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Research Paper

Tracing aquatic resource contributions to Tree and Barn Swallow nestling diets across a cropland and wetland gradient

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ABSTRACT. The nutritional quality of nestling diets, influenced by parental prey selection, determines offspring health and development. In agricultural landscapes, nestling diets may be impacted by changes in prey availability from agricultural intensification. In 2020 and 2021, we compared landscape-level effects on nestling prey resources in two sympatric species of breeding aerial insectivores, Tree Swallow (*Tachycineta bicolor*) and Barn Swallow (*Hirundo rustica*). Our study was conducted across an agricultural crop and wetland gradient in Saskatchewan, Canada. Using hydrogen stable isotope analyses ($\delta^2\text{H}$) of nestling feathers, as an indicator of differential diet composition of terrestrial vs. aquatic-emergent insects, we hypothesized that Tree Swallows, as aquatic insect specialists, would have lower feather $\delta^2\text{H}$ values indicative of more aquatic diets. We predicted that increasing annual-row crop and wetland cover around nests would differentially impact each species with Tree Swallows being more sensitive to landscape differences given known reliance on wetland-derived prey. Wetland waters and select aquatic and terrestrial insects showed high variation presumably due to seasonal stochastic evaporation requiring greater sampling effort. However, evidence of differential use of aquatic resources was consistently found between the two swallow species and between wet versus dry years. Lower average Tree Swallow nestling feather $\delta^2\text{H}$ values suggested their diet was more reliant on aquatic-emergent prey, unrelated to the land use around the nest (at 500–2000 m). In contrast, Barn Swallows had higher average feather $\delta^2\text{H}$, which decreased with greater standing water cover in proximity of the nest (< 500 m), suggesting more terrestrial diets with opportunistic use of aquatic-emergent prey resources. For both species, we found no effect of crop cover extent on the isotopic indicator of prey source. These results contribute to the growing body of evidence that multiple species of aerial insectivores rely on aquatic insect resources regardless of local agricultural land use. Our results highlight the importance of conservation of small, interspersed wetlands, especially in intensive cropland-dominated landscapes, to benefit multiple species of aerial insectivores.

Contribution des ressources aquatiques au régime alimentaire d'oisillons d'Hirondelles bicolores et d'Hirondelles rustiques sur un gradient de terres cultivées et de milieux humides

RÉSUMÉ. La qualité nutritionnelle du régime alimentaire des oisillons, en partie influée par la sélection des proies par les parents, détermine leur santé et leur développement. Dans les paysages agricoles, le régime alimentaire des oisillons peut être affecté par le changement de disponibilité de proies attribuable à l'intensification de l'agriculture. En 2020 et 2021, nous avons comparé les effets du paysage sur les ressources en proies destinées aux oisillons chez deux espèces sympatriques d'insectivores aériens nicheurs, l'Hirondelle bicolore (*Tachycineta bicolor*) et l'Hirondelle rustique (*Hirundo rustica*). Notre étude a été menée sur un gradient de terres cultivées et de milieux humides en Saskatchewan, au Canada. Au moyen d'analyses de l'isotope stable de l'hydrogène ($\delta^2\text{H}$) de plumes d'oisillons, comme indicateur de la composition différentielle du régime alimentaire d'insectes terrestres par rapport aux insectes aquatiques émergents, nous avons émis l'hypothèse que les Hirondelles bicolores, en tant que spécialistes des insectes aquatiques, auraient des valeurs de $\delta^2\text{H}$ plus faibles dans les plumes, indiquant un régime alimentaire aquatique accru. Nous avons supposé qu'une plus grande superficie de cultures annuelles et de milieux humides autour des nids aurait un effet différent sur chaque espèce, l'Hirondelle bicolore étant plus sensible aux différences de paysage en raison de sa dépendance connue à l'égard de proies tirées des milieux humides. L'eau des milieux humides et certains insectes aquatiques et terrestres ont montré une forte variation sans doute attribuable à l'évaporation stochastique saisonnière nécessitant un plus grand effort d'échantillonnage. Cependant, des indices d'une utilisation différentielle des ressources aquatiques ont été systématiquement trouvés entre les deux espèces d'hirondelles et entre les années humides et les années sèches. Les valeurs moyennes plus faibles de $\delta^2\text{H}$ des plumes des oisillons d'Hirondelles bicolores indiquaient que leur régime alimentaire est plus dépendant de proies aquatiques émergentes, sans lien avec l'utilisation des terres autour du nid (à 500-2000 m). En revanche, l'Hirondelle rustique avait un $\delta^2\text{H}$ moyen des plumes plus élevé, qui diminuait avec une plus grande superficie d'eau stagnante à proximité du nid (< 500 m), laissant entrevoir un régime alimentaire terrestre accru, comportant une utilisation opportuniste de proies aquatiques émergentes. Pour les deux espèces, nous n'avons trouvé aucun effet de l'étendue de la couverture végétale sur l'indicateur isotopique de la source des proies. Nos résultats contribuent au nombre croissant d'observations indiquant que de multiples espèces d'insectivores aériens dépendent des insectes aquatiques indépendamment de leur utilisation locale des terres agricoles. Nos résultats soulignent l'importance de la conservation de petits milieux humides intercalés, en particulier dans les paysages dominés par les cultures intensives, pour bénéficier à de multiples espèces d'insectivores aériens.

Key Words: *aerial insectivore; agriculture; deuterium; diet source; prairie pothole; segregation; stable isotope*

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INTRODUCTION

Early life-stages in altricial birds are among the most nutritionally and energetically demanding periods of their life cycle, and the quantity and quality of food provisioned by parents can influence nestling phenotype and subsequent fitness (McCarty and Winkler 1999, Twining et al. 2018a, Berzins et al. 2021). Diet quality and composition depends on several factors including, but not limited to, foraging strategies of the provisioning adults (e.g., distance and height of foraging; Orłowski and Karg 2013, Dreelin et al. 2018, Bumelis et al. 2022), nutritional demands of the young (Twining et al. 2021a), and the spatiotemporal availability of high-quality nutritional prey determined by the landscape structure and the quality of the habitat (Génier et al. 2021, Twining et al. 2021b).

In the last several decades, global changes in agricultural practices have been increasingly shifting toward high-input agriculture and the expansion of cropped areas (Matson et al. 1997), which has transformed and degraded aquatic and terrestrial habitats (Bélanger and Grenier 2002, Benton et al. 2002, Tschardt et al. 2005). Wetlands in agricultural lands are widely recognized for providing habitat and nutritional subsidies for terrestrial and riparian consumers (Fritz et al. 2017, Twining et al. 2019, Kowarik et al. 2021). However, wetlands are becoming scarcer (Hayashi et al. 2016, McKenna et al. 2019), and their quality has been deteriorating principally through land-use change and chemical pollution (Bartzen et al. 2010, Malaj et al. 2020). At a global scale, agricultural intensification practices have played a major role in shaping the structure, diversity, and phenology of aquatic and terrestrial arthropod communities (Euliss and Mushet, 1999, Campbell et al. 2009, Morrissey et al. 2015, Cavallaro et al. 2019, Sánchez-Bayo and Wyckhuys 2019), potentially affecting the diet and fitness of many farmland species that use this resource (Benton et al. 2002, Stanton et al. 2018).

Aerial insectivorous birds are a diverse guild that rely almost exclusively on flying insects, including aquatic-emergent and terrestrial taxa (Bellavance et al. 2018, Michelson et al. 2018, McClenaghan et al. 2019, Kusack et al. 2020, Bumelis et al. 2022). This guild has experienced severe and sustained declines in abundance in the last five decades in parts of their geographic ranges in North America (Smith et al. 2015, Sauer et al. 2017), with an estimated loss of 59% in Canada and close to 32% across North America (NABCI 2019, Rosenberg et al. 2019). Given the strong association of many aerial insectivore species with open habitats, agroecosystems, and riparian features, a reduction in availability of high-quality prey caused by agricultural intensification and climate change have been recently hypothesized as major drivers of population declines of this guild (Spiller and Dettmers 2019).

Relative to terrestrial insects, aquatic-emergent insects represent a high-quality prey source for several aerial insectivores as they are richer in physiologically important long-chain polyunsaturated fatty acids (LCPUFA) (Twining et al. 2019). Increased contribution of some LCPUFA-rich aquatic-emergent prey to the diet of nestlings improves health, growth and immunocompetence in different species of riparian songbirds, notably Tree Swallows (*Tachycineta bicolor*; Dodson et al. 2016, Twining et al. 2016, 2019, Berzins et al. 2021). Despite the reliance of aerial insectivores on

flying insect prey, the diet of different species of swallows and their reliance on aquatic-emergent prey as highly nutritious food for nestlings may vary depending on foraging strategies (Bumelis et al. 2022) and dietary needs, which are related to the conversion efficiency of insectivores to synthesize LCPUFA from precursors found in their diets (Twining et al. 2018b).

