

RESEARCH ARTICLE



Wetland occupancy by duck broods in cropland-dominated landscapes of the United States Prairie Pothole Region

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Abstract

The Prairie Pothole Region (PPR) is globally important for breeding waterfowl but has been altered via wetland drainage and grassland conversion to accommodate agricultural land use. Thus, understanding the ecology of waterfowl in these highly modified landscapes is essential for their conservation. Brood occurrence is the cumulative outcome of key life-history events including pair formation and territory establishment, nest success, and early brood survival. We applied new technological advances in brood surveying methods to understand brood use of wetlands and how land use and wetland-specific factors influenced brood use of 413 wetlands in crop-dominated landscapes in the PPR of Iowa, Minnesota, North Dakota, and South Dakota, USA, during summers of 2018–2020. Dynamic occupancy models combining information from 2 visits throughout the year revealed no difference among the 4 states or between private and public lands, resulting in a region-wide annual wetland occupancy estimate of 0.41 (95% credible interval [CrI] = 0.26, 0.58). We assessed aquatic invertebrate forage availability, wetland and upland vegetation communities, and various water chemistry metrics in a subset ($n = 225$) of these wetlands to evaluate how landscape and wetland-specific factors influenced occupancy. The amount of grassland surrounding wetlands was the only

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variable to influence occupancy at a landscape scale, while wetland size, invertebrates, fish, and vegetation communities influenced occupancy at finer scales. Closer scrutiny of wetland area revealed occupancy was greater in small wetlands after controlling for total wetland area. Our results indicate the greatest constraint on brood occupancy across crop-dominated landscapes of the PPR in the United States was the occurrence of semipermanent wetlands suitable for brood rearing. Other factors, such as wetland vegetation or surrounding land use, had minor intervening influences on duck brood use and ducks were distributed invariant of wetland ownership or broad spatial processes occurring among states. These results demonstrated wetland conservation and restoration strategies are likely to yield gains in annual duck broods across this vast, altered, and highly modified landscape.

KEYWORDS

brood, duck, occupancy, Prairie Pothole Region, waterfowl conservation, wetland

Demographic vital rates of breeding ducks can be affected by landscape conditions (Mack and Clark 2006, Simpson et al. 2007, Howerter et al. 2014, Koford et al. 2016), which has widespread implications for altered landscapes, including the Prairie Pothole Region (PPR) of the north-central United States and prairie Canada where most of the North American ducks breed annually (Batt et al. 1989). Extensive wetland drainage and grassland conversion to annual agriculture in this region (Dahl 1990, Doherty et al. 2013, Johnston 2013) have reduced the abundance of prairie wetlands and grasslands that provide habitat for breeding ducks (Crissey 1969, Greenwood et al. 1995, Walker et al. 2013a, Carrlson et al. 2018). Managing for breeding waterfowl habitat in this modified landscape thus requires an understanding of duck habitat-landscape relationships during key life phases (Greenwood et al. 1987, Drever et al. 2007).

Most previous research on breeding waterfowl has consisted of spatially extensive breeding pair surveys (Reynolds et al. 2006) or nest survival studies in restricted geographies (Stephens et al. 2005, Skaggs et al. 2020). These studies measure vital rates from early in the breeding period that are demographically important (Sargeant et al. 1984; Hoekman et al. 2002, 2006; Koons et al. 2006; Coluccy et al. 2008) but may not be accurate predictors of recruitment (Amundson et al. 2013, Kemink et al. 2021). Brood studies allow researchers to understand habitat use and production (Walker et al. 2013a) because brood occurrence is the culmination of multiple complex interactions including settling and territory establishment, nest success, brood survival, and habitat use. Researchers have focused largely on landscape-level factors such as surrounding land use or wetland characteristics influencing brood distributions (Bloom et al. 2011, Walker et al. 2013a, Carrlson et al. 2018) or used radio-marked females or broods to examine fine-scale movements (Krapu et al. 2000, Giudice 2001, Pietz et al. 2003). No research has simultaneously considered wetland and landscape characteristics that may influence brood occupancy across large landscapes, which could have important implications for wetland conservation, management, and restoration.

Brood habitat selection is a complex product of preceding life-history events and site characteristics (Casazza et al. 2020) and thus could be influenced by multiple hierarchical factors (Johnson 1980). Broad spatial trends in occupancy, such as variation among states or regions, could result from the clustered nature of duck distribution

during the breeding season (Crissey 1969, Johnson and Grier 1988, Janke et al. 2017). Factors that influence settling patterns of ducks at landscape scales could also influence nest success, brood survival, and ultimately brood occupancy, such as wetland densities, grassland area, or fragmentation (Stephens et al. 2005, Bloom et al. 2011, Walker et al. 2013b).

Breeding ducks cluster in the PPR (Janke et al. 2017) because of varying upland and wetland conditions (Miller 2000). Landscapes with large contiguous patches of grasslands and high densities of wetlands that can support greater concentrations of breeding pairs have traditionally been the focus of research and conservation in the PPR. But recent research has indicated landscapes capable of supporting high breeding pair densities are not a perfect correlate for brood occurrence, and by implication, recruitment (Kemink et al. 2021). Thus, wetlands outside these high wetland and grassland density areas that exist in a matrix of intensive row crop agricultural may be undervalued for waterfowl conservation (Carrlson et al. 2018).

Landscapes dominated by row crop agriculture may have increased concentrations of nests in fragmented patches of grass where mesopredators (e.g., striped skunk [*Mephitis mephitis*]; Phillips et al. 2003) can take advantage of edge effects (Pasitschniak-Arts et al. 1998) and where density-dependent factors (e.g., functional responses by predators; Ringelman et al. 2018) may become more apparent. Furthermore, grassland to row crop land conversion has led to disproportionate losses of smaller wetlands (Miller et al. 2011, Serran and Creed 2016, Krapu et al. 2018) and homogenized the size and distribution of remaining wetlands (Miller et al. 2011, Le and Kumar 2014, Van Meter and Basu 2015, Serran and Creed 2016). Consequently, these actions have reduced the abundance and quality of breeding and brood-rearing habitat (McCauley et al. 2015, Anteau et al. 2016).

At finer spatial scales, several wetland-specific factors may influence brood occurrence. First, larger wetlands have greater occupancy (Walker et al. 2013a, Carrlson et al. 2018). Food availability and factors that influence it within wetlands are also likely to affect occupancy. Waterfowl rely on invertebrates year-round (Bouffard and Hanson 1997), but stressful and energetically expensive events (e.g., clutch formation and brood growth) require an invertebrate-rich diet. Diets of ducklings are dominated by invertebrates, which facilitate growth (Chura 1961, Sugden 1973, Krapu 1974, Jarvis and Noyes 1986, Afton and Ankney 1991) and influence survival (Sedinger 1992). Ducklings feed primarily on surface, emergent vegetation-dwelling, and highly mobile invertebrates (Chura 1961, Hill et al. 1987, Gardarsson and Einarsson 1997, King and Wrubleski 1998, Nummi et al. 2000). Submersed aquatic vegetation is an important portion of duckling diets and proportions of plant material in their diets increase as they age (Chura 1961, Sugden 1973). Submersed aquatic vegetation and emergent macrophytes can also indirectly influence food availability by providing forage, cover, and attachment points for important invertebrates (Voigts 1976, Murkin et al. 1992, de Szalay and Resh 2000). Emergent vegetation may also influence brood survival by provisioning cover to escape weather or predators (Stafford and Pearse 2007) and influence brood occupancy (Walker et al. 2013a, Carrlson et al. 2018). Finally, biotic and abiotic factors within wetlands, especially fish communities (Hanson and Riggs 1995, Anteau et al. 2011) can influence plant and invertebrate communities and ultimately brood distribution or survival (Giles 1994, Zimmer et al. 2001).

Our research had 2 primary objectives: to describe occupancy dynamics in small wetlands (≤ 10 ha) in crop-dominated landscapes through space (states and land ownership within the U.S. PPR) and time (throughout the breeding season) and to understand local and landscape-level factors influencing brood occurrence on these wetlands. We hypothesized duck brood occupancy of wetlands would be lower in our study than documented in studies considering more intact grassland-wetland landscapes (Walker et al. 2013a) because of the myriad challenges of nesting and raising young in crop-dominated landscapes. Further, we hypothesized occupancy by broods at the landscape scale would be positively influenced by wetland abundance or density (Johnson and Grier 1988, Bloom 2010, Zimpfer et al. 2012) and amount of grassland surrounding wetlands (Greenwood et al. 1995, Reynolds et al. 2006). We predicted occupancy at the wetland scale would be positively associated with characteristics of individual wetlands that promote survival including the absence of fish (Hanson and Riggs 1995, Bouffard and Hanson 1997), abundance of invertebrate forage (Chura 1961, Sugden 1973, Cox et al. 1998),

submersed and emergent macrophyte abundance (Walker et al. 2013a, Carrlson et al. 2018), and wetland depth and size (Walker et al. 2013a, Carrlson et al. 2018).

