ARTICLE

Tree Swallow (*Tachycineta bicolor*) foraging responses to agricultural land use and abundance of insect prey

R.L. Stanton, C.A. Morrissey, and R.G. Clark

Abstract: Throughout North America, many species of aerial insectivorous birds have exhibited steep declines. The timing of these declines coincides with changes in agriculture, perhaps signaling a causal link. Increased agrochemical use, wetland drainage, and cropping intensity may indirectly influence insectivores by reducing the abundance of insect prey. Our objective was to determine whether changes in insect abundance and biomass on agricultural landscapes in the Canadian Prairies influence the foraging behaviour of breeding Tree Swallows (*Tachycineta bicolor* (Vieillot, 1808)). Swallows were studied at five sites with varying levels of agricultural intensity in Saskatchewan, where insect abundance and biomass were monitored daily with passive aerial samplers. Radio-frequency identification (RFID) technology was employed at Tree Swallow nest boxes to investigate adult foraging behaviour. Foraging rates (number of nest visits/h) were slightly higher on agricultural sites than at grassland sites, and were positively related to daily insect biomass and nestling age. Tree Swallows, especially males, breeding at agricultural sites spent more time away from the nest box, presumably foraging, resulting in reduced nest attentiveness. RFID technology provides an effective technique to measure behaviour in birds and these findings suggest mechanisms by which prey abundance and agricultural land use may affect declining aerial insectivorous bird populations.

Key words: aerial insectivore, agricultural intensification, radio-frequency identification, RFID, Tree Swallow, *Tachycineta bicolor*.

Résumé : De nombreuses espèces d'oiseaux insectivores aériens présentent des déclins marqués à la grandeur de l'Amérique du Nord. Le moment de ces déclins coïncide avec des changements aux pratiques agricoles, ce qui pourrait indiquer un lien de causalité. L'utilisation croissante de produits chimiques agricoles, l'assèchement des milieux humides et l'intensité des cultures pourraient exercer une influence indirecte sur les insectivores en réduisant l'abondance d'insectes qui leur servent de proies. Notre objectif consistait à établir si des modifications de l'abondance et de la biomasse d'insectes dans les paysages agricoles des Prairies canadiennes influencent le comportement d'approvisionnement des hirondelles bicolores (*Tachycineta bicolor* (Vieillot, 1808)) nicheuses. Des hirondelles ont été étudiées en cinq sites en Saskatchewan présentant différents degrés d'intensité agricole, où l'abondance et la biomasse d'insectes ont été surveillées quotidiennement à l'aide d'échantillonneurs aériens passifs. La technologie d'identification par radiofréquence (IRF) a été utilisée à des nichoirs d'hirondelles bicolores pour étudier le comportement d'approvisionnement des adultes. Les fréquences d'approvisionnement (nombre de visites au nid/h) étaient légèrement plus grandes dans les sites agricoles que dans les sites de prairie et présentaient une relation positive avec la biomasse quotidienne d'insectes et l'âge des oisillons. Les hirondelles bicolores, particulièrement les mâles, qui nichaient dans des sites agricoles passaient plus de temps loin du nichoir, probablement pour s'approvisionner, ce qui se traduisait par réduction de l'assiduité au nid. La technologie IRF fournit une méthode efficace pour mesurer le comportement des oiseaux, et les résultats donnent à penser qu'il existe des mécanismes par lesquels l'abondance de proies et l'utilisation agricole du territoire pourraient influencer les populations d'oiseaux insectivores aériens en déclin. [Traduit par la Rédaction]

Mots-clés : insectivore aérien, intensification de l'agriculture, identification par radiofréquence, IRF, hirondelle bicolore, *Tachycineta bicolor*.