Habitat features can determine the availability of different types of insect prey in the landscape, and with that the quality and composition of bird diets. For instance, in different species of aerial insectivores, such as Bank Swallows (*Riparia riparia*) and Tree Swallows breeding in the Great Lakes area in Eastern Canada, nestlings were provisioned with more aquatic-emergent prey when nesting closer to large waterbodies indicating that use of the aquatic-emergent prey can depend on the habitat surrounding the natal sites (Génier et al. 2021, 2022). In contrast, Barn Swallows (*Hirundo rustica*) appear to be less dependent on aquatic-emergent insects regardless of their natal habitat (Orłowski et al. 2014, McClenaghan et al. 2019, Génier et al. 2022, Kusack et al. 2022). Given the wide distribution of aerial insectivorous birds across North America and their diversity in natural history traits related to foraging and breeding ecology, it is important to compare species-specific reliance on aquatic-emergent prey for provisioning nestlings in different landscapes. Such comparisons can provide clues as to which common factors are limiting population growth of the guild and could help direct conservation efforts.

Hydrogen stable isotope analysis ($\delta^2\text{H}$) is a widely used tool to estimate the relative broad contribution of aquatic-emergent prey to the diet of birds and mammals (Voigt et al. 2015, Génier et al. 2021, 2022, Bumelis et al. 2022). Hydrogen atoms are incorporated into food webs from environmental waters to primary producers and subsequently transferred through all trophic levels (Fogel and Cifuentes 1993, Hobson 2007). In general, aquatic food webs from the same locations tend to be more depleted in $\delta^2\text{H}$ compared to terrestrial food webs due to differential evapotranspiration, with land plants experiencing higher rates compared to algal cells (Bortolotti et al. 2013, Doucett et al. 2007, reviewed by Vander Zanden et al. 2016). This distinction is generally transferred to higher levels of the food chain. Thus, differences in measurements of $\delta^2\text{H}$ in bird feathers can be compared among species and locations to estimate a relative broad contribution of aquatic prey to the diet during the period of feather growth (Vander Zanden et al. 2016, Bumelis et al. 2022, Génier et al. 2022). Although several hydrological processes can introduce variation, lower average $\delta^2\text{H}$ values in insect consumers should generally reflect higher use of aquatic compared to terrestrial prey in the diet.

Declines of aerial insectivores in North America vary geographically and among species (Michel et al. 2016). Barn Swallows declined by 69% between 1970 and 2019 in Canada (Smith et al. 2020) and were recently designated as Special Concern after being listed as “threatened” under Canada’s Species at Risk Act (COSEWIC 2011). Tree Swallows, which similarly inhabit agricultural landscapes, have been declining in part of their distribution though not as precipitously, with a loss of 35% of the population since 1970, with more drastic changes in northeastern North America (Shutler et al. 2012). Although

Canada-wide swallow populations are still experiencing steep declines (Barn Swallows: -2.34% per year, 95% CI +/- 0.30, Tree Swallows: -0.90% per year, 95% CI +/- 1.33; Smith et al. 2020), in the Prairie Pothole Region (PPR), both Barn and Tree Swallows have maintained relatively stable populations with a ~1.5% annual increase since 2009 (Smith et al. 2020). Most of the landscape in the PPR is dominated by annual crops and intensive farming practices, with 70% of native prairie and more than half of the region's wetlands having been lost due to the conversion of native grasslands and drainage of wetlands to increase the area of croplands (Bartzen et al. 2010, Watmough et al. 2017). Therefore, the trends of stable or increasing populations for both Barn and Tree Swallows in the PPR remain unexplained considering the growing evidence that agricultural intensification, including pesticide use and habitat alterations, causes shifts in abundance and composition of insect communities (Sánchez-Bayo and Wyckhuys 2019, Wagner et al. 2021), which may indirectly reduce prey quality and availability for aerial insectivores. However, variation in individual species reliance on wetlands and tipping points for wetland loss may not yet have been reached (Berzins et al. 2022).

By studying birds nesting across a gradient of agricultural intensity in the Saskatchewan Prairies and using nestling feather stable isotope ($\delta^2\text{H}_f$) values as intrinsic markers of relative contribution of prey to the diet of nestlings (Voigt et al. 2015, Vander Zanden et al. 2016, Génier et al. 2021, 2022), our first objective was to test if Barn and Tree Swallows differed in relative contributions of aquatic prey in their nestling diet. Second, we explored whether metrics of agricultural intensity around the nest site influenced intra-specific differences in aquatic prey contribution to the diet for each species. We predicted that annual crop coverage and proportion of standing water would influence the contribution of aquatic-emergent prey in nestling diets. Specifically, we predicted lower $\delta^2\text{H}_f$ (higher use of aquatic prey) in Tree Swallow nestlings than in Barn Swallows, and that $\delta^2\text{H}_f$ for both Tree and Barn Swallow nestlings would decrease with greater extent of wetland area or higher cropland area around the nest site due to increased availability or reliance on $\delta^2\text{H}$ -depleted aquatic-emergent prey. We hypothesized that these effects would be more pronounced in Tree Swallows given their known specialization in aquatic-emergent prey in other study systems.

METHODS

Study species

Tree Swallows are short to medium distance migratory birds that winter in the southern United States and Mexico (Winkler et al. 2011) and usually raise one brood a year of four to eight eggs. They are secondary cavity nesters (Rendell and Robertson 1989) but also use artificial nest boxes provided by humans. Barn Swallows are a long-distance migrant that breed across North America and winter in Central and South America. This species can be double-brooded and can lay four to six eggs. Barn Swallows nest colonially using human structures such as barns, sheds, and abandoned buildings. Historically, Barn Swallows nested in caves, but with the expansion of human settlements in North America, they have adapted to use homesteads and farm buildings (Brown and Brown 2019).

Study area

Fieldwork was conducted at 16 sites in 2020 and 2021 within 70 km east and south of the city of Saskatoon, Saskatchewan, in the vicinity of Dundurn (51° 48' 34.56" N, 106° 30' 27.36" W), Hanley (51° 37' 40.8" N, 106° 26' 22.2" W), Kenaston (51° 30' 2.16" N, 106° 16' 14.16" W), and Allan (51° 53' 38.4" N, 106° 3' 19.8" W). This area is characterized by mixed annual row crops (primarily canola, lentils, and wheat), natural grasslands, and planted forages. Wetlands of varying size and permanency were abundant, especially in the Allan Hills area, east of Highway 11, but were increasingly rare toward the west. Brightwater Reservoir and Blackstrap Lake are the main large permanent waterbodies located with 3–4 km from the closest study site (Appendix 1).

We studied 12 colony sites in 2020 and 14 in 2021. Tree Swallow boxes (8–10) were installed within 100–200 m around each Barn Swallow colony spaced at least 30 m from each other. This study design allowed us to investigate the diets of nestling individuals of both species, breeding sympatrically.

Land use classification

The landscape surrounding each nest or building was classified by land cover types: annual row crop, perennial forages (including natural grasslands and forage crops), standing water (wetlands), urban, and trees. To determine the appropriate scale at which the land covers of interest could influence our response variable, we used 20 concentric buffers spanning from 500 to 2000 m around each nest or colony. These buffers were used to calculate the relative percentage of each land cover class at each buffer scale. Land cover types were classified using the 2020 Annual Crop Inventory spatial dataset (30 m resolution) available from Agriculture and Agri-food Canada (AAFC 2020). Cropland cover included area under canola, wheat, lentils, flaxseed, barley, and other crops that were combined into an annual row crop category (hereafter crop), which we used as a proxy of agricultural intensity from landscape simplification (Malaj and Morrissey 2022). Pastureland and area under grasses, including lands seeded to perennial forages and hay, were combined into a "perennial grasses" category. The Canadian Wetland Inventory (Mahdianpari et al. 2020) provided a more accurate classification of the standing water relative coverage (10 m resolution) because it includes the shallow/open water category. Although we recognized that marshes, which often include ephemeral wetlands, can be important refugia for insects, this type of wetland was excluded from the classification due to higher evaporation prior to the breeding season and the difficulty of confirming their presence and identifying their boundaries through visual inspection of satellite imagery. Digitized land cover data were compared with Copernicus Satellite-2 imagery (10 x 10 m resolution; European Space Agency 2021) from 26 June 2020 and 01 July 2021, which also corresponded with the breeding peak for both the focal species during the years of the study. The Canadian Wetland Inventory has not been completed for the whole study area; therefore, where coverage was not available ($n = 5$ sampled sites), we relied on satellite imagery from Sentinel-2, along with personal observations and knowledge of wetlands extent and permanence, to carefully delineate wetland boundaries.

Our study colonies were located in a gradient of agricultural land cover where crop coverage ranged between 0.25% and 94% in a 500 m radius from the nests (mean \pm SD = 40.0 \pm 27.3%; Fig. 1;

Appendix 2) and was negatively correlated with the perennial grass cover that ranged between 0.24% and 88% ($41.7 \pm 22.1\%$). Standing water area ranged between 0 and 13% ($3.0 \pm 3.4\%$). Trees and urban areas were present in the landscape surrounding the nests but did not represent a major component of the landscape, except for one site where tree coverage was relatively more abundant (SSP11, $14.3 \pm 3.4\%$).

Water sample collection

Water samples were collected in 2021 only, from at least one natural wetland or artificial pond (i.e., dugouts) at each site to characterize the isotopic environmental water baseline. Samples were collected two or three times during the breeding season (mid-May, mid-June, mid-July) from the nearest permanent wetland (within 500–1000 m from the main swallow colony). In sites where wetlands were not present near the colony, we collected water samples from artificial ponds. Water was collected within 1 m of the wetland or pond edge and approximately 10 cm below the surface.