STUDY AREA

We conducted our research in intensively cropped portions of the PPR of Iowa, Minnesota, North Dakota, and South Dakota, USA, during summers of 2018–2020 (Figure 1). This region was characterized by poorly drained glacial till soils with gently rolling topography and millions of small, depressional pothole wetlands that are remnants from the receding Wisconsin Pleistocene glacier 12,000–14,000 years ago. These potholes historically covered upwards of 20% of the PPR by land area with wetland densities exceeding 40 basins/km² in some areas (Kantrud et al. 1989, Johnson and Higgins 1997); however, the PPR has lost large percentages of wetlands because of drainage and subsequent land conversion for agriculture and urban development. Dahl (1990) estimated 35%, 50%, and 90% of wetlands were lost in South Dakota, North Dakota, and Iowa, respectively, before the 1980s. In Minnesota, upwards of 85% of wetlands have been drained (Johnson et al. 2008, Oslund et al. 2010). The portion of the PPR in the United States is an estimated 32.9 million ha, yet only 1.6 million ha (4.9%) consists of emergent herbaceous wetlands. A majority of the remaining land area comprised cropland with an estimated 21.3 million ha (64.7%; Homer et al. 2020). Wetland vegetation in this region was a mix of submersed and emergent macrophytes including coontail (*Ceratophyllum demersum*), pondweeds (*Potamogeton* and *Stuckenia* spp.), bladderwort (*Utricularia macrorhiza*), cattail (*Typha* spp.), bulrushes (*Schoenoplectus* and *Scirpus* spp.), and smartweed (*Polygonum* spp.).

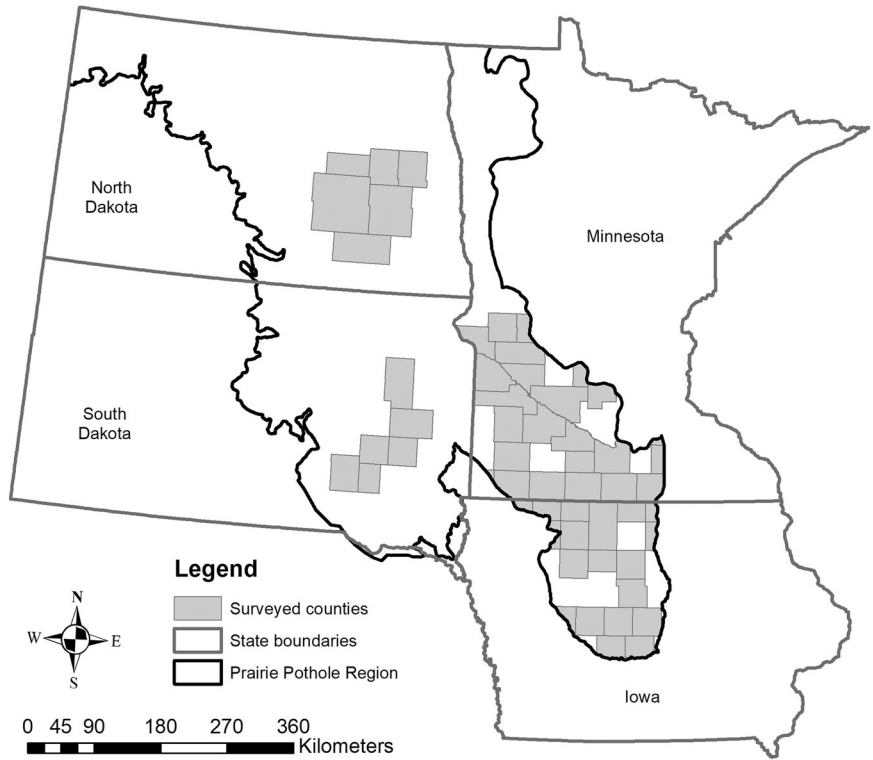


FIGURE 1 Location of our study area where we assessed duck brood occupancy of small (≤ 10 ha) wetlands in crop-dominated landscapes within the United States Prairie Pothole Region (black outline) during summers 2018–2020. Gray shaded polygons represent counties in which we surveyed ≥ 1 wetland.

The predominant aquatic mammals included American beaver (*Castor canadensis*), muskrat (*Ondatra zibethicus*), and American mink (*Mustela vison*). Breeding ducks in our study area primarily consisted of upland-nesting dabbling ducks. Elevation across the study area ranges from 360 m to 550 m. Continental climate in the region has 4 seasons and a north-south temperature and east-west precipitation gradient. Warmer, wetter conditions prevail in Iowa and Minnesota and cooler, drier conditions prevail in more northern latitudes (Johnson et al. 2005). Periods of drought and flood are typical in this region in irregular decadal patterns (Millett et al. 2009), resulting in further hydrological variability. Mean summer (May–Aug) temperature was approximately 19°C across our study area (National Oceanic and Atmospheric Administration 2021). This area had an average annual temperature of about 9°C and average annual rainfall of about 76 cm (National Oceanic and Atmospheric Administration 2021).

METHODS

Sample selection

We focused our research in crop-dominated landscapes in the PPR of Iowa, Minnesota, North Dakota, and South Dakota (Figure 1). We used ArcMap 10.6.1 (Esri, Redlands, CA, USA) to define crop-dominated landscapes by centering candidate sites over 9.7-km × 9.7-km moving windows (94 km²) where ≥60% of the uplands contained crops during ≥3 of the previous 4 years between 2014–2017 based on the National Land Cover Database (Homer et al. 2020) and annual cropping patterns from the Cropland Data Layer (U.S. Department of Agriculture 2018, Mitchell 2021).

We sought to ensure a wide range of landscape-level wetland conditions in our sample of candidate sites, so we used the National Wetlands Inventory (NWI; Wilen and Bates 1995) to stratify cropland-dominated landscapes into areas with high, low, and functionally no suitable amounts of brood-rearing habitat. We defined suitable brood-rearing habitat from NWI as wetlands with a semi-permanent hydrology with the presence of persistent emergent vegetation and stratified candidate sites into low and high wetland densities (Mitchell 2021). We used the focal statistics tool in ArcMap to sum the number of cells representing suitable brood-rearing habitat within a 3.2-km × 3.2-km moving window (a scale routinely used in wetland research this landscape; Reynolds et al. 2006) of each land-use pixel and then multiplied this wetland raster by the cropland raster to yield candidate site centers. We reclassified this layer to stratify candidate sites into areas with low wetland density (≥5 ha but ≤40 ha), high wetland density (>40 ha but ≤518 ha), or no data (<5 ha or >518 ha). The 5-ha minimum ensured adequate potential wetlands to sample and the 518-ha upper limit excluded areas where wetlands comprised >50% of the study area, which were generally lakes or larger wetlands outside the objectives of this study.

We used the create spatially balanced points tool in ArcMap to place 50 points across low and high wetland strata in each state to serve as sites on which to select wetland locations. Sites were within 220 km of housing locations in each year (Humboldt, IA and Madelia, MN in 2018; Humboldt, IA, Madelia, MN, Jamestown, ND, Huron, SD in 2019; Ames, IA and Glenfield, ND in 2020). Twenty-seven potential sites occurred in low wetland density strata and 23 potential sites occurred in high wetland density strata in each state. We randomly ordered all sites within each stratum and proceeded to map wetlands and seek landowner permission for access; we replaced sites that could not be sampled with the next site on the randomized list.

We used ArcMap to manually digitize candidate wetlands >0.01 ha and ≤10 ha because those are most at risk of degradation and drainage according to the Prairie Pothole Joint Venture (Brice et al. 2016) and the focus of conservation and restoration practices on private lands in our study area. We started mapping wetlands on the 4 Public Land Survey Sections (1 section = 259 ha) nearest to the randomized point and expanded sites adding sections in each direction in concentric rings up to 36 sections in pursuit of 3–15 candidate wetlands. We used a combination of NWI and historical and current aerial imagery to map candidate semi-permanent wetlands. We randomly ordered wetlands in the sites and sought permission from landowners to survey up to 10 wetlands on each site.

Brood surveys

We conducted 2 temporally separated periods of repeat-visit brood surveys (4 visits/wetland) similar to Carrlson et al. (2018). During each period, 1 visit occurred between sunrise and 1000 hours (morning) and another occurred between 1600 hours and sunset (evening) in a 24-hour period. There were a few instances where we surveyed a wetland once in the morning (or evening) and not again until the following morning (or evening). We avoided surveying during midday (i.e., between 1000 and 1600 hours) because broods seek thermal refuge in emergent vegetation during this time (Diem and Lu 1960, Ringelman and Flake 1980). We used 2 survey windows within the year to capture different nesting chronologies among species and more accurately characterize the occupancy state of wetlands throughout the breeding season. The first period was timed to target early-nesting species (e.g., mallards [*Anas platyrhynchos*]) and spanned from late May to mid-July, while the second period was timed to target re-nesting and later-nesting species (e.g., blue-winged teal [*Spatula discors*]; Klett et al. 1986) and spanned from early July to mid-August. We excluded wetlands that lacked surface water during the first survey period because the probability of a dry wetland becoming inundated later in summer (e.g., during round 2) was low. We selected a new sample of study sites and wetlands each year of this study.