Introduction

Agricultural intensification, defined as "increased production of agricultural commodities per unit area" (Donald et al. 2001), includes changes that have occurred to farmland management and operations worldwide over the last several decades. These changes involve increased mechanization and reliance on agrochemicals, decreased habitat heterogeneity with fewer mixed-farming systems, and loss of natural habitat such as field margins and wetlands (Fuller et al. 1995; Chamberlain et al. 2000; Benton et al. 2003). Avian species associated with agricultural habitats are currently experiencing declines more severe than birds associated with any other biome (Sauer et al. 2000; Murphy 2003). In Canada specifically, grassland bird populations have declined, on average, by almost 40% (NABCI Canada 2012). Furthermore, declines of aerial insectivores, an avian guild with high reliance on aerial insects as prey, the common trait of an otherwise ecologically diverse group, may also be influenced by agriculture and the associated widespread reductions in insect abundance (Nebel et al. 2010; Nocera et al. 2012).

Arthropod species richness is greater in areas of less intensive agriculture (Benton et al. 2002; Attwood et al. 2008), and areas of

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Table 1. Summary of site and land-use characteristics for grassland and agricultural cropland sites in south-central Saskatchewan.

Site	% Crop[a]	% Human use[b]	% Natural[c]	% Pasture[d]	% Trees[e]	% Water[f]	Neonicotinoid concentration[g]	RFID females[h]	RFID males[i]
Grassland									
Allan	0.0 (0)	0.8 (0–3.4)	64.3 (4.7–91.3)	10.3 (0–81.9)	8.2 (5.5–12.2)	16.4 (3.2–42.0)	<DL (<DL)	4	2
St. Denis	19.9 (0–82.9)	0.4 (0–1.7)	42.7 (1.5–92.4)	19.0 (0–77.5)	3.6 (0.3–12.1)	14.5 (2.5–26.1)	2.0 (1.6–3.6)	5	3
Cropland									
Burr	75.4 (51.2–87.9)	8.4 (0–8.8)	15.3 (1.5–33.5)	0.0 (0)	2.1 (0–6.9)	5.1 (0.4–7.9)	97.5 (1.2–410.3)	8	7
Colonsay	82.5 (72.2–92.5)	10.4 (0–11.1)	5.1 (1.3–7.3)	0.0 (0)	2.3 (0–4.2)	8.3 (0.3–16.9)	21.4 (10.2–30.5)	3	0
Humboldt	60.9 (34.6–82.2)	6.8 (0.0–9.2)	12.7 (4.2–22.9)	0.0 (0)	3.1 (0.5–9.1)	20.7 (3.9–50.9)	360.8 (89.7–710.8)	6	5

Note: Land use is displayed as a percentage of total area in 8–10 quarter sections surrounding the nest boxes at each site. The range in percentage of each land-use category across quarter sections is shown in parentheses. Mean (range) in total neonicotinoid insecticides (sum of acetamiprid, imidacloprid, clothianidin, and thiamethoxam) concentrations were measured in 3–5 wetlands per site.

[a]Land under cultivation.
[b]Buildings, roads, other human structures.
[c]Grass, dried wetlands.
[d]Pasture area for livestock.
[e]Trees or shrubs.
[f]Surface water.
[g]Mean total neonicotinoid concentration (ng/L) in wetland water samples from 2012 to 2014. Concentrations below the detection limit (DL) were set at 0.1 ng/L, which is an arbitrary value that is equal to the lowest DL for any single neonicotinoid.
[h]Number of females monitored with a radio-frequency identification (RFID) reader.
[i]Number of males monitored with a RFID reader.

vegetation adjacent to cropland can provide essential resources for a variety of insects (Dennis and Fry 1992). Likewise, Gruebler et al. (2008) determined that aerial insect abundance was higher in areas with trees, hedgerows, and native grassland compared with areas of cereal crop. Dipterans (true flies), which comprise 62.5% of the food provided to Tree Swallow (*Tachycineta bicolor* (Vieillot, 1808)) nestlings in some regions, are almost twice as abundant in fields that do not receive insecticides during the Tree Swallow breeding season (Rioux Paquette et al. 2013); in untreated fields, dipteran abundance is positively related to the presence of nearby water sources, such as rivers and ditches (Morris et al. 2005). This is a critical relationship, as many wetlands such as those in Prairie Canada are experiencing long-term degradation and drainage for conversion to agriculture (Bartzen et al. 2010).