Insect sampling

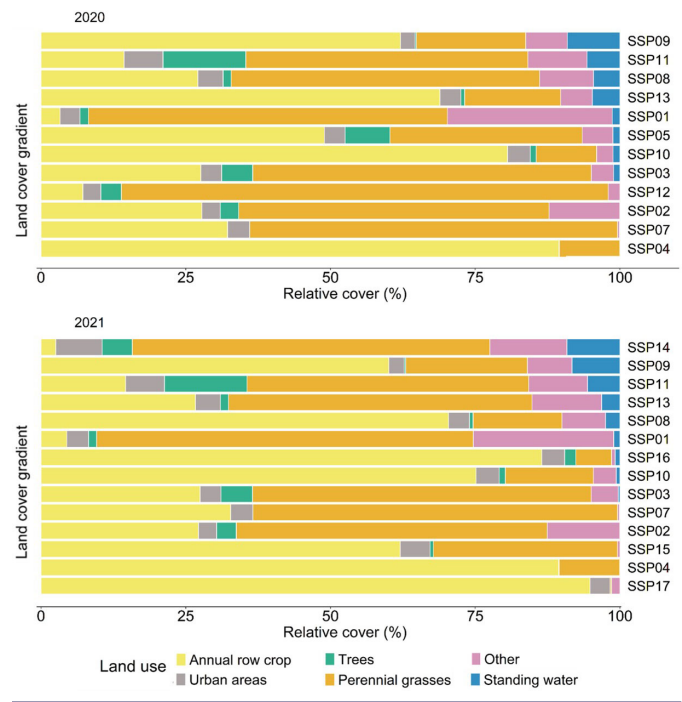
In 2020, standardized sweep netting was conducted in each site, using conical insect nets (Ward’s Professional Insect Net, VWR International catalogue # 470018-488, Radnor, Pennsylvania, USA). Sweep netting was conducted every 10 to 15 days, from the last week of May until the first week of August, to cover the whole swallow breeding period. On each site, four 50 m long sweep-net transects were conducted within 500 m from the main Barn Swallow colony in cropland, grassland, field, or road margin, and within 2 m from wetland shorelines, where available. Samples were stored in plastic bags, placed on ice in a dark cooler in the field, and upon returning to the lab were stored at -20°C until later identification.

Samples were thawed and identified to order, following a dichotomous key (Triplehorn et al. 2005). After identification, samples were refrozen for 24 h at -80°C and subsequently freeze-dried for a minimum of 48 h. We selected two representative groups of invertebrates as terrestrial and aquatic prey: Coleoptera, focusing on terrestrial beetles, and Nematocera (i.e., chironomids, midges), which are aquatic-emergent insects. Nematocera has been previously identified as one of the favored prey groups for swallows and the order Coleoptera has been detected by DNA metabarcoding in nestling fecal DNA samples (Mengelkoch et al. 2004, Orłowski and Karg 2011, McClenaghan et al. 2019, Harris 2023). Both groups were analyzed for $\delta^2\text{H}$ to estimate the degree of site-level variance and the isotopic discrimination with water samples.

Nest monitoring

Barn and Tree Swallow colonies were visited every three to four days starting May 15, to check for signs of occupancy and nesting activity in barns and nest boxes. To reduce disturbance to Barn Swallow adults and nestlings, we used a lighted mirror attached to an extension pole to check nests. Nests were visited approximately every two days to estimate clutch initiation date and day of hatching. The day the first nestling hatched was considered Day 0 for the whole brood.

Fig. 1. Land cover gradient measured across the 16 study sites for each of the 2 study years (2020 and 2021). In the plot, sites are ordered from high to low amounts of area of standing water (i.e., wetlands). The plot shows percentage of relative land use cover within 500 m radius from nest, extracted from the Annual Crop Inventory (AAFC 2020). The category of standing water reflects open water wetlands and was obtained from the Canadian Wetland Inventory (Mahdianpari et al. 2020) and Sentinel-2 Satellite imagery (European Space Agency 2021). The category “Other” includes area of marshes and ephemeral wetlands, which were excluded from the analysis due to the high seasonal variability and difficulty to ground-truth.



Feather sampling

On Day 12 or 15, three nestlings were randomly chosen from each nest to sample feathers and blood. We collected five to six body feathers and stored them in paper coin envelopes for future lab processing and analysis. The previously described methods were used to follow first broods. However, in 2020 due to high nest failure rates caused by intense rain events and frequent predation events at Barn Swallow nests, some second attempts (i.e., a new clutch after the first nest or clutch failed) and second broods (i.e., new brood after successful fledgling) were used to increase sample size. When a Barn Swallow nest failed, adults would typically build or repair a nest located close to the failed nest. Similarly, because Barn Swallows can be double-brooded, adults rarely used the same nest to start a second brood (Safran 2006). Accordingly, first broods and first attempts were categorized as “first” and late broods and/or second attempts were called “late.” We were not able to observe and follow every nesting attempt in the barns and not all Barn Swallow adults were marked leading to uncertainty about whether clutches were second attempts or just late broods. So, we calculated the 5–

95% quantile range of hatching date of a set of nests from 2021 that were known as true first broods. All nests with a hatching date later than the 95% quantile (Barn Swallows, day 189- July 8; Tree Swallows, day 180- June 30) were then assigned to the late category. Only early broods were included in analyses.

Stable isotope analyses

Water samples were analyzed for $\delta^2\text{H}$ by off-axis integrated cavity output spectroscopy (OA-ICOS) using a Los Gatos Research DLT-100 lasers spectrometer in the Stable Isotope Lab at the National Hydrology Research Center (NHRC) in Saskatoon. To normalize raw delta values to the VSMOW-SLAP scale, two calibrated reference waters were used (INV1 $\delta^2\text{H} = -217.7\text{‰}$, $\delta^{18}\text{O} = -28.5\text{‰}$, and ROD3 $\delta^2\text{H} = -3.9\text{‰}$, $\delta^{18}\text{O} = -1.0\text{‰}$). To reduce carryover between samples, nine aliquots were analyzed from each sample, but only the last five were used to obtain the raw delta values (Koehler 2019).

Insect samples from 2020 were freeze-dried after insects were identified to order except for Diptera, in which we selectively focused on the Nematocera suborder. Samples collected from June 11 to July 16, 2020 were manually homogenized by taxa using a pestle directly within vials, ensuring a consistent particle size. The homogenized samples were then pooled to obtain the target mass necessary for hydrogen isotope analysis (0.35 mg). For the analysis, only chitinous tissues (wings and legs) were used for large insects, while entire bodies were used for smaller specimens. Two to eight pooled sub-samples per site were encapsulated into silver capsules.

Body feathers were soaked overnight in 2:1 chloroform:methanol, decanted, rinsed, and dried under a fume hood for 24 h, as described by Wassenaar and Hobson (2000). Then feather barbs (not rachis) were analyzed for stable hydrogen isotope by weighing subsamples (0.35 mg) into silver capsules. Samples and standards were processed by KAH at the LSIS-AFAR Stable Isotope Laboratory, University of Western Ontario for $\delta^2\text{H}$ analysis. There, samples were loaded in a Uni-Prep (Eurovector, Milan, Italy) heated carousel (60°C) coupled with an Eurovector elemental analyser and combusted on a glassy carbon reactor at 1350°C. The resultant H_2 gas was analyzed using a coupled Thermo Delta V Plus (Thermo Scientific®, Bremen, DEU) isotope-ratio mass spectrometer in continuous-flow mode via a Conflo interface.

Pre-calibrated in-house keratin standards (CBS; 197 ‰; KHS: -54.1 ‰) were used to derive the $\delta^2\text{H}$ value of the non-exchangeable H fraction, according to the comparative equilibration technique described by Wassenaar and Hobson (2003). Results were expressed in the standard delta (δ) notation in parts per thousand (‰) deviation from the Vienna Standard Mean Ocean Water (VSMOW). Based on within-run replicate measurements of each keratin standard (5 standards for every 38 unknown samples), analytical error of isotopic measurements (standard deviation, SD) was estimated to be $\pm 2\text{‰}$.

Statistical analyses

We used linear mixed-effect models (LMM) to test for differences in stable isotope composition between aquatic vs. terrestrial insects in each site. We also used LMM to test for differences in relative contributions of aquatic versus terrestrial prey to the diet of Barn and Tree Swallows, and the effects of land use on their

diet source. Before the analyses, we standardized all the continuous variables (mean = 0, SD = 1; Grueber et al. 2011). We used the Akaike information criterion for small sample size (AIC_c) to determine the best-approximating model. In cases where a single best-fitting model could not be determined and no other models had $\Delta\text{AIC}_c < 2$, the effects of individual variables were estimated via multi-model inference (Burnham and Anderson 2002), and model predictions were calculated using conditional model averaging whereby parameters are only averaged over models in which they occur (Grueber et al. 2011). Explanatory variables with unconditional 95% CI overlapping zero were noted as uninformative (Arnold 2010). We performed all statistical analyses using R (version 4.0.3) and RStudio (v. 1.3.1093, RStudio 2020). We used the R package “lme4” to fit LMMs (Bates et al. 2015) and package “MuMIn” to perform model selection, and model averaging (Bartoń 2025). We assessed the collinearity between variables using the VIF function from the “car” package and the normality of residuals by normal Q-Q and residual plots. Subsequently, using the “performance” package in R, calculated marginal R^2 and conditional R^2 of top models ($\Delta\text{AIC}_c < 2$), to evaluate the variance explained by the fixed effects, and the variance explained by both fixed and random effects, respectively (Nakagawa and Schielzeth 2013).