We used quadcopter drones (DJI Matrice 200 or 210; DJI, Shenzhen, China) equipped with thermal imaging cameras (Zenmuse XT2 or Zenmuse XT, 19-mm lens, 640 × 512-pixel resolution) and visual cameras (Zenmuse XT2, 8-mm lens, 4,000 × 3,000-pixel resolution or Zenmuse X4S, 9-mm lens, 5,472 × 3,684-pixel resolution) to search wetlands for broods. We used the white hot thermal setting such that reflective objects or objects omitting heat appeared white and all other objects appeared gray to black. This color palette provided the best contrast between broods and non-target subjects (e.g., red-winged blackbirds [*Agelaius phoeniceus*]). We satisfied all Federal Aviation Administration (FAA) regulations by gaining prior authorization for flights in controlled airspace and recording weather and flight conditions in a flight log. We conducted all flights by or under the direct supervision of a licensed remote pilot in command under FAA Part 107 regulations.

We launched the drone a minimum of 100 m from the wetland edge as suggested by Vas et al. (2015) to minimize physical and audial disturbances. Upon take-off, the drone ascended to 43 m before making movements towards the wetland. This height provided adequate detection capabilities with the thermal camera, while simultaneously maximizing our field of view to reduce survey time and provide sufficient resolution to discern non-target species (e.g., American coot [*Fulica americana*]). We started each brood survey in an arbitrary edge of the wetland, usually along a relatively straight edge if available, and manually flew transects with about 25% overlap until we searched the entire wetland. The overlap served as a safety net to observe any broods that attempted to avoid detection. Flight speeds were between 5–10 m/second depending on how much emergent vegetation was present in each wetland. This speed allowed us to survey each wetland quickly (mean = 4.7 ± 4.7 [SD] min, median = 3.0 min), thus minimizing disturbance while ensuring detection.

We recorded all duck broods seen on each survey. Upon detecting a brood with the thermal camera (Figure 2), we switched to visual display (Figure 2) and slowly descended the drone (i.e., ~5 m/sec) to no lower than 10 m to record species, age class (Gollop and Marshall 1954), and number of ducklings in the brood. If we encountered ducklings with no adult female, we classified the brood as an unknown dabbling duck or unknown diving duck based on their reaction to the drone. Dabbling ducks tended to seek emergent vegetative cover, whereas diving ducks moved towards open, deeper water. We excluded hooded merganser (*Lophodytes cucullatus*) broods from all analyses because of their unique ecology and habitat requirements that ordinarily preclude them from habitat conservation strategies in the region (Brice et al. 2016). We captured photos of each brood for post-flight identification confirmation. Using ocular estimates via drone camera, we estimated percentage of emergent vegetation ($\pm 10\%$) and cover type (Stewart and Kantrud 1971) once during the first survey period, and estimated percent wet ($\pm 10\%$) once during each survey period.



FIGURE 2 Blue-winged teal brood captured with thermal camera (left; DJI Zenmuse XT2) and visual camera (right; DJI Zenmuse XT2) via quadcopter drone (DJI Matrice 200) as part of a duck brood occupancy study on small (≤ 10 ha) wetlands in crop-dominated landscapes within the United States Prairie Pothole Region during summers 2018–2020. Image captured on 23 June 2019 in Palo Alto County, Iowa, USA.

Wetland sampling

During 2019 and 2020, we conducted additional wetland sampling to measure local wetland characteristics. We divided each wetland into 4 quadrants using cardinal directions to establish 4 transects to sample wetland biotic and abiotic characteristics. We randomized which cardinal direction transect received a specific distance (0, 30, 60, 90), with each distance representing a percentage towards the center of the wetland along each transect (e.g., 90 was 90% towards wetland centroid). Estimates and variances for sampled metrics (e.g., invertebrate abundance) did not differ significantly between 3 randomly selected sampling locations and all 4 sampling locations within a wetland. As a result, we used 3 sampling locations in 2020 at 0, 45%, and 90% distances along 3 randomly selected cardinal directions. At each sampling location, we sampled aquatic invertebrates, fish, submersed aquatic vegetation (SAV), and depth. We sampled wetlands within 48 hours after the second brood survey to avoid biasing occupancy estimates, while allowing us to characterize wetland conditions near the time of surveys.

We sought to characterize invertebrate availability for surface and near-surface foraging ducklings using surface activity traps (SATs), which have been used to characterize nektonic invertebrate assemblages in other prairie wetland studies and offer many logistical advantages in the field and laboratory (Murkin et al. 1983, Hanson et al. 2000). We modified our SATs (25.4 cm \times 25.4 cm \times 16.5 cm; 6.4-mm plexiglass) from the design in Hanson et al. (2000) by adding a full-length fish guard (6.4-mm galvanized wire) to reduce the risk of predation by fish and large predatory invertebrates (Elmberg et al. 1992). We bracketed each SAT to a t-post and partially submerged it such that 4 cm of the trap was out of the water. We deployed SATs for 24 (± 2) hours to capture diel migrations of invertebrates. We transferred SAT contents into a 500-micron wash bucket, enumerated and released fish, tadpoles, or non-target invertebrates, and transferred remaining contents into a Whirl-Pak bag (Nasco, Fort

Atkinson, WI, USA; 11.5 cm × 23 cm or 19 cm × 30 cm) before preserving with a 70% ethanol solution dyed with Rose Bengal.

We placed a dual entrance Gee-style fish trap (0.64-cm mesh) at the 2 deepest sampling locations within each wetland for the same 24-hour period SATs were deployed. In pilot research, we found that when fish were detected in the wetland, ≥1 of the 2 fish traps in the deepest sampling locations captured ≥1 fish 91% of the time ($n = 20$ out of 22). Thus, our approach to sampling fish only at the 2 deepest sampling locations and quantifying captures of small-bodied fish (e.g., fathead minnow [*Pimephales promelas*]) in our SATs sufficiently characterized fish presence in our wetlands. We enumerated fish by species and immediately released them.

We used a rake method to sample SAV (Kenow et al. 2007). We dragged a 15-tine metal rake along the substrate and enumerated the number of tines covered for 3 attempts at each sampling point within a wetland to derive an index of SAV abundance. We measured depth (cm) at all sampling locations and recorded the deepest point we encountered in each wetland up until the water became too deep to wade (max. 120 cm).

Invertebrate processing

We emptied each invertebrate sample into a 500-micron sieve, rinsed it, and removed large plant materials. We then transferred the sample, along with some tap water, into a 100-mm × 15-mm square petri dish to facilitate systematic searches under a dissecting microscope at 10 times magnification. We enumerated all large or rare invertebrates and used a fixed-area count (25%) to estimate abundance of more numerous taxa like zooplankton (e.g., *Daphnia* spp., Order Cladocera; modified from King and Richardson 2002). We identified invertebrates to taxonomic levels typical in the waterfowl research literature to facilitate estimation of sample biomass (mg) and enumeration of key forage taxa (Table S1, available in Supporting Information; Mitchell 2021). We preserved all invertebrates from each sample in a 100% ethanol solution dyed with Rose Bengal in a 20-mL plastic scintillation vial.

James et al. (2012) reported dry masses of invertebrates were correlated with energy density, which we used as a composite index of overall forage availability (i.e., biomass). We therefore converted counts to biomass by multiplying the average count among traps for all taxonomic groupings by their respective dry masses (Table S1; Mitchell 2021) and summed these values to calculate total average biomass (mg) per wetland. We calculated all invertebrate metrics as an average of values derived from all SATs in each wetland.

Geospatial analysis

We sought to characterize metrics for grassland and wetland availability surrounding surveyed wetlands to evaluate relationships between landscape composition and wetland occupancy by broods. Grasslands have been considered important determinants of duck nesting success in many studies (Greenwood et al. 1995, Reynolds et al. 2006, Pearse et al. 2022). Bloom (2010) demonstrated female mallards selected areas with greater wetland densities to raise a brood, presumably because of reduced duckling survival with increased overland travel in areas with few wetlands (Rotella and Ratti 1992b, Ball et al. 1995), increased competition from conspecifics in low wetland density areas (Krapu et al. 1997), or fewer available inundated wetlands as dry summer conditions progress.