A decline in avian food supply associated with agricultural intensification can result in more time spent away from the nest and altered foraging strategies to locations that are more reliable, but also more distant from the nest (Winkler et al. 2013). For example, Barn Swallows (*Hirundo rustica* L., 1758) actively forage in vegetated field boundaries rather than in field centres during periods of cold temperatures, strong winds, and rain, although this switch from field centres to boundaries is not seen during good weather (Evans et al. 2003). This suggests that changes in abundance of aerial insects in fields can affect foraging behaviour and energy balance. Changes in foraging behaviour and increased flight time for breeding adults can adversely affect reproduction, physiology, survival, and nestling growth rates (Holmes 1995; Siriwardena et al. 2000; Monaghan et al. 2009).

In areas of Eastern Canada where cropping regimes and agricultural practices can reduce abundance of dipteran insects, Tree Swallows have lower nest-box occupancy, clutch size, and number of fledged nestlings, and impaired adult immune responses (see Ghilain and Bélisle 2008; Robillard et al. 2012; Pigeon et al. 2013; Rioux Paquette et al. 2013). However, the generality of these results is unclear. The Prairie region is Canada's most important crop production area and the region uses 70% of the nation's commercial fertilizers and 80% of the pesticides (Kissinger and Rees 2009); therefore, investigations into threats associated with agricultural intensification are strongly needed. We evaluated the hypothesis that a reduction of insects may be an important driver in disrupting food webs in agricultural landscapes and we predicted that adult Tree Swallows would alter their foraging and nest attendance behaviour in response to prey abundance. This work is an important step in understanding if a causal mechanism exists between prey abundance at agricultural cropland sites and declines of farmland aerial insectivorous bird populations.

Materials and methods

Characterization of site type from land use and pesticides

Land use was classified at five sites with Tree Swallow nest-box colonies (*n* = 32 boxes/site) in south-central Saskatchewan in 2014: Allan (51.6206°N, 105.9706°W) and St. Denis (52.2101°N, 106.0760°W) served as grassland (reference) sites, whereas Burr (51.9710°N, 105.0996°W), Colonsay (52.0272°N, 105.9183°W), and Humboldt (52.2122°N, 105.2903°W) were characterized as agricultural sites (Table 1). Daily temperature, precipitation, and wind speed were recorded at all sites, as weather influences aerial insect abundance (McCarty 1995; Gruebler et al. 2008). Temperature data were collected from local weather stations. Precipitation and wind speed were measured using a rain gauge and an anemometer, respectively, at each site.

Land use was characterized using aerial photographs for 8–10 agricultural quarter sections per site, depending on the distribution of the boxes. A quarter section is the dominant land tenure parcel in Prairie Canada and it consists of 160 acres or 0.65 km². Land uses included crop, human use (such as roads and buildings), pasture, herbaceous cover, trees and shrubs, and standing water (Table 1). ArcGIS was used to delineate the land use within these areas. As part of a larger study, total neonicotinoid (insecticide) concentrations were also repeatedly measured in water samples collected from 3 to 5 wetlands/site in June 2012–2014. Neonicotinoid concentrations are representative of the extent of agrochemical use as they are the main insecticides used across the Canadian Prairies. These compounds are also known to exert toxicity to a range of aquatic insects that are important prey for Tree Swallows (Morrissey et al. 2015). Although other pesticides were not measured, we reasoned that neonicotinoid concentrations in water may be considered an indicator of agricultural intensity. Water samples were analyzed for neonicotinoids using the liquid chromatography – mass spectroscopy (LC–MS/MS) at the National Hydrology Research Centre (Saskatoon, Saskatchewan, Canada), as previously described by Main et al. (2015).