To assess differences in insect $\delta^2\text{H}$ values we used a LMM model that included insect $\delta^2\text{H}$ values as the response variable, taxa as fixed factor, and site as the random effect.

We first tested for isotopic differences between swallow species, without including any of the landscape variables. We used a LMM with $\delta^2\text{H}_i$ as a response variable and included species, year, brood size (number of young when sampling), and hatching date (day of year) as fixed effects. Hatching day was included to account for seasonal effects on $\delta^2\text{H}_i$. By including brood size as a covariate, we controlled for potential differences in parental selection of food sources or travel times dependent on the number of nestlings raised and the demands on nest provisioning (Ardia 2007). Based on likelihood tests among random intercept-only models, we found that the best random effect structure for our model included nest identity nested within site identity by year ($p < 0.001$; Zuur et al. 2009). Including site-specific identity each year accounted for site-level differences among years such as local crop types and cropping specific practices that could have affected insect emergence and availability. The random effects structure also accounted for the non-independence of nestlings within nests.

To evaluate the effects of land use on $\delta^2\text{H}_i$ values, we used the relative area coverage of annual crops and standing water as proxies of agricultural intensification. We initially chose 500 m buffers as an appropriate area of interest to evaluate the effect of annual row crop based on previous studies that have reported breeding swallows foraging range (McCarty and Winkler 1999, Ambrosini et al. 2002, Elgin et al. 2020). Both species are central-place foragers and forage mostly within 500 m of the nests (McCarty and Winkler 1999). This is also supported by the adult foraging data obtained with GPS pinpoint tags deployed in Tree and Barn Swallows during the rearing period in our study area (Harris et al. 2024) and by previous work conducted in the same region with adult female Tree Swallows (Elgin et al. 2020), which confirmed that 75 percent of the foraging trips for both species occurred within 500 m but can be upward of 2000 m. However,

given the evidence that Tree Swallows preferentially foraged in wetlands when traveling farther from the nest (Elgin et al. 2020, Harris et al. 2024), we aimed to determine the optimal scale at which standing water could influence our response variable ($\delta^2 H_p$). For each species, we used a scale-of-effect approach (Kusack et al. 2020) by fitting a set of LMM for our response variable using a set of fixed factors (i.e., brood size, hatching date, and year) as well as crop cover at 500 m and standing water coverage at multiple nested scales (from 500 to 2000 m radii, every 100 m). We used the best random effect structure, which as above, included nest identity nested within site-year identity. Scale-of-effect models were fitted using maximum likelihood. We selected the most appropriate scale for standing water relative coverage based on the model with the lowest AIC_c value.

To test our prediction that the contribution of aquatic-emergent prey to the diet of Barn and Tree Swallow nestlings was higher on landscapes with higher water or crop coverage, we used a set of pre-designed LMM candidate models for each species to compare with a null model with no fixed predictors and only a random intercept structure of nest ID within site-year ($1 + |site-year/nest$). All candidate models included hatching date, brood size, and year (biological model). The candidate set of models also included fixed factors of crop cover within 500 m, water, or an interaction between year and water. Standing water cover was included in the models at the most appropriate scale based on the scale of effect analysis. The interaction of standing water and crop cover could not be tested due to model convergence. All models included nest identity nested within site-year identity as random effects, as used in the scale-of-effect models.

RESULTS

A total of 679 Barn Swallow and 711 Tree Swallow nestlings from 164 and 129 nests, respectively, were monitored. However, more than 15% of Barn Swallows and 10% of Tree Swallows died before fledging due to predation, heat stress, rain events, or unknown causes. We studied an average of 6.0 ± 2.7 (mean \pm SD) Barn Swallow nests per farm site in 2020 and 2021. Average Tree Swallow occupancy was $61.7\% \pm 27.1$ in 2020 and 2021, and the average number of Tree Swallow nests followed per site was 4.8 ± 1.4 in 2020 and 5.6 ± 2.9 in 2021.

Isotopic characterization of environmental water and invertebrate prey $\delta^2 H$

Surface water $\delta^2 H$ values collected in natural wetlands ($n = 6$) ranged widely between -57 and -129 ‰ and those from artificial ponds (i.e., dugouts, $n = 6$) lower ranged between -68 and -150 ‰. As expected, values of water $\delta^2 H$ showed seasonal increases at most sites relative to May samples, with highest values in samples collected in July ($\beta_{June} = 15.46 \pm SE 5.41$; 95% CI = 4.79 - 25.87, $\beta_{July} = 26.02 \pm SE 5.23$; 95% CI = 15.55 - 36.02; Appendix 3). Water collected from smaller artificial ponds was on average more depleted in $^2 H$ than samples collected in natural larger wetlands ($\beta_{natural} = 50.28 \pm SE 9.94$; 95% CI = 31.05 - 69.58, Appendix 3). Invertebrate $\delta^2 H$ values similarly showed high variance. Mean terrestrial insect (Coleoptera, $n = 70$) $\delta^2 H$ values were -185.18 ± 14.82 ‰ but ranged between -161.2 ‰ and -223.2 ‰ and mean aquatic-emergent insect (Nematocera, $n = 70$) were -186.59 ± 19.59 ‰ but values ranged between -152.5 ‰ and -248.3 ‰ (Appendix 4). Given the large inter-and intra-site differences in

isotopic values of wetlands and Nematocera and Coleoptera insect $\delta^2 H$ values after controlling for site ($\beta_{Nematocera} = -1.54 \pm SE 9.94$; 95% CI = -6.76 to 3.69), these data could not detect clear isotopic differences between terrestrial and aquatic insect taxa.

Comparison of $\delta^2 H_f$ values of nestling Tree and Barn Swallows

We used feathers from 258 Barn and 313 Tree Swallow nestlings to test the effect of agricultural intensity on aquatic-terrestrial source contributions of insect prey to the diet (Table 1). A summary of $\delta^2 H_f$ and sampling dates by species and year is provided in the Appendix 5.

Table 1. Summary statistics for Tree Swallow (*Tachycineta bicolor*) and Barn Swallow (*Hirundo rustica*) nestlings $\delta^2 H_f$ values separated by species, year, site, and number of feathers analyzed (n). The sites are listed in order of increasing relative standing water cover, from low to high percentage of wetland area. A dash (-) indicates that samples were not collected.

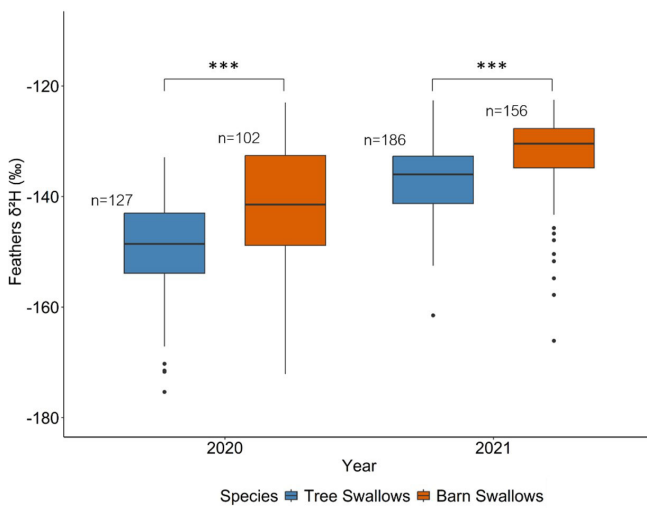
Site	Year	Tree Swallows		Barn Swallows	
		$\delta^2 H_f$ (mean \pm SD ‰)	n	$\delta^2 H_f$ (mean \pm SD ‰)	n
SSP04	2020	-139.8 \pm 5.8	9	-130.5 \pm 4.1	8
	2021	-132.0 \pm 4.6	3	-129.4 \pm 3.7	15
SSP12	2020	-150.3 \pm 8.5	9	-140.2 \pm 4.5	5
	2021	-	0	-127.6 \pm 2.4	7
SSP02	2020	-142.6 \pm 4.4	3	-146.5 \pm 18.8	6
	2021	-134.1 \pm 3.1	21	-127.6 \pm 2.1	10
SSP07	2020	-155.0 \pm 17.7	6	-139.5 \pm 8.7	12
	2021	-134.8 \pm 5.8	19	-	0
SSP16	2021	-	0	-133.5 \pm 5.6	18
SSP17	2021	-135.7 \pm 4.4	11	-131.7 \pm 5.0	12
SSP03	2020	-139.4 \pm 5.1	9	-138.4 \pm 9.4	6
	2021	-132.3 \pm 3.6	29	-128.9 \pm 5.3	12
SSP10	2020	-153.3 \pm 7.7	12	-141.9 \pm 1.3	3
	2021	-134 \pm 2.8	23	-128.1 \pm 1.8	6
SSP01	2020	-151.2 \pm 16.6	9	-149.0 \pm 6.6	13
	2021	-140.4 \pm 2.4	3	-143.3 \pm 9.9	9
SSP13	2020	-156.0 \pm 7.9	18	-141.8 \pm 9.3	14
	2021	-141.9 \pm 4.8	23	-131.5 \pm 4.0	13
SSP08	2020	-151.0 \pm 11.6	15	-151.1 \pm 16.0	11
	2021	-150.8 \pm 9.4	3	-141.9 \pm 14.7	6
SSP11	2020	-148.1 \pm 7.7	15	-136.2 \pm 7.1	11
	2021	-137.9 \pm 5.3	10	-130.1 \pm 5.5	13
SSP09	2020	-151.0 \pm 5.5	9	-156.9 \pm 8.7	17
	2021	-143.2 \pm 3.3	26	-134.9 \pm 7.7	18
SSP14	2021	-136.7 \pm 2.3	15	-135.9 \pm 6.8	26

