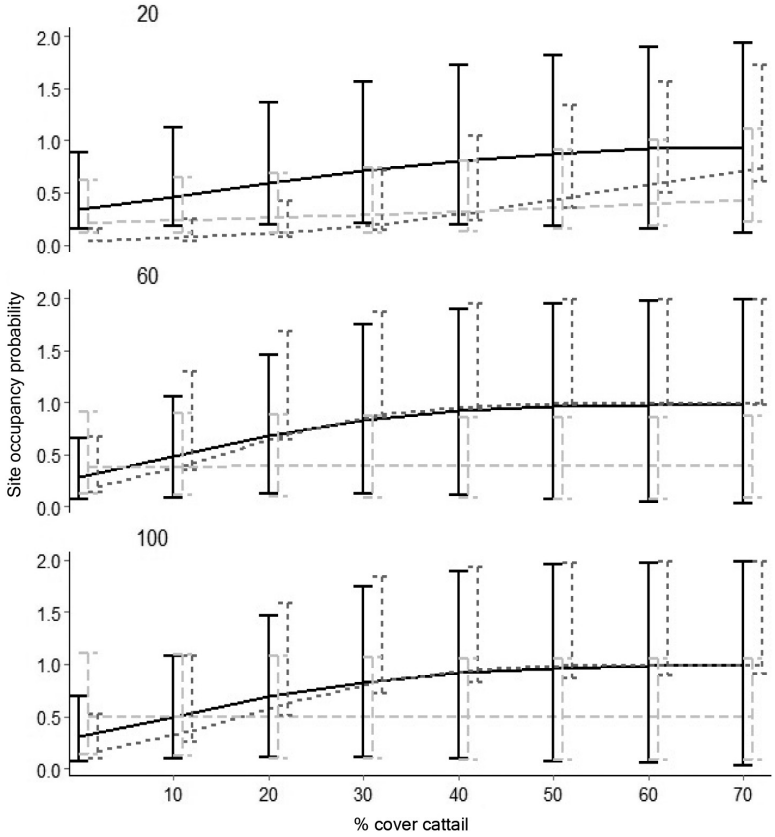

Fig. 1. Site occupancy probability (95% CI) of Marsh Wren (ΨA), site occupancy probability of Yellow-headed Blackbird in the presence of Marsh Wren (ΨBA), and site occupancy probability of Yellow-headed Blackbird in the absence of Marsh Wren (ΨBa) in response to percent cover of cattail at three spatial scales: ≤20 m (20), ≤60 m (60), and ≤100 m (100). Solid line represents ΨA, dashed line represents ΨBA, and dotted line represents ΨBa.

The consequences of interspecific interactions at small, local spatial scales such as those mentioned above can also have population impacts at larger scales (e.g., regional; Martin 1986). Breeding territory size for Marsh Wrens ranged from 225 to 3483 m^2 (Verner 1965), which ranges from 8 to 33 m in diameter. Similarly for Yellow-headed Blackbirds, breeding territory size ranged from 120 to 4000 m^2 (Twedt and Crawford 1995) which ranges from 6 to 35 m in diameter. In our example, we considered the distance bands out to 100 m as the local spatial scale to encompass the breeding territory size of both species and because aggressive interspecific interactions and competition for food resources at this scale can reduce individual fitness (Martin 1986, 1987). This local spatial scale can be applied to other marsh birds (Johnson and Dinsmore 1985, Bogner and Baldassarre 2002) as well as a variety of other passerines (Odum and Kuenzler 1955, Morse 1976, Wiens et al. 1985). Local populations of Yellow-headed Blackbirds are reduced, or perhaps driven to local extirpation, by the presence of Marsh Wrens, particularly if resources shared between these two species are limited. This not only reduces the amount of suitable habitat available to Yellow-headed Blackbirds within the entire patch, but also potentially limits colonization of suitable habitats at the above distances from an active Marsh Wren nest and also reduces other potential colonizing Yellow-headed Blackbird populations. Reduced or limited populations of Yellow-headed Blackbirds at the local level drive population dynamics at the regional level. If Marsh Wrens are driving Yellow-headed Blackbirds out of suitable habitat patches, Yellow-headed Blackbirds are thus forced to settle at other less suitable patches on the landscape. Typically, Yellow-headed

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Blackbirds are found on larger wetlands and occupy the deepwater areas of these wetlands (Weller and Spatcher 1965). However, Brown (1985) found that Yellow-headed Blackbird colonies were not uniformly distributed on the landscape relative to available wetlands, and that Yellow-headed Blackbirds were nesting on wetlands <1 ha in size. This could be the result of Yellow-headed Blackbirds being excluded from suitable habitat at larger wetlands by Marsh Wrens. However, it is likely that Yellow-headed Blackbirds are able to persist in some numbers at the larger wetlands because they arrive and establish territories in Iowa prior to the arrival of Marsh Wrens, and Levin (1974) suggests that relatively high initial densities could insulate a local population from extirpation as a result of interspecific competition.

Site occupancy and coexistence of species are influenced by several different factors that can vary both spatially and temporally (Martin 1986). Few studies have evaluated competitive interactions using the newly-developed co-occurrence model framework, and none to our knowledge have applied this model to evaluate scale-dependent species co-occurrence. Considering spatial scale when evaluating species co-occurrence is important when making inferences about competitive exclusion (Richmond et al. 2010). Here, we present a new approach to evaluating species co-occurrence across multiple spatial scales that uses an established model framework. This approach requires a measure of the distance to individuals of each study species. Depending on the study design, this piece of information is relatively simple to collect in the field. For birds, traditional survey methods involve the use of point counts or line-transect counts, both of which are methods that could easily incorporate measuring distance to individuals. Furthermore, this approach retains the ability of the co-occurrence model to include habitat covariates on parameters of interest which allows the evaluation of scale-dependent habitat associations and elevates our understanding of how co-occurring species partition habitat characteristics within a patch. A potential disadvantage of this approach is that truncating encounters based on established distances may reduce the number of detections and nondetections in encounter histories to the point that the model cannot obtain parameter estimates. Therefore, careful consideration of spatial scales and the number of potential detections therein is important when designing a study with the intent to use this approach. In other words, scales should be large enough to ensure adequate detections and also biologically relevant to the species of interest and the study question. Occupancy models require replicate visits to sites throughout the survey season. Therefore, this issue could be resolved by increasing the number of site visits when possible. The advantages, however, of scale-dependent co-occurrence models have significant implications when considered in the context of multiple species management, aiding decisions on habitat restoration and management for multiple species by providing information needed to increase habitat heterogeneity within a patch to benefit competing and ecologically similar species.

The two-species co-occurrence occupancy model is a valuable tool that allows researchers to evaluate the presence of competitive interactions between species, and incorporating spatial scale into these models provides information on how species partition resources at different spatial scales within a patch. The scale-dependent species co-occurrence approach presented here will have broad application to evaluations of co-occurrence in birds and possibly other taxonomic groups. Understanding species co-occurrence patterns across multiple spatial scales provides valuable information that is useful for: (1) better understanding the mechanisms of competitive interactions between two species; and (2) aiding the restoration and management of habitat for multiple species.

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