Data on land use were analyzed using multivariate analysis of variance (MANOVA) with land-use variables (crop area, human use, pasture, herbaceous cover, trees, water) and total neonicotinoid insecticide concentrations (sum of acetamiprid, imidacloprid, clothianidin, and thiamethoxam) as response variables and

site type (agricultural or grassland) as the explanatory variable. The analysis confirmed statistically ($F_{[1,21]} = 33.4$, $p < 0.0001$) that site types differed primarily in the amount of crop (Student's t test, $t_{[27]} = 13.6$, $p < 0.0001$) and neonicotinoids in wetlands ($t_{[27]} = 4.7$, $p < 0.0001$), which were higher in agricultural sites, whereas herbaceous cover ($t_{[27]} = -4.4$, $p < 0.001$) and pasture ($t_{[27]} = -3.0$, $p = 0.005$) were more prevalent on grassland sites.

Insect availability: deriving biomass and abundance indices

Insects were collected using aerial insect passive samplers ($n = 3$ per site), as described in Hussell and Quinney (1987). Glass collection jars filled with a 70:25:5 mixture of ethanol:water:glycerol (to prevent evaporation) were changed every 24–48 h during the swallow breeding season. Samples were filtered, and insects were then stored in 70% ethanol (30% water) until counted, and then placed in a drying oven at 95 °C until completely dry, and weighed (nearest 0.01 mg) on an analytical balance to obtain dry biomass. Insects longer than 13 mm (excluding antennae and ovipositors) are considered rare in a Tree Swallow's diet and were removed prior to processing (Quinney and Ankney 1985; McCarty and Winkler 1999). Insect dry biomass was adjusted for sampling duration and mean wind speed during the sampling period, by first dividing the insect dry mass (mg) by total sampling duration (s), and further dividing by mean wind speed (m/s) over the sampling time period then standardized to 1 day by multiplying by 86 400 s (= 24 h) to derive an "insect biomass index". This measure provides a wind-corrected estimate of insect availability over each 24 h period. To relate temporal differences in food supply to Tree Swallow foraging behaviour, the insect biomass index was calculated to match each Tree Swallow observation period.

Tree Swallow nest monitoring and capture

Starting in early May, nest building was monitored every other day until the first egg was laid, and thereafter, nests were checked daily until the clutch was complete. Nests were not disturbed until the end of the incubation period (about 12 days). When the first egg hatched, nests were checked daily until hatch was completed. Adults were trapped in nest boxes using a trap door within a few days after hatch, banded with a metal band (or identified, if recaptured), and wing chord and ninth primary lengths were measured with a wing rule (nearest 0.5 mm), head–bill length was measured with dial calipers (nearest 0.01 mm) and body mass was taken with a Pesola spring scale (nearest 0.5 g). Females were aged as second year or after second year, based on plumage (Hussell 1983).

Foraging behaviour

A randomly selected subsample of breeding adults (Table 1) was monitored through use of radio-frequency identification (RFID) readers placed at the nest box during the chick-rearing period (Bridge and Bonter 2011). At capture, the adult male and female at each nest were temporarily marked with a unique passive integrated transponder (PIT) by gluing the PIT to the bird's interscapular feathers with nontoxic VetBond™. A sham RFID antenna made of copper and bronze wire was placed around the nest-box opening at least 24 h prior to marking to allow swallows to habituate to the experimental set up before data collection began. A subset of Tree Swallows was casually observed before and after placement to confirm that the use of sham antenna placement did not disrupt normal nest visitation behaviour. After this period, the automated RFID reader was placed under the nest box and connected to the real antenna placed around the nest-box opening. The RFID reader was programmed to log date and time of nest visits by each uniquely tagged male and female, providing information about how often each parent visited the nest and the duration between visits. The number of nest visits provides a reliable index of food

Table 2. Summary statistics for the best-approximating models (based on the lowest AIC_c (Akaike's information criterion corrected for small sample size) value) to explain variation in foraging rate and trip duration for adult Tree Swallows (*Tachycineta bicolor*) nesting on agricultural and grassland sites in Saskatchewan.