Across sites and years, Barn Swallow $\delta^2 H_f$ values were on average 5.8 ‰ higher than in Tree Swallows ($\beta_{Barn} = 5.82 \pm SE 0.91$ ‰, $df = 179.81$, $p < 0.001$; Table 1) and, for both species, feathers were 11.3 ‰ more enriched in $^2 H$ in the drier 2021 year relative to 2020 ($\beta_{2021} = 11.38 \pm SE 1.90$ ‰, $df = 23.11$, $p < 0.001$; Fig. 2).

Effect of land use on $\delta^2 H_f$ values in Barn and Tree Swallows

The scale-of-effect analysis indicated that the models with strongest support ($\Delta AIC_c < 2$) included water coverage within a buffer of 500 m for Barn Swallows. Although for Tree Swallows all scale of effect models (from 500 m–2000 m) were competitive ($\Delta AIC_c < 2$; Appendix 6), we used 500 m as the most appropriate scale to test the effect of amount of water in the surrounding landscape on feather $\delta^2 H$ values because the model with that scale had the lowest AIC_c .

Fig. 2. Boxplot of nestling Tree (*Tachycineta bicolor*) and Barn Swallow (*Hirundo rustica*) $\delta^2\text{H}$ feather values (‰) sampled in 2020 (wetter year) and 2021 (drier year) from 16 agricultural study sites in central Saskatchewan. Each box represents the interquartile range with the lower and upper edges of the box indicating the 25th and 75th percentiles, respectively. Blue and orange boxes represent Tree and Barn Swallow $\delta^2\text{H}$ feather values (‰), respectively. Data points outside this range are considered outliers and are plotted individually as dots. Highly significant differences ($p < 0.001$) are indicated with three stars (***)



When evaluating the effect of land use on Tree Swallow $\delta^2\text{H}_f$ values, two models had $\Delta\text{AIC}_c < 2$, but neither of them included the crop cover variable (Table 2). Model-averaged estimates indicated that Tree Swallow $\delta^2\text{H}_f$ values had a positive relationship with year ($\beta = 11.52 \pm \text{SE } 1.80$; 95% CI: 7.97 to 15.06) and were higher in the drier 2021 year (Table 3; Fig. 3). Feather $\delta^2\text{H}$ values increased later in the season and decreased with brood size (Table 3). Standing water cover was included in the averaged models; however, it was uninformative because the CI overlapped zero (Table 3).

When we tested the effects of cropland and water cover at 500 m, for Barn Swallow $\delta^2\text{H}_f$ values, three models had a $\Delta\text{AIC}_c < 2$, and the models included crop, standing water, or both (Table 2). Model-averaged estimates indicated that, as predicted, Barn Swallow $\delta^2\text{H}_f$ values were lower where there were more wetlands around the nest ($\beta = -4.82 \pm \text{SE } 1.56$; 95% CI: -7.89 to -1.74) and were related to year, with higher $\delta^2\text{H}_f$ values in the drier 2021 year ($\beta = 11.66 \pm \text{SE } 1.83$, 95% CI: 8.08 to 15.24; Table 2, Fig. 3). Although crop cover and the interaction of standing water and year were included in the top models, we considered these parameters uninformative given that the CI overlapped 0 (Table 3, Fig. 3).

DISCUSSION

Using nestling $\delta^2\text{H}_f$ measurements, and in line with our predictions, we found that Tree Swallows in Saskatchewan's agricultural landscape had lower $\delta^2\text{H}_f$ values than Barn Swallows, which is consistent with a diet composed of more aquatic-

emergent prey. This suggests an ecological differentiation between the two species even though they were breeding sympatrically, with Barn Swallows only increasing their aquatic food sources when wetland water sources were more available. These results are important given previous assumptions that shifts in availability of high-quality prey caused by agricultural intensification and climate are a shared driver for population declines of different species of aerial insectivores (Spiller and Dettmers 2019).

Our results also suggest that Barn and Tree Swallows in the Saskatchewan Prairie region are both affected by climate patterns affecting the presence of wetlands on the landscape, with lower $\delta^2\text{H}_f$ values of both species suggesting greater aquatic resource use in that wetter year. However, these species are affected differently by shifts in the composition of invertebrate communities caused by agricultural intensification including wetland drainage and disturbance, and the use of agrochemicals (Cavallaro et al. 2019). We found species-specific effects of wetland abundance, but no effect of crop cover on the relative contribution of aquatic-emergent prey in diet. These observed effects were likely driven by differences between species in their reliance on riparian habitats, diet preferences, and parental care strategies. It further suggests that swallows consistently depend on wetland resources where croplands dominate as a reliable source of high-quality prey (Berzins et al. 2022).

Hydrogen isotope variability and dietary inference in prairie ecosystems

There is sufficient foundational evidence on isotopic differences between aquatic and terrestrial prey in the literature (Doucett et al. 2007, Voigt et al. 2015, Soto et al. 2016) and the observed isotopic differences between the two species of swallows studied in sympatry are consistent with evidence of differential relative consumption of aquatic versus terrestrial prey, as $\delta^2\text{H}_f$ values integrate signals from the aerial insectivores' diet (Génier et al. 2021). However, the use of $\delta^2\text{H}_f$ as a tracer of diet and the interpretation of results based on this metric involve important caveats, especially in highly seasonal environments like the Canadian PPR. We observed high variability in water $\delta^2\text{H}$ among different types of wetlands with different seasonal standing water levels (Appendix 3), consistent with other studies in the PPR (Bam and Ireson 2019, Bortolotti et al. 2013, Cavallaro et al. 2022). Similar to Bortolotti et al. (2013), we also found high variability in $\delta^2\text{H}$ values of insects between the two taxa and across sites (Appendix 4), which precludes detection of a clear aquatic-terrestrial difference that may be apparent in less hydrologically dynamic areas (Génier et al. 2022).

The differences in $\delta^2\text{H}$ values between artificial ponds and natural wetlands are notable and somewhat unexpected, with natural wetlands showing higher $\delta^2\text{H}$ values than artificial ponds. These variations may not be solely attributed to evaporation rates, which tend to be higher in smaller water bodies, but could also be influenced by the source of water in the dugouts. Natural wetland waters in Prairie Canada predominantly originate from melted snow and precipitation, while artificial ponds, such as dugouts, are mainly produced by groundwater with limited contributions from surface run-off. The majority of groundwaters worldwide have lower $\delta^2\text{H}$ (and $\delta^{18}\text{O}$) values than annual precipitation (Jasechko et al. 2014), potentially explaining the different isotopic signatures.

Table 2. Model selection table for linear mixed-effect models to evaluate effects of crop and water coverage (%) on feather hydrogen stable isotope ($\delta^2\text{H}_f$) values in Tree (*Tachycineta bicolor*) and Barn Swallow (*Hirundo rustica*) nestlings. Shown are the top candidate models for each species ($\Delta\text{AIC}_c < 2$). Our global model included the water cover interaction with year, crop cover, hatching date, and brood size. All models included site-year ID and nest as random effects, following a nested structure. Models with $\Delta\text{AIC}_c < 2$, indicated in bold, were included in the model averaging (see Table 3). Log likelihood and weight are reported for context but not used in model selection.