We created a 2-km buffer around the perimeter of each wetland based on the average maximum linear distance traveled by mallard broods in eastern North Dakota (Krapu et al. 2006). Within each wetland buffer, we calculated the proportion in grassland using the Cropland Data Layer (U.S. Department of Agriculture 2018). We summed the area of cells (30 × 30-m resolution) containing grass (hay, clover, wildflowers, switchgrass, grassland, and pasture) and divided it by the area of the buffer excluding the area of the focal wetland. We modified NWI by reclassifying all wetland types that corresponded with our original inclusion criteria plus lakes (1) and excluding all

others (0). We included all permanent and semi-permanent Lacustrine (i.e., Littoral and Limnetic) unconsolidated bottom and aquatic bed wetlands and those therein that were diked or impounded (h modifier). We also included all permanent and semi-permanent Palustrine unconsolidated bottom, aquatic bed, and persistent emergent wetlands and including those with modifiers indicating they were partly drained or ditched (d modifier) or diked and impounded (h modifier). We excluded all temporary, seasonal, and artificial wetlands and those considered as excavated wetlands (i.e., dugouts; x modifier). We summed the area of these reclassified cells (30 × 30 m resolution) and divided it by the area of the buffer excluding the area of the focal wetland to calculate wetland density surrounding each surveyed wetland. We validated this approach by digitizing all permanent and semi-permanent wetlands within our 2-km wetland buffers in Iowa and Minnesota and discovered high correspondence (adjusted $R^2 = 0.85$) with our reclassified NWI layer.

Data analysis

We used occupancy modeling to understand duck brood occupancy dynamics across a range of ecological conditions and across the large geographic scale of our study. Static (i.e., single-season) and dynamic (i.e., multi-season) models are the 2 prevailing approaches to occupancy modeling (Kéry and Schaub 2011), and we used both to answer separate questions about our system. We used dynamic occupancy models to draw inference about wetland occupancy throughout the entirety of a single brood-rearing season with data from 3 summers: 2018–2020. We used static occupancy models to examine patterns of occupancy relative to landscape and wetland covariates measured during individual survey rounds during the latter 2 years of the study: 2019 and 2020. In both static and dynamic approaches, the occupancy model is a hierarchical model containing 2 separate, albeit related, processes: a submodel for the observational data (detection model) conditional on the latent variable (true occupancy) and a submodel for the partially observed state process (occupancy model; Royle and Kéry 2007). The input structure of the models is a vector of 1 s and 0 s indicating visit-specific detections (1 s) or absences (0 s) by round.

Data collection for occupancy studies involves repeated visits and periods of closure with 4 key assumptions (MacKenzie et al. 2006). First, we ensured occupancy state was closed during a sampling period by conducting repeat visits within 24 hours. Second, we ensured detections at 1 wetland or visit were independent from detections at another wetland or visit by surveying each wetland in the same systematic manner (e.g., similar speed, same amount of overlap) while attempting to impose as little survey bias as possible (e.g., slower flight speeds on the second visit if a brood was detected on the first visit). Third, we ensured detection and occupancy probabilities were adequately described by model covariates by measuring covariates deemed influential by *a priori* hypotheses and previous brood studies in the region. Finally, we ensured there were no false positives or misidentifications of broods with protocols that called for capturing numerous photos of each potential brood to compare with our field observations and verify identification.

Annual occupancy dynamics

We used dynamic occupancy models to explain the overall occurrence of duck broods on wetlands over the course of the entire brood-rearing period rather than during 1 period typical of past work in these systems (Walker et al. 2013a). This metric, which we derived from a dynamic occupancy model and called annual occupancy, revealed the contribution of individual wetlands in crop-dominated landscapes to duck production annually. Dynamic models estimate colonization and persistence probabilities after an initial visit, which removes the closure assumption between primary sampling periods. We used this approach to quantify occupancy patterns throughout the entire brood-rearing season treating our 2 rounds of surveys as primary sampling periods. We fit a model to evaluate

whether systematic differences existed in brood use of wetlands across geopolitical boundaries in the region (4 states) or across different ownership regimes (private lands vs. public lands). We fit this state and ownership model to provide decision makers with information to consider in conservation schemes across geopolitical borders where wetland conservation occurs on a mix of private and public lands.

We empirically estimated 3 parameters with the model: initial occupancy, persistence, and colonization probabilities. Initial occupancy was the probability of occupancy in the first period. Persistence was the probability an occupied wetland in the first period remained occupied in the second period (e.g., the same brood was present during the second survey period or a new brood moved to the wetland to replace the brood observed in the first survey period). Colonization was the probability an unoccupied wetland in the first period became occupied during the second period (e.g., a brood moved to a wetland that was unoccupied in the first survey period). We derived a fourth parameter from model estimates called annual occupancy probability. Annual occupancy probability was the probability a wetland was occupied by ≥ 1 brood throughout the entire survey window and was thus equal to:

$$\Psi_{i,\text{annual}} = \Psi_{i,1} + (1 - \Psi_{i,1})\gamma_{i,2},$$

where $\Psi_{i,1}$ was the probability a wetland i was occupied in period 1 (initial occupancy), and $\gamma_{i,2}$ was the probability of colonization for wetland i in period 2 (colonization probability). This derived value reveals the probability that a wetland was ever used by a duck brood throughout the brood-rearing season and is arguably a more informative measure of wetland use than occupancy derived from a single survey round within the season.

A few ($n = 29$) wetlands that were inundated during period 1 were not in period 2, which created a challenge for the hierarchical dynamic occupancy model because occupancy in these wetlands was 0, but the observation process giving rise to that 0 was different from that giving rise to unoccupied inundated (and thus usable) wetlands. Thus, we incorporated a binary indicator variable for wetness (1 if wet, 0 if dry) to fix colonization, persistence, and detection probabilities at 0 in instances when the wetland was dry during the second period. This solution allowed us to draw inferences to annual occupancy dynamics among all wetlands that were wet at the onset of the brood rearing period (i.e., period 1) without obscuring estimation of detection probabilities on wet wetlands.

We used Bayesian hierarchical occupancy models in Program R (R Core Team 2020) and the jagsUI package (Kellner 2019). We included a term for the timing of the survey (morning = 1, evening = 0) in the detection models because previous analyses with these data revealed that to be the only consequential predictor of detection (Mitchell 2021). We fit the model with an effect parameterization approach, where the intercepts represented the whole-group mean and state and ownership terms indicated the additive effect of those groups' means. This approach allowed for direct comparison of each level (state or ownership) on mean estimates of annual occupancy and other parameters. We used a uniform $-5, 5$ prior on intercepts and normally distributed priors with mean = 0 and standard deviation = 5 for all coefficients. We ran 3 Markov chains with 200,000 iterations in each chain. We used our array indicating wetness for initial values because it was impossible for a dry wetland to be occupied. We removed the first 100,000 iterations in each chain to reduce the influence of initial values on parameter estimates and evaluated convergence by inspecting trace plots for each chain and by confirming the Gelman-Rubin statistic was < 1.1 (Gelman et al. 2004). We empirically compared mean estimates for each group with the overall mean to interpret variation among states and ownership types.

Static occupancy models

We used static occupancy models to explore relationships between brood occupancy and covariates describing conditions in and around wetlands. We parsed covariates and data into 2 categories and fit 2 models: 1 for landscape-scale covariates and 1 for local or wetland-specific covariates (Table 1). We hypothesized variation in occupancy at these scales was attributable to covariates describing differences in habitat characteristics that influenced settling patterns of breeding ducks, reproductive success of breeding females, and foraging conditions on wetlands for broods, all based on a synthesis of the literature (Table 1).

TABLE 1 Covariates included in occupancy models used to assess relationships between wetland or landscape features and duck brood occupancy of small (≤ 10 ha) wetlands in crop-dominated landscapes within the United States Prairie Pothole Region during summers 2019 and 2020.