Response variable	Factors	Estimate ± SE	p
Foraging rate	Site type	0.66±0.21	**0.05**
	Insect biomass	18.30±7.03	**0.02**
	Nestling age	0.13±0.04	**0.001**
Trip duration	Site type	−1.43±2.09	0.54
	Sex	−5.06±2.24	**0.048**
	Insect biomass	−99.50±43.50	**0.03**
	Site type × sex	6.55±2.72	**0.04**

Note: Factors are defined as follows — site type: agriculture or grassland; insect biomass: wind-corrected daily biomass of insects collected on the day of behavioural monitoring; brood size: number of nestlings in a brood; nestling age: age of the nestlings on the day of the foraging measurements; sex: male or female. Global models included effects of site type, insect biomass, brood size, nestling age, sex, and site type × sex interaction. The p values in boldface type are significant at $p < 0.05$.

provisioning to nestlings, as swallows feed nestlings on 95%–98% of their visits to the nest box (McCarty 2002; Whittingham et al. 2003).

We analyzed foraging rate, the number of nest visits per individual over 17 h (0500 to 2200), and trip duration, the time spent between visits inside or at the entrance to nest boxes, which is assumed to include foraging, territory defense, or other activities. Foraging rate included only trips away from the box with intervals >12 s and <3600 s (1 h). If parents did not enter the nest box for a period longer than 12 s, then they were assumed to be foraging, whereas trips longer than 3600 s were rare (0.41%). Trip duration was analyzed using the mean time interval between nest visits for each individual.

Linear mixed-effects models were used to determine whether there were differences in foraging rate and trip duration between nest-box visits for individual birds at agricultural versus grassland site types and the main factors that could influence these responses. Foraging rate and trip duration data were square-root transformed prior to analysis to improve normality. Global models included fixed effects of site type, daily insect biomass, brood size, nestling age, sex, and the interaction between site type and sex. An interaction between site type and insect biomass was also tested, but nonsignificant interaction terms were removed. The models all included a hierarchical random effect of nest-box identity nested within site to account for the structure of the data set where male and female pairs sampled within each of the five study sites are likely to be more similar in their responses. Modelling was done in R version 3.0.3 (R Core Team 2014) using the lme function of the nlme package (Pinheiro et al. 2015), and model selection was determined by lowest AIC_c (Akaike's information criterion corrected for small sample size) scores, model weights, and deviance scores (Supplementary Table S1),[1] following Burnham and Anderson (2002).
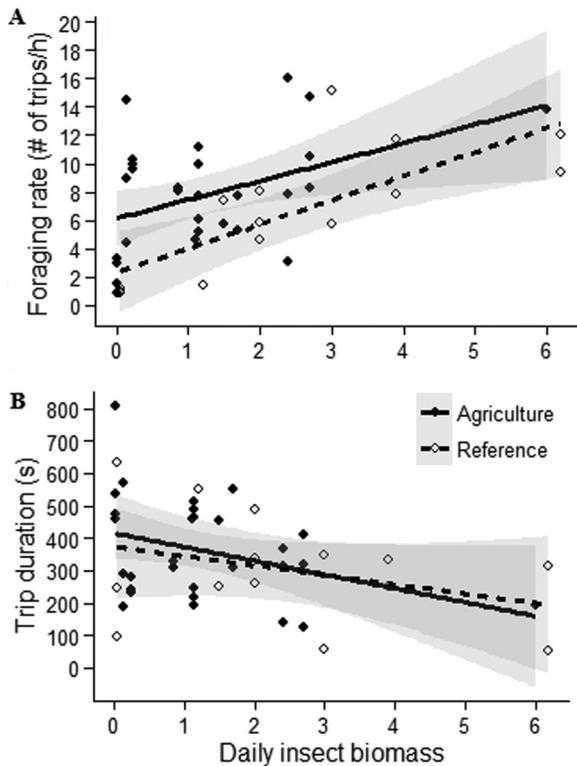
Results

Foraging rate and duration between site types

Birds on grassland sites had a mean (±SE) foraging rate of 6.6 ± 1.2 trips/h compared with birds on agricultural sites with 7.8 ± 0.7 trips/h. The best-supported model for foraging rate incorporated effects of site type, insect biomass index, and nestling age (Table 2). Model-based parameter estimates indicated more frequent foraging rates with higher insect biomass (Fig. 1A; $\beta = 18.3 \pm 7.03$, $p = 0.02$). Foraging rate also increased for nest boxes with older