Response variable	Models	K	ΔAIC_c	Log-likelihood	weight
Tree Swallow $\delta^2\text{H}_f$	year+ hatching date + brood size (<i>biological model</i>)	7	0	-1054.68	0.41
	water + year + hatching date + brood size	8	0.56	-1053.91	0.31
	crop + year + hatching date + brood size	8	2.10	-1054.68	0.14
	crop + water + year + hatching date + brood size	9	2.63	-1053.88	0.11
	water*year + crop + hatching date + brood size	10	4.76	-1053.88	0.04
	(<i>null model</i>)	3	24.91	-1070.25	0
Barn Swallow $\delta^2\text{H}_f$	water*year + crop + hatching date + brood size	10	0	-908.80	0.37
	water + year + hatching date + brood size	8	0.29	-911.10	0.32
	water + crop + hatching date + brood size	9	0.48	-910.12	0.29
	year + hatching date + brood size (<i>biological model</i>)	7	8.64	-916.34	0
	crop + year + hatching date + brood size	8	10.64	-916.27	0
	(<i>null model</i>)		19.53	-924.93	0

Different factors could have driven the variation in insect $\delta^2\text{H}$ values, and they are likely not mutually exclusive. In food webs, hydrogen isotopic composition of tissues depends on biotic and environmental factors such as habitat and other natural history traits of organisms such as diet and metabolic rates (Jardine et al. 2009, Hobson et al. 2012, Nordell et al. 2016, Vander Zanden et al. 2016, Reese et al. 2018). In aquatic food webs, tissue isotopic values also reflect the variability in environmental waters from where they were synthesized (Hobson et al. 1999, Doucett et al. 2007, Solomon et al. 2009, Finlay et al. 2010, Soto et al. 2013, 2016, Vander Zanden et al. 2016), which are strongly influenced by climate and hydrological processes (i.e., temperature, evaporation, groundwater inputs; Vander Zanden et al. 2016).

In aquatic-emergent insects, the chitinous tissues represent the isotopic composition of the aquatic larval stages, which are influenced by the algae isotopic values in the waterbodies where insects emerge from. Even though many adult aquatic-emergent insects do not feed as adults, the natal environmental isotopic signature of terrestrial and aquatic insects that feed as adult flying insects could be replaced over time by dietary or drinking water sources (Myers et al. 2012).

Numerous families of terrestrial Coleoptera are predaceous (e.g., Carabidae, Cicindelidae, and Gyrinidae). For example, the Carabidae family is riparian and feed mainly on aquatic insects, obtaining food by preying on adult aquatic insects or scavenging on dead insects (Paetzold et al. 2005). Their feeding behaviors result in the integration of isotopic signals from diverse aquatic sources and contribute to additional variability in the isotopic composition of terrestrial Coleoptera.

Another issue that can affect the $\delta^2\text{H}$ values of insect prey used by swallows is their lipid content. Lipids tend to be depleted in ^2H compared to other macronutrients (reviewed by Vander Zanden et al. 2016) and differential lipid content between insect groups can bias prey $\delta^2\text{H}$ values. For this reason, lipid removal from prey tissues (Soto et al. 2013) of insects may reduce some variation. Therefore, in our study system, complex life-history traits, habitats, and physiology, including trophic position and lipid content, use of diverse wetland subject to evaporative water loss could have contributed to the high variation in $\delta^2\text{H}$ in the sampled insects (Vander Zanden et al. 2016).

Species-specific dietary responses to landscape composition

Consistent with our predictions, nestling Tree Swallow $\delta^2\text{H}_f$ values were lower than in Barn Swallows and that relationship held throughout the two years of the study, suggesting that Tree Swallows consume on average, more aquatic-emergent prey than Barn Swallows. Similarly, in Ontario, Tree and Cliff Swallow (*Petrochelidon pyrrhonota*) nestling $\delta^2\text{H}_f$ values were lower relative to Barn Swallow feathers, indicating dietary segregation between sympatric species of swallows, and different reliance on the aquatic prey (Bumelis et al. 2022). Previous studies have found that the majority of Tree Swallow diet consists of aquatic-emergent prey (Michelson et al. 2018), with a high contribution of Nematocera to the diet (McCarty and Winkler 1999, Winkler et al. 2011). Barn Swallows have greater dietary flexibility consuming a wide variety of terrestrial and aquatic prey (McClenaghan et al. 2019).

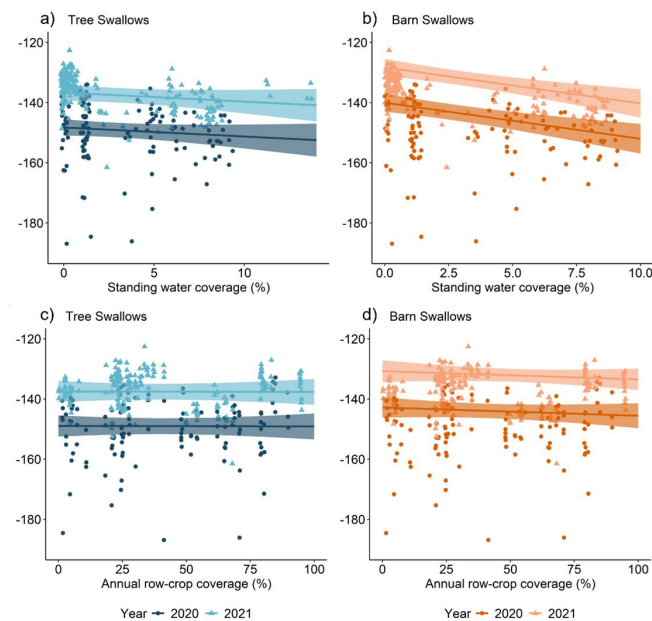
Across our cropland and wetland gradient, we observed species-specific impacts of wetland cover on relative contribution of aquatic-emergent prey to the diet. However, no discernible effect of crop extent was identified across either of the studied species. Increasing cropland area may not be as impactful to the diet of swallows if wetlands are retained. As predicted, Barn Swallow nestling $\delta^2\text{H}_f$ values were lower when the relative area of standing water in the vicinity of the nest (500 m) increased. These results differ from a similar study conducted in the Great Lakes area of Ontario, in which Barn Swallow nestling $\delta^2\text{H}_f$ did not differ between inland and lakeshore locations, indicating a predominantly terrestrial diet independent of the large scale (> 5 km) surrounding nesting habitat (Génier et al. 2022). In Southern Ontario, the availability of aquatic prey is primarily limited to riparian zones and large lakes shores (Lake Ontario, Lake Erie, and Lake Huron). In contrast, Saskatchewan's PPR is characterized by numerous smaller, dispersed wetlands. These wetlands, with their different hydrological regimes, may provide a more continuous and widespread availability of aquatic-emergent prey across the landscape, contributing to the regional differences in Barn Swallow source selection.

If higher wetland cover in agricultural lands increases the availability of aquatic-emergent prey (Lewis-Phillips et al. 2020),

Table 3. Averaged model coefficients with adjusted standard error (SE) and unconditional 95% confidence intervals (CI) from the best-fit models ($\Delta AICc \leq 2$ units) for Tree (*Tachycineta bicolor*) and Barn Swallow (*Hirundo rustica*) nestling feather isotope values (δ^2H_f). A dash (-) indicates that explanatory variables were not included in the model averaging. Estimates with 95% confidence intervals not overlapping with zero are in bold marked with asterisks (*).

Explanatory variables	Tree Swallows			Barn Swallows		
	Estimate	Adjusted SE	Uncond. 95% CI	Estimate	Adjusted SE	Uncond. 95% CI
Intercept	-149.09	1.29	-151.61 – -146.57	-143.88	1.34	-146.50 – -141.25
water cover	-1.02	0.75	-2.51 – 0.46	-4.82	1.56	-7.89 – -1.74*
crop cover	-	-	-	-1.07	0.96	-2.96 – 0.80
2021	11.52	1.80	7.97 – 15.06*	11.66	1.83	8.08 – 15.24*
hatching date	1.01	0.46	0.10 – 1.92*	-0.97	0.62	-2.19 – 0.22
brood size	-0.99	0.42	-1.83 – -0.14*	0.423	0.6	-0.77 – 1.62
water cover*year	-	-	-	3.35	1.91	-0.40 – 7.12

Fig. 3. Model predicted δ^2H_f values for Tree Swallow (*Tachycineta bicolor*; a and c) and Barn Swallow (*Hirundo rustica*; b and d) nestlings and plotted against standing water and annual row-crop coverage at 500 m (%). Points represent individual feather data. The model predicted δ^2H_f values and 95% CIs are based on the most parsimonious model from the top models (lower $\Delta AICc$), which included each of the land use variables. Raw values from 2020 are shown with dots and raw values from 2021 are shown with triangles. Predicted δ^2H_f values from 2020 are shown with dark-colored lines and the lighter lines are showing 2021 predicted values.



our results suggest that, at least in our study area, Barn Swallows can increase their reliance on more aquatic-emergent insects opportunistically, without full dependence. This flexibility may buffer them from the effects of intensive agriculture. Barn Swallows, which often breed colonially in barns or other structures, commonly forage nearer their nest site compared to Tree Swallows (Harris et al. 2024) and select large actively flying Diptera, but adjust their provisioning depending on prey

availability even if it means sacrificing larger or preferred prey (Turner 1982, Brown and Brown 2019). Opportunistic foraging behavior may explain why Barn Swallows in Saskatchewan’s wetland-rich landscapes show different dietary selection compared to those in Ontario.

It remains unclear whether aquatic-emergent insects represent an additional nutritional benefit over terrestrial prey for Barn Swallows, or if the increased use of aquatically derived prey simply reflects their relative abundance. Linking these results to measures of prey availability, reproductive metrics, and nutritional value (i.e., LCPUFA prey composition and specific-specific conversion efficiency) may help better understand the role of aquatic-prey resource dependence for Barn Swallows.