Covariate	Description	Models	n	Mean	Median	SD	Min.	Max.
Date	Day of the year since 1 Jan of the survey	Landscape	671	190	192	20.53	151	226
Wetland area (ha)	Area of the wetland based on aerial imagery	Landscape and local	349	1.49	0.99	1.44	0.09	7.64
Wetland prop	Percent of a 2-km-radius buffer around wetland in semipermanent wetland	Landscape	349	2.07	0.96	3.01	0.00	20.21
Grass prop	Percent of a 2-km-radius buffer around wetland in grassland	Landscape	349	14.10	12.10	11.75	0.00	53.79
Percent emergent	Percent of the wetland surface area covered with emergent vegetation	Local	225	55.47	60.00	22.34	10.00	90.00
Deepest point (cm)	Deepest point in the wetland (truncated at 120 cm)	Local	225	80.64	81.00	28.11	21.00	120.00
SAV (count)	Count of rake tines obstructed with submersed aquatic vegetation (SAV) out of 45 possible	Local	225	17.74	15.33	15.43	0.00	45.00
Zooplankton	Average count of zooplankton captured in traps	Local	225	614.26	246.67	1,033.31	10.50	6,970.25
Dipteran	Average count of dipterans captured in traps	Local	225	32.05	16.75	49.42	0.00	539.25
ETO	Average count of ephemeropterans, tricopterans, and odonates captured in traps	Local	225	3.98	2.00	6.33	0.00	52.00
Coleopteran	Average count of coleopterans captured in traps	Local	225	3.66	2.67	3.55	0.00	19.50
Hemipteran	Average count of hemipterans captured in traps	Local	225	23.71	10.75	33.56	0.00	233.25
Biomass (mg)	Average total biomass of invertebrates captured in traps	Local	225	451.47	274.36	609.28	21.90	6,399.29
Fish	Binomial covariate indicating presence (1) or absence (0) of fathead minnows or black bullheads	Local						

Our landscape model aimed to assess the influence of external, upland characteristics (e.g., grassland availability, wetland density) on occupancy and included all inundated wetlands we surveyed. We included a quadratic covariate for ordinal date in the landscape model to account for an influence of nesting chronologies. Our local model aimed to assess the influence of internal, wetland-specific covariates (e.g., forage availability, water depth) on occupancy. We used a square root transformation for all invertebrate abundance metrics and biomass to minimize the influence of extreme values commonly found in forage studies (Straub et al. 2012). We calculated SAV amount as an average of each 3-trial sum across all sampling locations in each wetland. We incorporated quadratic terms for maximum depth and wetland macrophyte coverage because we predicted non-linear relationships with occupancy for each term. We incorporated a binary covariate depicting presence (or absence) of fathead minnows or black bullhead (*Ameiurus melas*) based upon ≥ 1 capture in ≥ 1 SAT or fish trap. We focused on these species because they have been demonstrated to adversely affect prairie wetland ecosystems at high densities (Hanson and Riggs 1995, Zimmer et al. 2001).

We included a covariate for wetland area (log-transformed) in each model because researchers have reported wetland area to be an important predictor of wetland occupancy and we wanted to control for variable wetland sizes in the analysis (Walker et al. 2013a, Carrlson et al. 2018). Wetland area was the estimate of the typical wetland extent based on apparent vegetation, topography, and water derived from a geographic information system. We z-standardized all numerical covariates to be centered on the mean with a standard deviation of 1. For correlated variables ($|r| \geq 0.6$), we included the covariate that made the most biological sense in accordance with our hypotheses. We used a uniform $-5, 5$ prior on intercepts and normally distributed priors with mean = 0 and standard deviation = 5 for all coefficients. We created a vector with the observed occupancy state at each wetland and used this for the initial values. We ran 3 Markov chains with 200,000 iterations in each chain and removed the first 100,000 iterations in each chain to reduce the influence of initial values on parameter estimates. We evaluated model convergence by inspecting trace plots for each chain and by confirming the Gelman-Rubin statistic was < 1.1 (Gelman et al. 2004). We inspected posterior predictions for model coefficients and plotted mean predicted occupancy with 95% credible intervals (CrI) among important terms with all other covariates held at their mean. All JAGS, R code, and data used in these analyses are available for download at the link referenced in the data availability statement of this manuscript.

RESULTS

Wetland and brood observations

We conducted brood surveys on 413 wetlands across Iowa ($n = 120$), Minnesota ($n = 111$), South Dakota ($n = 38$), and North Dakota ($n = 144$) on 57 study sites from 2018 through 2020. Most of these wetlands were on private property ($n = 52$ in 2018, $n = 115$ in 2019, $n = 113$ in 2020; Table 2). The remaining wetlands occurred on public property ($n = 12$ in 2018, $n = 85$ in 2019, $n = 36$ in 2020) and were managed by the Iowa or Minnesota Department of Natural Resources, County Conservation Boards, or the United States Fish and Wildlife Service. Brood surveys commenced from late May to early July (2 Jul 2018, 4 Jun 2019, 30 May 2020) and ended in late July to mid-August

TABLE 2 Count of publicly and privately owned small (≤ 10 ha) wetlands surveyed for duck broods in crop-dominated landscapes across 4 states in the United States Prairie Pothole Region during summers 2018–2020.

Ownership	Iowa	Minnesota	North Dakota	South Dakota
Public	84	45	3	1
Private	36	66	141	37

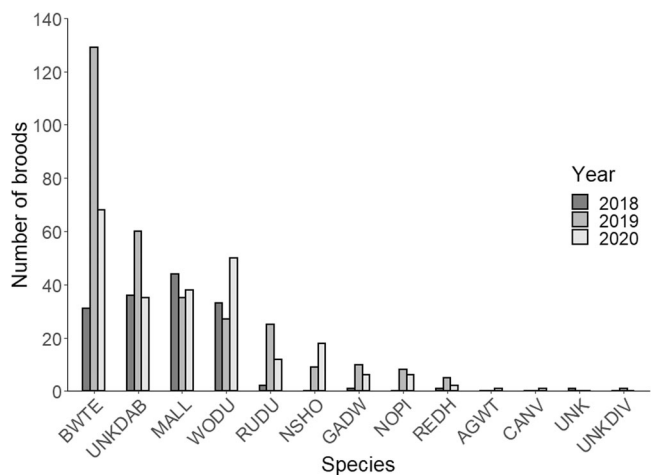


FIGURE 3 Species count from a duck brood occupancy study on small (≤ 10 ha) wetlands in crop-dominated landscapes within the United States Prairie Pothole Region during summers 2018–2020. The species codes are as follows: BWTE = blue-winged teal, UNKDAB = unknown dabbling duck, MALL = mallard, WODU = wood duck, RUDU = ruddy duck (*Oxyura jamaicensis*), NSHO = northern shoveler (*Spatula clypeata*), GADW = gadwall (*Mareca strepera*), NOPI = northern pintail (*Anas acuta*), REDH = redhead (*Aythya americana*), AGWT = American green-winged teal (*Anas carolinensis*), CANV = canvasback (*Aythya valisineria*), UNK = unknown duck species, UNKDIV = unknown diving duck.

(15 Aug 2018, 14 Aug 2019, 31 Jul 2020). The mean time between visits to a wetland within a round was 12.5 hours (range = 7.6–35 hours, median = 12.3 ± 3.3 [SD] hours). The average time between round 1 and round 2 surveys was 32 days (range = 24–46 days, median = 30 ± 5.4 days). We recorded 695 broods ($n = 148$ in 2018, $n = 309$ in 2019, and $n = 237$ in 2020; Figure 3). We observed 10 species including 7 dabbling duck and 3 diving duck species (Figure 3). Blue-winged teal ($n = 228$) were the most abundant brood, followed by mallard ($n = 117$), and wood duck (*Aix sponsa*; $n = 110$; Figure 3). We never observed a brood on 250 (60%) wetlands. Among the 163 wetlands with broods, the highest count obtained in the 4 surveys ranged from 1 ($n = 82$) to 9 ($n = 1$) with a mean maximum count of 2.1 ± 1.5 broods. We conducted wetland sampling on 225 of the wetlands.

Annual occupancy dynamics

We included 413 unique wetlands in our dynamic occupancy model (Table 2). The detection submodel estimated higher detection in morning surveys (0.77, 95% CrI = 0.70, 0.83) than evening surveys (0.64, 95% CrI = 0.57, 0.71). The mean difference in detection between morning and evening surveys was 0.12 (95% CrI = 0.05, 0.20). Mean initial occupancy was 0.30 (95% CrI = 0.15, 0.49), mean persistence was 0.67 (95% CrI = 0.45, 0.84), mean colonization was 0.15 (95% CrI = 0.06, 0.29), and mean derived annual occupancy was 0.41 (95% CrI = 0.26, 0.58; Figure 4).

Main effect terms for state and ownership did not predict significant variation from means among all 4 parameters we estimated or derived (Table 3). To explicitly compare group differences, we compared the difference between the estimated mean annual occupancy parameter and each group estimate. The difference between the overall mean annual occupancy and the state mean in the posteriors was -0.05 (95% CrI = -0.16 , 0.06) in North Dakota, -0.00 (-0.13 , 0.13) in South Dakota, 0.01 (95% CrI = -0.11 , 0.13) in Iowa, and 0.04 (95% CrI = -0.07 , 0.16) in Minnesota. Similarly, ownership means were not different from the overall mean, with a mean difference of -0.02 (95% CrI = -0.15 , 0.11) for public ownership and 0.01 (95% CrI = -0.13 , 0.14) for private ownership.