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Fig. 1. Relationship between Tree Swallow (*Tachycineta bicolor*) foraging rate (A) and trip duration (B) with wind-corrected insect biomass index measured at five agricultural (solid line, solid symbols) and grassland (broken line, open symbols) sites in south-central Saskatchewan in 2014. Lines indicate best-fit linear trends with 95% confidence intervals (shaded areas).

tances or longer time periods to locate sufficient or desired prey. Britschgi et al. (2006) similarly observed that adult Whinchats (*Saxicola rubetra* (L., 1758)) exhibited comparable nestling feeding rates between intensively farmed landscapes and traditionally managed grassland, but that birds in the intensive landscape foraged over longer distances.

Differences in habitat characteristics, including access to water, natural areas, vegetated buffers, or trees, across the site types may have influenced access to suitable insect prey. The grassland sites had more pasture and herbaceous cover than the agricultural sites, which may have improved foraging opportunities. The presence of hills and valleys at the grassland sites, compared with the much flatter agricultural sites, may have also contributed to the differences in foraging strategy. Tree Swallows often forage in areas that are sheltered from the wind where insects gather (McCarty and Winkler 1999). If insects tend to congregate in low areas between hills or in areas of dense natural vegetation, then it may be easier for Tree Swallows on grassland sites to find and collect prey, reducing lengths of foraging trips. Agricultural sites had higher concentrations and frequency of detections of neonicotinoid insecticides in the wetlands. Heavier agricultural pesticide use may have reduced overall prey biomass and availability given Tree Swallows eat mostly insects of aquatic origin (Quinney and Ankney 1985; McCarty and Winkler 1999). In addition, the grassland sites, on average, had more trees, possibly creating profitable foraging opportunities for Tree Swallows in nearby areas where insects gather to avoid wind.
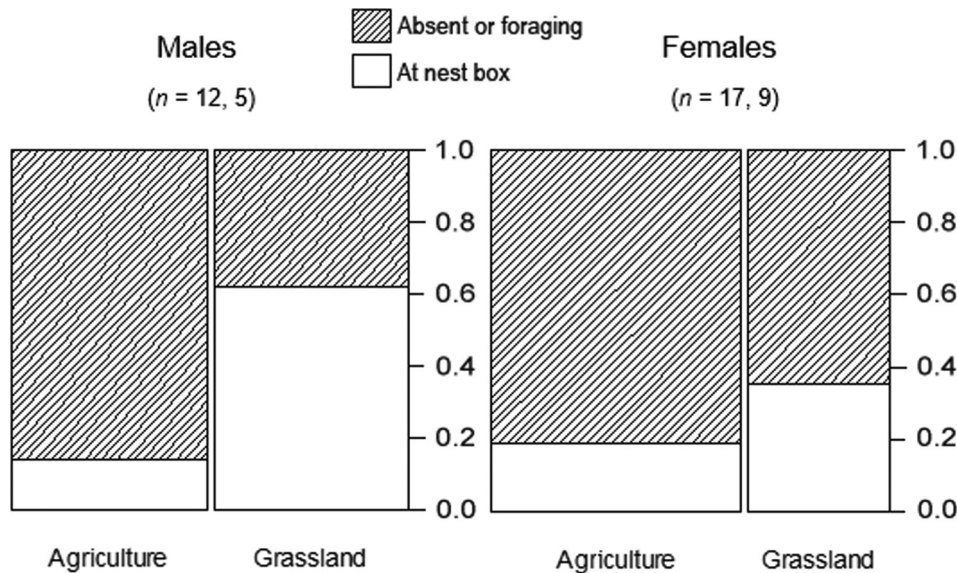
Although equal feeding rates between the sexes have been reported in some systems (Quinney 1986; Dunn and Robertson 1992), Tree Swallows generally show female-biased parental care, which is often related to quality of foraging conditions. Our results suggested that the sexes were behaving differently. In particular, males generally spent more time away from the nest at agricultural sites, possibly foraging, compared with males at grassland sites who more frequently remained at or near the nest box. Males appear more sensitive to reductions in prey at agricultural sites and increased time spent away from the nest may have been due to the greater need to feed themselves rather than engage in nest attendance activities. This may suggest that grassland sites have sufficient resources to support optimal maintenance of both adults and nestlings.