Contrary to our predictions, land-use measurements of cropland cover and water extent evaluated as a proxy of agricultural intensity or landscape simplification (Malaj and Morrissey 2022) were not directly related to δ^2H_f in Tree Swallows, indicating no effect on their selection of prey source. Previous isotopic studies in the PPR, using $\delta^{13}C$ and $\delta^{15}N$ but not δ^2H measurements, did not find clear evidence of differences in apparent aquatic diet composition between Tree Swallows nesting at cropland and grassland sites (Michelson et al. 2018), but those isotopes are generally a poorer indicator of use of aquatic vs. terrestrial prey (reviewed by Vander Zanden et al. 2016). However, there is a growing body of evidence that wetland area and abundance plays a disproportionately large role in the diet and foraging ecology of Tree Swallows by providing a subsidy of high-quality insect prey (Elgin et al. 2020, Berzins et al. 2021, 2022) in turn leading to increased reproductive success and survival (Clark et al. 2018, Twining et al. 2018a).

Previous research in the PPR found that Tree Swallows preferentially forage over wetlands disproportionately to their availability relative to terrestrial habitats (Elgin et al. 2020, Harris et al. 2024), and that selection for wetlands rises with increasing foraging distance from the nest. Although, in other systems, Tree Swallow diet quality increased with proximity to waterbodies with presumably higher abundance of aquatic prey (Génier et al. 2022), Tree Swallows in our study sites with a relatively small gradient of wetlands cover (0–13%), may still have sufficient access to aquatic-emergent insects from wetlands. This is likely due to proximity to wetlands and a mix of aerial plankton carried by the wind, making the availability of aquatic-emergent prey not

limiting. Some other potential mechanisms to mitigate the effect of agricultural intensity on nestling diet might involve changing parental care strategies by increasing feeding rates (Garrett et al. 2022), traveling to farther wetlands to find high-quality food sources (Elgin et al. 2020, Harris et al. 2024), adjusting foraging effort, or increasing the time away from the nest to forage for preferred prey (Stanton et al. 2016). This trade-off has been shown to represent a potential cost to the body condition or fitness of parents (Saino et al. 1999, Ardia 2005, Harrison et al. 2011, Stanton et al. 2017, Clark et al. 2018).

Wetlands in the PPR vary in size and hydrologic regime, exhibiting diverse biotic and abiotic characteristics that enhance the habitat heterogeneity and shape wetland communities (Euliss et al. 2004). These variations influence the phenology of aquatic-emergent insects, which can change daily and seasonally depending on the species and local weather resulting in short-term and local shifts in the insect community composition and structure (Euliss and Mushet 1999, Wrubleski and Ross 2011, Mantyka-Pringle et al. 2019, Shipley et al. 2020, 2022, Mclean et al. 2022). In our region, the asynchrony of the peaks of insect emergence during the early summer and the highly mobile condition of aerial insects (Muehlbauer et al. 2014) influenced by winds (Pasek 1988) could favor the constant flow and diffusion of aquatic-emergent prey into terrestrial and riparian environments and may also help offset lower insect availability associated with a declining abundance of wetlands and more intense agricultural practices locally. Our results contribute to the growing body of evidence that wetlands in the agricultural landscapes of the PPR are critical for supporting breeding populations of some aerial insectivores as sources of high-quality prey (Michelson et al. 2018, Berzins et al. 2021, 2022).

Limitations and future directions

Using only $\delta^2\text{H}$ in feathers as a tracer of the contribution of aquatic-emergent prey involves challenges given the strong link of stable hydrogen isotopes with the hydrological cycle and ambient temperatures, especially in a hydrologically dynamic region such as the PPR. However, despite the known causes of variance in $\delta^2\text{H}$ in food webs, the comparative nature of our research successfully allowed us to capture the isotopic variance of two species by simultaneously measuring them at the same sites and under the same environmental conditions. Future studies using multiple dietary tracers in concert (e.g., multiple isotopes, fecal eDNA, LCPUFA) could help address any shortcomings identified and can provide greater insight into the spatio-temporal shifts in aerial insectivore diet composition (Nielsen et al. 2018, Hoenig et al. 2022a, b, Génier et al. 2022).

CONCLUSION

With increasing evidence of global changes in the composition, abundance, and phenology of insect communities associated with agricultural intensification (Campbell et al. 2009, Morrissey et al. 2015, Cavallaro et al. 2019, Stenroth et al. 2015, Shipley et al. 2022), the availability of highly nutritious insect prey may be approaching thresholds that could negatively impact insect consumers, particularly for more specialized species like Tree Swallows. Although Barn Swallows consumed more terrestrial prey, it is apparent that they also facultatively use aquatic-emergent prey when wetland water sources are more available,

such as during wet years. The availability of aquatic-emergent insect prey appears to buffer populations against many of the threats associated with agriculture. Declining insectivore population trends, as has been reported for other parts of Canada and North America, may be indicative of changes in aquatic insect resource availability rather than simply overall insect declines. Therefore, to support aerial insectivores breeding in farmland habitats, we recommend agricultural policies and incentives for conserving and protecting the remaining wetlands and other remaining natural habitat features to benefit multiple species facing population declines.

Author Contributions:

AMD, KAH, and CAM designed the study, AMD collected and analyzed data. KAH (Western) conducted Stable Isotope Analysis. AMD wrote the first manuscript draft and all authors assisted with manuscript refinement and editing.

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Data Availability:

Datasets including (1) Insect, water, and feather isotope data collected in 2020 and 2021 and (2) R code for the statistical analyses are available in the Federated Research Data Repository at <http://doi.org/10.20383/103.01210>.

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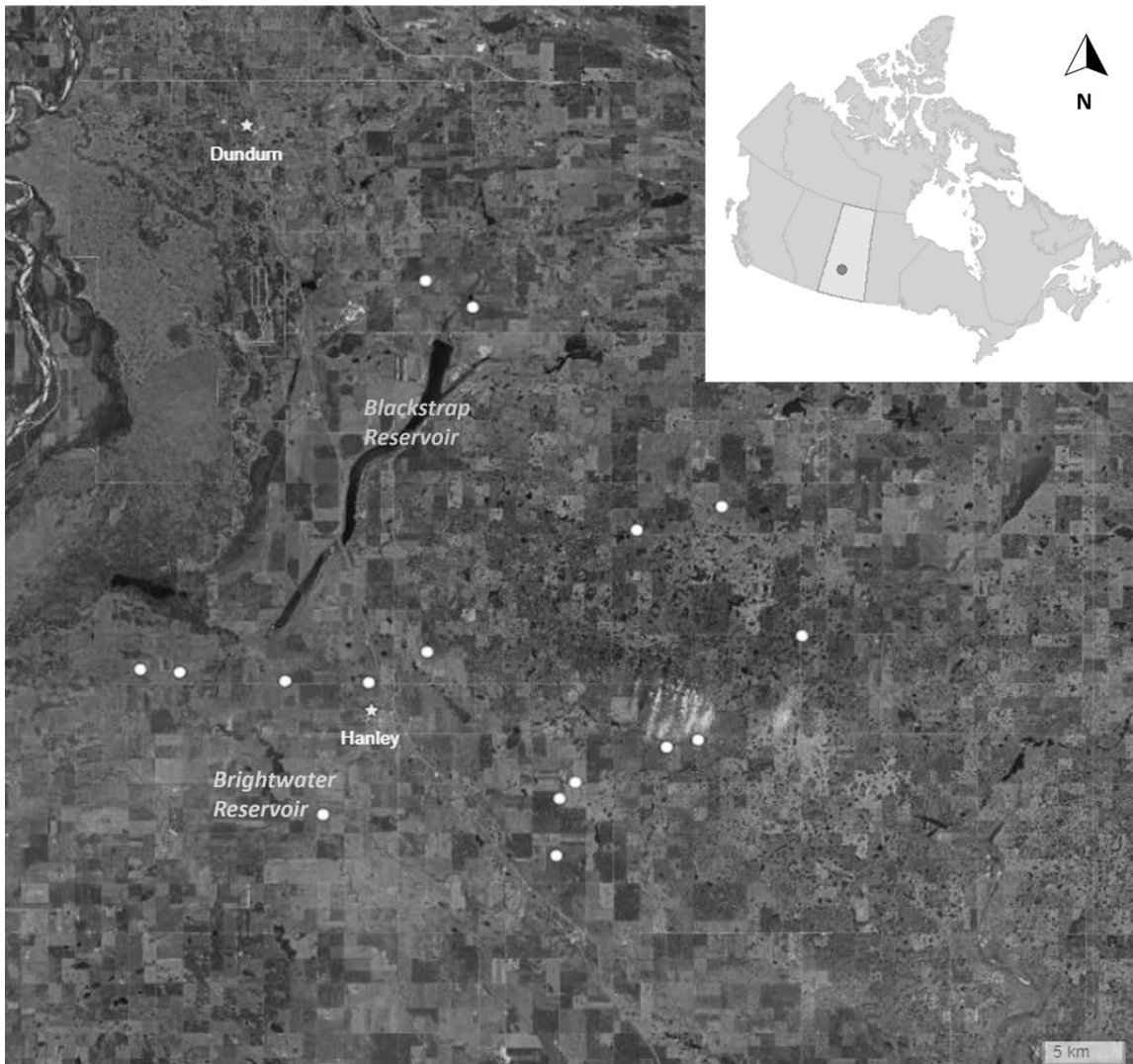
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Appendix 1. Location of the Barn and Tree Swallow study sites in 2020 and 2021. Sites were within 100km southeast of the city of Saskatoon in Central Saskatchewan.