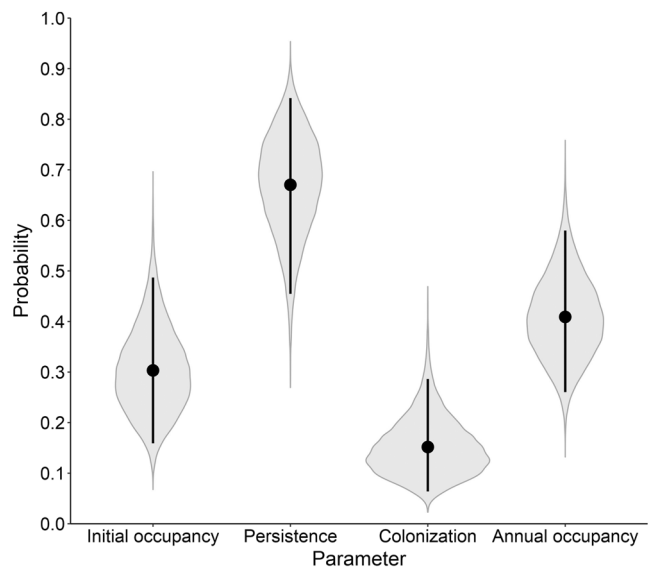


FIGURE 4 Mean duck brood dynamic occupancy model parameter posterior estimates among small (≤ 10 ha) wetlands in crop-dominated landscapes within the United States Prairie Pothole Region during summers 2018–2020. Initial occupancy was the probability of occupancy in the first period. Persistence was the probability an occupied wetland in the first period remained occupied in the second period. Colonization was the probability an unoccupied wetland in the first period became occupied prior to the second period. Annual occupancy was the sum of initial occupancy probability and the probability the wetland was unoccupied in the first period but became colonized before the second period. The points and error bars correspond with the means and 95% credible intervals of the posteriors, respectively.

Factors affecting occupancy

We included 349 wetlands surveyed 671 times in our landscape-scale occupancy analysis. Log-transformed wetland area was the strongest variable in the model (Figures 5 and 6). A 1-ha wetland had a probability of occupancy of 0.31 (95% CrI = 0.25, 0.36), whereas a 7-ha wetland had a probability of being occupied of 0.72 (95% CrI = 0.62, 0.81). The mean difference between 1-ha and 7-ha wetlands was 0.41 (95% CrI = 0.33, 0.5). Occupancy probability increased from 0.25 (95% CrI = 0.18, 0.32) to 0.32 (95% CrI = 0.26, 0.39) for a mean difference of 0.07 (95% CrI = 0.00, 0.13) when the proportion of the 2-km buffer in grassland increased from 0 to 20% (Figures 5 and 6). Occupancy probability peaked around mid-July (11 Jul; 0.30, 95% CrI = 0.24, 0.36; Figures 5 and 6).

We included 225 wetlands surveyed 439 times in the local-scale model. Log-transformed wetland area was the strongest variable in the model but was included only as a control term to inspect the influence of other variables on wetland occupancy. Wetlands with fish had higher occupancy (0.51, 95% CrI = 0.37, 0.65) than wetlands without fish (0.40, 95% CrI = 0.31, 0.49). The mean difference in occupancy between wetlands with fish and without was 0.11 (95% CrI = -0.02, 0.23). Most (95%) posterior draws estimated higher occupancy in wetlands with fish than those without. Remaining terms measured on a continuous scale had variable influences on wetland occupancy at the local scale (Figures 6 and 7). Occupancy was greatest around 40% percent emergent vegetation on the wetland and decreased thereafter. Occupancy probability at 10% emergent vegetation was 0.34 (95% CrI = 0.18, 0.55) and an average of -0.09 (95% CrI = -0.25, 0.09) off from occupancy at 40% emergent (mean = 0.44, 95% CrI = 0.34, 0.55). Occupancy probability at 90% was 0.15

TABLE 3 Model parameter estimates for a dynamic occupancy model estimating duck brood occurrence in small (≤ 10 ha) wetlands in crop-dominated landscapes across 4 states in the United States Prairie Pothole Region during summers 2018–2020.

Parameter	Group	Mean	Lower 95% credible interval	Upper 95% credible interval
Initial occupancy	Iowa	0.306	0.169	0.472
	Minnesota	0.361	0.211	0.538
	North Dakota	0.255	0.135	0.415
	South Dakota	0.296	0.142	0.495
	Public ownership	0.299	0.185	0.435
	Private ownership	0.301	0.200	0.419
Persistence	Iowa	0.731	0.524	0.885
	Minnesota	0.664	0.450	0.840
	North Dakota	0.606	0.377	0.809
	South Dakota	0.668	0.407	0.869
	Public ownership	0.685	0.488	0.849
	Private ownership	0.658	0.495	0.802
Colonization	Iowa	0.163	0.068	0.305
	Minnesota	0.149	0.061	0.283
	North Dakota	0.143	0.060	0.269
	South Dakota	0.156	0.055	0.317
	Public ownership	0.127	0.055	0.235
	Private ownership	0.175	0.098	0.275
Annual occupancy ^a	Iowa	0.419	0.278	0.577
	Minnesota	0.456	0.308	0.617
	North Dakota	0.362	0.231	0.516
	South Dakota	0.406	0.242	0.595
	Public ownership	0.388	0.270	0.521
	Private ownership	0.424	0.319	0.537

^aAnnual occupancy is a derived quantity taken from the sum of the probability the wetland was occupied in round 1 (initial occupancy) plus the probability the wetland became occupied in round 2 $[(1 - \text{initial occupancy}) \times \text{colonization}]$.

(95% CrI = 0.08, 0.28) with a mean difference from 40% emergent vegetation of -0.28 (95% CrI = -0.43 , -0.12 ; Figures 6 and 7). Hemipteran abundance was negatively associated with occupancy, with occupancy estimated at 0.50 (95% CrI = 0.37, 0.63) in wetlands with 0 hemipterans and occupancy at 0.25 (95% CrI = 0.14, 0.39; Figures 6 and 7) in a wetland with 120 hemipterans, though values that high were rare in our sample (Table 1). Occupancy was higher at lower levels of SAV (0 rake tines obstructed mean = 0.48 95% CrI = 0.36, 0.60) than at higher levels (45 tines obstructed mean = 0.29, 95% CrI = 0.18, 0.43) with an average difference of 0.18 (95% CrI = 0.00, 0.37) between the highest and lowest values of the index (Figures 6 and 7).

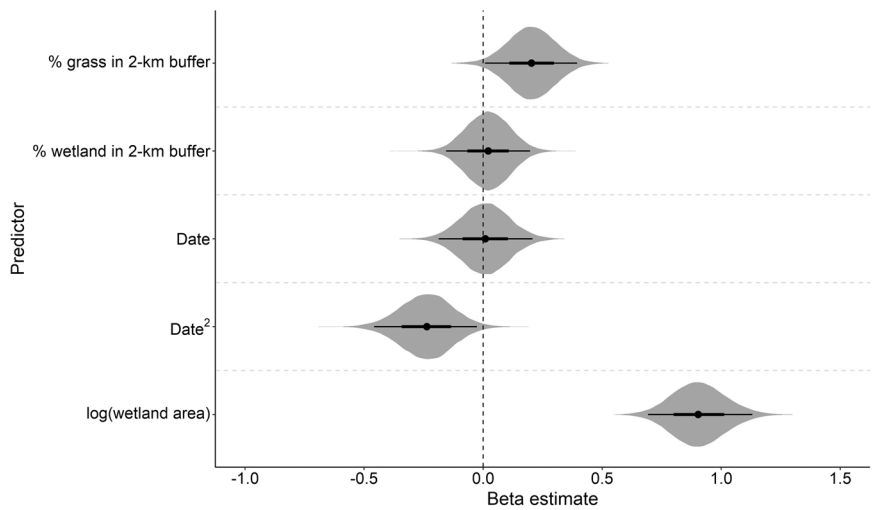


FIGURE 5 Logit-scale coefficient posterior distributions from our static occupancy model estimating duck brood occupancy of small (≤ 10 ha) wetlands in crop-dominated landscapes among covariates measured at the wetland or landscape (2-km radius) scale in the United States Prairie Pothole Region during summers 2019 and 2020. We modeled occupancy in relation to the proportion of the 2-km buffer composed of grassland, the proportion of the 2-km buffer composed of wetlands, ordinal date (1 Jan = 1) with a linear (date) and quadratic (date²) effect, and log-transformed area of the individual wetland. Points represent the posterior means. Thick black lines represent the 66% credible intervals and thin black lines represent the 95% credible intervals.

DISCUSSION

Small (≤ 10 ha) wetlands in crop-dominated landscapes in the PPR supported duck broods at occupancy rates comparable to those observed by other researchers in this region across a broader range of wetland sizes and land cover compositions (Walker et al. 2013a). Annual occupancy was invariant among the 4 primary states in the PPR and wetland ownership type despite the range of wetland conditions and management practices likely used across this vast crop-dominated landscape. We observed weak to marginal evidence of influences of landscape and local factors on wetland occupancy, though observed patterns indicated broods could benefit from management efforts to create hemi-marsh conditions in areas with surrounding grasslands for nesting. These findings indicate conservation and restoration of small wetlands in crop-dominated landscapes, where wetlands may be a limiting landscape feature, would be an effective waterfowl conservation strategy largely independent of broader landscape contexts.