Previous studies (Jones 1988; Bryant and Tatner 1991) have suggested that the positive relationship between feeding rates and prey availability may not be based solely upon higher foraging success and associated lower foraging costs. Schifferli et al. (2014) found that adult Barn Swallows increased their nestling provisioning rate when foraging conditions were favourable, and reduced it when conditions were poor. Under favourable conditions, parents probably increase their own food intake and forage more intensively and efficiently. This type of strategy may have evolved in response to the short-term fluctuations in food availability due to changes in weather that Tree Swallows commonly experience (Gruebler et al. 2008).

Birds at agricultural sites may be optimizing their own energy expenditure by reducing parental care in response to lower food availability. Consistent with this hypothesis, we found longer trip durations with lower insect biomass. Nestling Tree Swallows raised on our grassland sites also had higher body condition than those on the agricultural sites (Michelson 2016). Adult Tree Swallows breeding on agricultural sites may not be compensating for lower food availability, but rather pass on these costs to their nestlings. Indeed, Red-backed Shrikes (*Lanius collurio* L., 1758) produced similar brood sizes in agriculturally intensive and low-intensity landscapes, but nestlings and adults weighed less and parents increased foraging times in the intensive landscape (Leugger-Eggimann 1997).

Our main findings suggest that subtle differences in prey availability, quality, or composition produce shifts in parental forag-

nestlings ($\beta = 0.13 \pm 0.04$, $p = 0.001$) and was higher on agricultural sites than on grassland sites ($\beta = 0.66 \pm 0.21$, $p = 0.050$).

When examining trip duration, males on agricultural sites spent 14% of their time at or near the nest box compared with 62% for grassland males (Fig. 2); agricultural females spent 19% of the time at the nest box compared with 36% for grassland females (Fig. 2). The best-approximating model for trip duration included fixed effects of site type, sex, insect biomass index, and an interaction between site type and sex (Table 2). Males had shorter mean trip durations than females ($\beta = -5.06 \pm 2.24$, $p = 0.048$). Model-predicted least-squares mean (±SE) trip durations were 364 ± 2.8 and 197 ± 4.2 s for females and males at grassland sites, respectively, and 312 ± 1.6 and 367 ± 2.1 s for females and males at agricultural sites, respectively. Trip duration was also negatively associated with insect biomass index (Fig. 1B; $\beta = -99.5 \pm 43.5$, $p = 0.03$), suggesting reduced insect availability increased the time spent away from the nest to presumably forage.

Discussion

Our approach for assessing foraging behaviour of Tree Swallows using RFID technology successfully recorded more frequent visits to the nest (i.e., feeding trips) and shorter absences during periods of higher prey availability, with tagged birds responding positively to prey biomass and increasing their provisioning of nestlings when food conditions were favourable. The increase in foraging rate with higher prey biomass was most pronounced in birds inhabiting grassland sites, whereas responses at agricultural sites were somewhat dampened. Although agricultural sites had slightly higher mean foraging rates, the trip duration indicated breeding Tree Swallows, particularly males, at agricultural sites spent more time away from the nest, possibly foraging over greater dis-

Fig. 2. Proportion of time spent at the nest box (duration ≤12 s) or absent or foraging (duration >12 s) for male and female Tree Swallows (*Tachycineta bicolor*) on agricultural and grassland sites in south-central Saskatchewan in 2014. Sample size is shown in parenthesis (*n* = agriculture, grassland).

ing behaviour. Additional work is required to more completely understand the indirect effects of intensive agricultural practices on food quality and quantity, and how this may influence aerial insectivores. Subtle indirect habitat effects are often overlooked when assessing threats to aerial insectivore and grassland bird populations, but incorporating these considerations into agricultural management strategies may provide a promising approach for conservation of birds associated with farmland habitats.

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