Appendix 2. Summary of site-specific information on land use cover and colony size/nest box occupancy by year of the study. Shown are mean % and standard deviation of land use cover per site per year calculated from the land use relative cover surrounding Tree and Barn Swallow nests within a 500 m radius. This table also includes a summary of numbers of nestlings (nests) followed in 2020 and 2021, including nests that failed after laying at least one egg. For Tree Swallows, nest box occupancy (%) is also reported based on the percentage of boxes that were occupied.

Site	Year	Land use relative cover (500 m radius)			Barn Swallow	Tree Swallow	
		Standing water (%)	Annual row crop (%)	Perennial grasses (%)	Nestlings	Nestlings	Nest box occupancy
SSP01	2020	1.34 ± 0.16	3.28 ± 2.12	61.87 ± 4.81	23 (6)	25(4)	44
	2021	1.06 ± 0	4.40 ± 0	64.25 ± 0	-	5(1)	12
SSP02	2020	0.00 ± 0.01	27.68 ± 2.03	53.48 ± 0.94	34(7)	16(3)	
	2021	0.01 ± 0.02	27.13 ± 2.89	53.62 ± 1.69	32(7)	41(8)	89
SSP03	2020	1.16 ± 0.02	27.57 ± 3.28	58.42 ± 3.51	31(6)	18(4)	70
	2021	0.29 ± 0.03	27.43 ± 4.33	58.44 ± 4.49	37(8)	53(10)	100
SSP04	2020	0.01 ± 0.03	89.24 ± 2.78	10.42 ± 2.76	32(8)	18(3)	44
	2021	0.02 ± 0.04	89.14 ± 2.92	10.41 ± 2.81	23(7)	11(2)	22
SSP05	2020	1.22 ± 0.05	48.84 ± 2.80	33.14 ± 2.31	16(5)	32(6)	68
	-	-	-	-	-	-	-
SSP07	2020	0.088 ± 0	32.18 ± 3.36	63.48 ± 3.41	23(5)	16(3)	56
	2021	0.088 ± 0	32.70 ± 4.38	62.91 ± 4.48	14(3)	40(7)	78
SSP08	2020	4.76 ± 0.55	68.76 ± 1.67	16.55 ± 1.49	24(5)	29(5)	100
	2021	2.49 ± 0.12	70.21 ± 3.25	15.32 ± 2.96	17(4)	14(3)	29
SSP09	2020	9.07 ± 0.26	62.01 ± 3.68	18.87 ± 3.82	43(9)	25(5)	56
	2021	8.27 ± 0.23	59.97 ± 4.95	20.99 ± 5.14	35(7)	54(9)	100
SSP10	2020	1.19 ± 0.14	80.45 ± 1.56	10.48 ± 0.70	12(3)	37(6)	67
	2021	0.63 ± 0.44	75.00 ±	15.19 ± 13.84	13(3)	39(8)	89
SSP11	2020	5.69 ± 0.85	14.31 ±	48.63 ± 5.59	26(6)	28(5)	89*
	2021	5.61 ± 0.85	14.59 ± 7.52	48.57 ± 5.44	28(6)	26(5)	40*
SSP12	2020	0 ± 0	7.22 ± 3.61	84.0 ± 3.88	7(2)	21(4)	75
	2021	-	-	-	-	-	-
SSP13	2020	4.56 ± 2.23	27.04 ± 3.65	53.18 ± 4.12	56(12)	45(8)	70
	2021	3.15 ± 1.99	26.60 ± 3.54	52.32 ± 6.74	36(8)	45(8)	80
SSP14	2020	-	-	-	-	-	-
	2021	9.14 ± 1.97	2.54 ± 0.57	61.66 ± 1.20	58(13)	33(6)	75
SSP15	2020	-	-	-	-	-	-
	2021	0 ± 0	61.92 ± 8.89	31.74 ± 8.68	11(3)	4(2)	12
SSP16	2020	-	-	-	-	-	-
	2021	0.84 ± 0	85.88 ± 0	6.12 ± 0	26(6)	-	-
SSP17	2020	-	-	-	-	-	-
	2021	0 ± 0	94.64 ± 0.18	0.24 ± 0	17(5)	21(4)	44
All		3.0 ± 3.4	41.6 ± 28.0	40.6 ± 21.9	25 ± 12.9	25 ± 13.9	61.7 ± 27.1

(*) indicates the only site where a Tree Swallow colony was previously established, and where the number of boxes available was >20.

Appendix 3. $\delta^2\text{H}$ water values at three collection periods during the breeding season (mid-May, mid-June, and mid-July 2021). Water samples were obtained primarily from the nearest permanent wetland within 500-1000 m from the main swallow colony. In the absence of nearby natural wetlands, water samples were obtained from artificial ponds. Water was collected within 1m of the wetland edge and approximately 10cm below the surface. (-) indicates samples were not collected at that collection period.

Site	Type of wetland	First collection	$\delta^2\text{H}$ (‰)	Second collection	$\delta^2\text{H}$ (‰)	Third collection	$\delta^2\text{H}$ (‰)
SSP14E	natural	-	-	2021-06-10	-73	2021-06-25	-62
SSP14W	natural	2021-05-18	-70	2021-06-10	-64	2021-06-25	-59
SSP09	natural	2021-05-18	-73	2021-06-09	-70	2021-06-25	-64
SSP11	natural	2021-05-18	-68	2021-06-10	-64	2021-06-25	-57
SSP13	natural	2021-05-21	-129	-	-	2021-06-25	-57
SSP08	natural	2021-05-18	-80	2021-06-09	-61	2021-06-25	-73
SSP01	artificial	-	-	2021-06-10	-140	2021-06-25	-132
SSP10	artificial	2021-05-18	-103	2021-06-10	-83	2021-06-25	-68
SSP03	artificial	2021-05-18	-138	2021-06-09	-114	2021-06-25	-92
SSP07	artificial	2021-05-18	-150	2021-06-09	-138	2021-06-25	-126
SSP04	artificial	-	-	2021-06-09	-123	2021-06-25	-103
SSP02	artificial	-	-	2021-06-09	-131	2021-06-25	-128

Appendix 4. Summary statistics for stable hydrogen isotope ($\delta^2\text{H}$) of insects separated by taxa, and site. Insect samples analyzed were collected from June 11 to July 16, 2020, and were homogenized and pooled to obtain the target mass necessary for hydrogen isotope analysis.

Site	Coleoptera $\delta^2\text{H}$ (<i>mean</i> \pm <i>SD</i> ‰)	n	Nematocera $\delta^2\text{H}$ (<i>mean</i> \pm <i>SD</i> ‰)	n
SSP01	-183.8 \pm 3.5	4	-167.6 \pm 5.0	6
SSP02	-213.0 \pm 22.2	6	-181.1 \pm 6.5	5
SSP03	-159.6 \pm 5.3	6	-180.0 \pm 4.0	6
SSP04	-218.4 \pm 41.9	6	-176.1 \pm 9.6	2
SSP05	-188.7 \pm 4.6	8	-189.2 \pm 16.9	6
SSP07	-183.2 \pm 16.3	6	-176.3 \pm 11.1	6
SSP08	-181.6 \pm 2.0	6	-216.4 \pm 5.4	6
SSP09	-202.2 \pm 22.3	4	-184.2 \pm 18.5	7
SSP10	-181.2 \pm 13.0	6	-197.6 \pm 8.9	7
SSP11	-177.8 \pm 7.6	6	-180.9 \pm 7.3	7
SSP12	-169.7 \pm 6.5	6	-184.6 \pm 5.3	6
SSP13	-205.3 \pm 4.9	6	-180.6 \pm 5.1	6
General	-185.18 \pm 14.82	70	-186 \pm 19.58	70

Appendix 5. Summary of $\delta^2\text{H}$ feather values (mean \pm SD) for Barn and Tree Swallows sampled at 17 sites in Saskatchewan, Canada, during the breeding seasons of 2020 and 2021.

Year	Species	First day of feather sampling	Last date of feather sampling	Mean \pm SD (‰)	No. nestlings	No. nests
2020	Barn Swallow	2020-06-26	2020-07-22	-143.7 \pm 12.4	102	36
2020	Tree Swallow	2020-06-23	2020-07-16	-149.7 \pm 10.2	127	58
2021	Barn Swallow	2021-07-02	2021-07-23	-132.2 \pm 6.7	156	44
2021	Tree Swallow	2021-06-19	2021-07-12	-136.9 \pm 5.8	186	65

Appendix 6. Scale of effect showing model fits for nestling δ^2H_f values. The top plots (a) show ΔAIC_c values resulting from the linear mixed effect models at each nested scale (500 to 2000 m radii, every 100 m), and using crop cover at 500 m, year, hatching date, and brood as fixed effects and site ID and nest as random effects. The dashed lines in top plot (a) indicate the threshold of $\Delta < 2.0 AIC_c$ used to identify competitive models. The bottom plot (b) shows parameter estimates (β) from models.