Our dynamic occupancy models allowed us to ask novel questions about brood occupancy dynamics across space and time (i.e., within a season). The probability of a brood occupying a small wetland in crop-dominated landscapes of our study was relatively high (0.41, 95% CrI = 0.26, 0.59), invariant of ownership type, and not systematically variable among the 4 primary states of the PPR. Walker (2011) reported occupancy probabilities ranging from 0.09–0.35 depending on species. Our initial occupancy probability estimate was 0.30 (95% CrI = 0.16, 0.49), and allowing for colonization of unoccupied wetlands later in the season, raised the annual estimate to over the range Walker (2011) reported.

There was no difference in annual occupancy probability by state, which indicates that throughout the PPR brood occupancy in crop-dominated landscapes was reliant on wetland availability or smaller-scale factors, and not systematic landscape-level variation. Thus, our results point towards a phenomenon where wetlands at relatively low densities spread across expanses of private land that comprise most of the region (Doherty et al. 2013) are consistently supporting duck broods. This result aligns with research on spring migrating ducks that reported

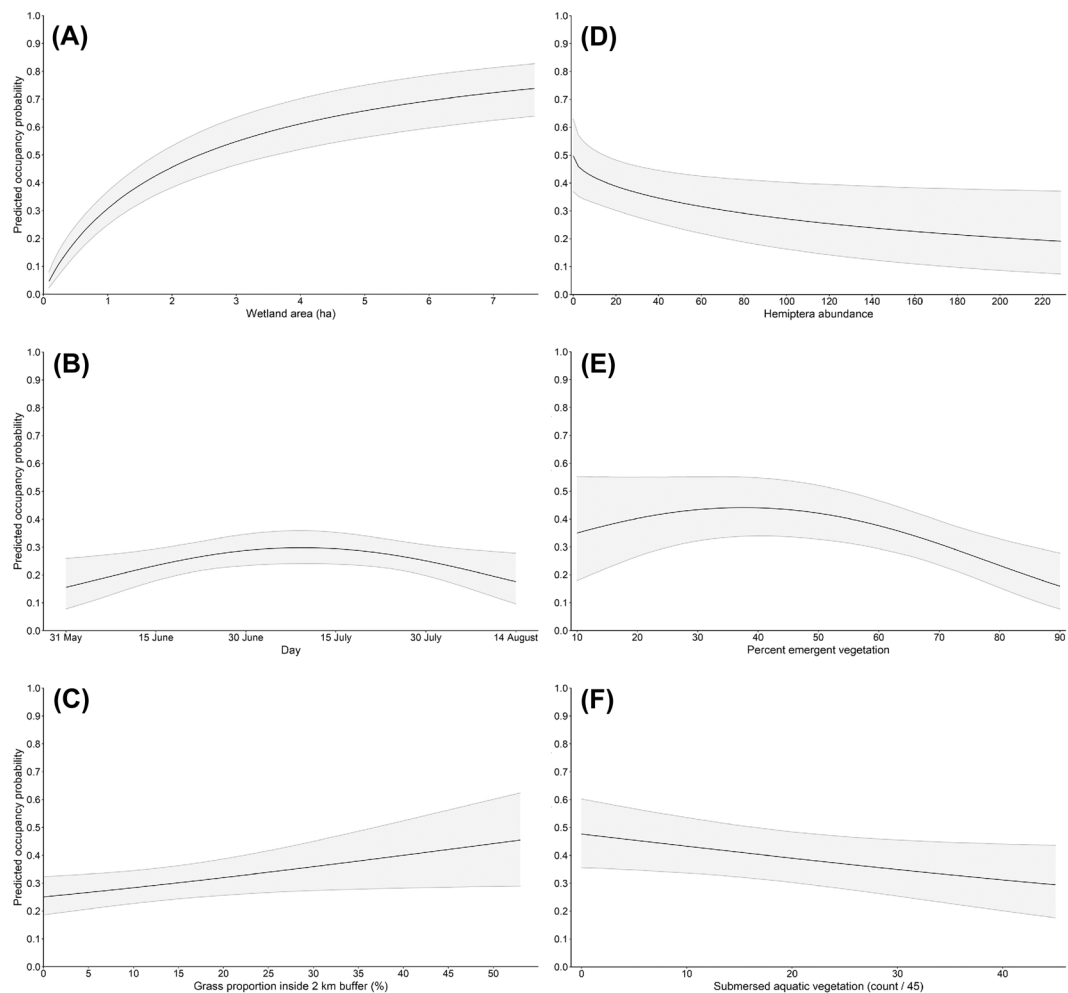


FIGURE 6 Predicted mean probability of occupancy of small (≤ 10 ha) wetlands by duck broods in crop-dominated landscapes within the United States Prairie Pothole Region during summers 2019 and 2020, in relation to a range of covariate values on the x-axes. For each plot, we held corresponding equations from landscape models (A–C) and local models (D–F) at their means to explore variation across the range of conditions observed on the x-axis. Black lines represent the posterior mean and the gray shaded area represents the 95% credible interval.

comparable contributions of wetlands in agricultural landscapes (Janke et al. 2019) relative to grassland-dominated landscapes that have traditionally been the focus of conservation in this region (Reynolds et al. 2006, Walker et al. 2013a). Important research questions remain, especially regarding how these wetlands contribute to annual recruitment beyond occupancy alone.

Our static occupancy models provide a fine-grained lens to understand how smaller-scale factors (e.g., surrounding land use, wetland vegetation, wetland size) influenced occupancy in light of evidence for limited systematic landscape-scale variation. Similar to Walker et al. (2013a), wetland area was the strongest and most consistent predictor of occupancy. Other researchers also reported a consistent pattern of asymptotic wetland occupancy (Walker et al. 2013a) or use by broods (Talent et al. 1982, Rotella and Ratti 1992a, Raven et al. 2007, Bloom 2010) with increasing wetland area, though abundance responses in past work were more variable (Carrlson et al. 2018, Kemink et al. 2019). Although the relationship between occupancy probability and wetland area may

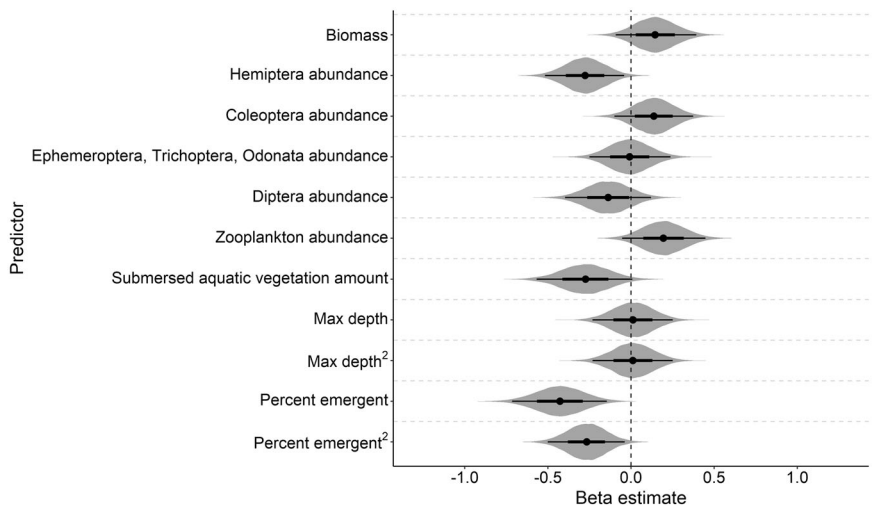


FIGURE 7 Logit-scale coefficient posterior distributions from our static occupancy model estimating duck brood occupancy of small (≤ 10 ha) wetlands in crop-dominated landscapes among covariates measured within wetlands (local scale) in the United States Prairie Pothole Region during summers 2019 and 2020. We modeled occupancy in relation to biomass (mg) of key forage taxa (biomass), abundance of hemipterans (Hemiptera abundance), abundance of larval and adult coleopterans (Coleoptera abundance), abundance of larval ephemeropterans, trichopterans, and odonates (Ephemeroptera, Trichoptera, Odonata abundance), abundance of larval, pupae, and adult dipterans (Diptera abundance), abundance of zooplankton (zooplankton abundance), average amount of submersed aquatic vegetation (submersed aquatic vegetation amount), maximum depth (cm) with a linear (max depth) and quadratic (max depth²) effect, and the amount of emergent vegetation with a linear (percent emergent) and quadratic (percent emergent²) effect. All covariates were z-standardized to have a mean of 0 and standard deviation of 1. Points represent the posterior means. Thick black lines represent the 66% credible intervals and thin black lines represent the 95% credible intervals.

indicate larger wetlands are better, we suggest more nuance in this interpretation is merited. Imagine being given 7 ha of wetlands, either split among 7 unique 1-ha wetlands (each with an occupancy probability of 0.31) or combined as a single 7-ha wetland (with an occupancy probability of 0.73). We can use our posteriors to compare an estimate that ≥ 1 of the 1-ha wetlands were occupied by taking 1 minus the probability none of them were occupied ($[1 - 0.31]^7$). This yields a probability of 0.92 (95% CrI = 0.86, 0.96), which is 0.20 (95% CrI = 0.12, 0.29) greater than the probability a single 7-ha wetland was occupied in our study. This aligns with a body of work that argues total area of habitat is a more important driver of species occurrence than measures of isolation or size of individual patches (Fahrig 2013). These results have important implications for wetland conservation and restoration strategies in crop-dominated landscapes because they indicate, at least for occupancy, the size of an individual wetland is less consequential than total wetland area in a management unit. Different findings may result from consideration of total brood abundance, especially among larger wetlands than those considered in our study.

Our result of a positive association between occupancy and the proportion of a 2-km buffer in grassland was consistent with other brood studies in this region. Carrlson et al. (2018) and Kemink et al. (2019) reported increased abundance of broods as the amount of grassland cover increased around each wetland, and the strength of our trend closely matched that from Walker et al. (2013a). Sovada et al. (2000) observed a positive relationship between grassland patch size and duck nest success, primarily due to increased predator efficiencies and marginal nest success in small, isolated patches. Other researchers also reported increased nest survival with more grassland (Duebbert and Kantrud 1974, Greenwood et al. 1995, Stephens et al. 2005) though recently that relationship has been challenged by Pearse et al. (2022).

We report a non-linear effect of percent emergent vegetation, with lowest occupancy probabilities at highest coverage of emergent macrophytes and relatively static occupancy probabilities up to 40%. This result was loosely consistent with the negative relationship with vegetation reported in Walker et al. (2013a) and non-linear relationships reported in studies of brood abundance (Carrlson et al. 2018). The influence of emergent vegetation on wetland use has been widely studied in this region among waterfowl (Bishop et al. 1979, Bloom 2010, Ballard et al. 2021) and other marsh birds (Harms and Dinsmore 2013, Vanausdall and Dinsmore 2019). Other researchers reported peak abundance (Weller and Spatcher 1965, Weller and Fredrickson 1974, Vanausdall and Dinsmore 2019) and greatest breeding-pair densities (Kaminski and Prince 1981) of waterfowl and waterbirds in wetlands with approximately 50% emergent vegetation and open water. Additionally, Voigts (1976) and McLean et al. (2021) reported the ratio of open water to emergent vegetation to be a strong and consistent driver of invertebrate communities. Our results align with this past work and indicate ideal conditions for broods are around 50% emergent vegetation and open water, and decline considerably as wetlands become more dominated by emergent macrophytes where visibility, mobility, forage resources, or other factors constrain brood use.

Our result of higher occupancy in wetlands with fish than those without was not consistent with our predictions. Researchers have reported negative relationships between fish and duck broods (Giles 1994, Zimmer et al. 2001) and prairie wetland function generally (Hanson and Riggs 1995, Anteau et al. 2011). But our wetlands were considerably smaller than those where the effects of fish have been most studied, and in our case, presence of fish may simply be a proxy for wetland permanence, which is important for broods late in the season (Krapu et al. 2006). Our results at least indicate that fish at the densities we observed in relatively small wetlands in crop-dominated landscapes were not detrimental to brood occurrence.

We observed marginal variation in occupancy with respect to invertebrate metrics. The strongest relationship was a negative one with hemipterans, although the significance of this correlation is unclear given the relatively low abundances we observed (Table 1) and that hemipterans are not a preferred forage (Chura 1961, Street 1977). Dipterans are an important forage taxon for ducklings (Chura 1961, Street 1977), yet we observed weak evidence for a negative effect on occupancy. Streever et al. (1995) observed more abundant dipterans in wetlands with >50% emergent vegetation. This indicates that perhaps dipterans were likely most abundant in wetlands used proportionally less by broods and aligns with our results of a stronger influence of emergent cover on occupancy than invertebrate metrics overall. We expected invertebrate biomass to be associated with occupancy by serving as a composite index of overall forage availability, which may result in higher duckling survival (Sedinger 1992, Cox et al. 1998). But our limited support for a positive effect of this metric perhaps also indicates an opportunistic foraging strategy on available invertebrate taxa in wetlands (Cox et al. 1998), or that females were not selecting for nest or brood-rearing sites with high invertebrate forage available in wetlands. Finally, because invertebrate populations experience frequent turnover and intra-annual fluctuations in abundance (Murkin and Kadlec 1986), our sampling methodology may have been inadequate to detect an influence of invertebrates on occupancy that may play out at finer spatial or temporal scales.

The negative relationship between SAV and occupancy was not consistent with our predictions, which were based on the assumption that high SAV density would provide greater forage. Ducklings transition to a more herbivorous diet as they grow (Chura 1961, Sugden 1973) and SAV provides forage and refugia for invertebrates (Voigts 1976, Diehl and Kornijow 1998). Our results showed occupied wetlands were more likely to lack SAV, which may stand as a proxy for other wetland conditions rather than indicate avoidance of SAV per se. For example, Weisner et al. (1997) reported a positive association between water depth and SAV biomass. Wetlands in our study with greater amounts of SAV were perhaps too deep and did not provide sufficient shallow water zones for feeding (Hanson et al. 2000). It is also plausible that dense SAV hinders locomotion and foraging, particularly for diving ducks (Hochbaum 1944, Monda and Ratti 1988).

We did not observe an effect of surrounding wetland density on occupancy, which was not consistent with our predictions. The association between spring pond counts (i.e., wetland density) and settling patterns of the breeding ducks is well documented (Johnson and Grier 1988, Doherty et al. 2015), and breeding ducks congregate in

wetland-dense areas to nest (Krapu et al. 1983, Bloom 2010). Increased wetland density has also been associated with brood and female survival (Krapu et al. 2000, Devries et al. 2003). Thus, we postulated wetland density would result in greater brood occupancies. But similar occupancy in wetland-sparse landscapes may reflect constrained choices ducks settling in those landscapes are left with for brood habitat. Regardless, this result has important implications for wetland conservation for waterfowl, indicating at least for occupancy, wetland occurrence is more important than landscape context (i.e., a wetland is a wetland).

Collectively, lack of spatial variation and generally weak support for landscape and local factors indicate wetland availability was the greatest constraint on brood occupancy. Wetland availability is primarily influenced by geomorphic history, drainage, and climate (Sofaer et al. 2016). Thus, wetland protection, restoration, or management schemes that focus on landscapes where climate conditions allow basins to be inundated into the brood-rearing period are likely to have the greatest positive effect on occupancy and thereby production. Climate models have projected that the western PPR may become too dry to provide productive breeding waterfowl habitat (Johnson et al. 2005, Rashford et al. 2016), though these projections are variable and remain uncertain (Niemuth et al. 2014, Sofaer et al. 2016, McKenna et al. 2021). Understanding factors that favor wetland occurrence over the long term will be an important focus of future research for conservation strategies in the region (Anteau et al. 2016). Future research on these factors could also help clarify whether occupied wetlands vary with respect to abundance of broods or with respect to survival and ultimate recruitment of broods into the fall flight.

MANAGEMENT IMPLICATIONS

Our finding that small (≤ 10 ha) wetlands in crop-dominated landscapes that prevail in the eastern and southern portions of the PPR in the United States were widely used by broods indicates targeted efforts to restore wetlands there would increase waterfowl productivity. That brood occurrence probability was largely independent of wetland size after controlling for total wetland area indicates that paradigms that favor widespread wetland restoration will have the greatest net benefit to waterfowl. In addition to restoring individual wetlands, our results also indicate some smaller scale features, such as increasing water permanence, bolstering the prevalence of grasslands around wetlands, or focusing on restoration or management practices that favor proliferation of intermediate-to-low levels of emergent vegetation and SAV may also enhance duck brood occurrence. Collectively, our results underscore the importance of wetland availability above all other features, which can be managed through protection or restoration schemes in these landscapes where small wetlands also play critical roles in flood mitigation, water quality, and wildlife-associated recreation.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

All sampling and handling of fish, amphibians, and birds described in this study was reviewed and approved by the Institutional Animal Care and Use Committee at Iowa State University (protocol number IACUC-18-152).

DATA AVAILABILITY STATEMENT

The R and JAGS code needed to reproduce our results are openly available at <https://doi.org/10.6084/m9.figshare.c.6324944.v1>.

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SUPPORTING INFORMATION

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