

Indirect effects of agricultural intensification on tree swallow (*Tachycineta bicolor*) foraging behaviour, body condition, and physiology

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ABSTRACT

Throughout North America, many species of aerial insectivorous birds – birds that capture flying insects – have exhibited sharp declines, with tree swallows (*Tachycineta bicolor*) experiencing a 2.8% annual decline in Canada since 1989. The timing of these declines coincides with major changes in agriculture, perhaps signaling a potential causal link. Declines may be influenced indirectly by agriculturally-driven reductions in the abundance of the swallow's main diet of aerial insects through increased agrochemical use, wetland drainage and cropping intensity. My objectives were to determine how aerial insect abundance and biomass vary across an agricultural landscape in the Canadian Prairies, and determine how breeding tree swallows respond in terms of (i) foraging behaviours and return rates, (ii) body condition, and (iii) selected physiological responses (i.e. oxidative stress and feather corticosterone). Artificial nest-boxes were erected at each of 5 sites with varying levels of agricultural intensification in south-central Saskatchewan, 2012-2014. Insect abundance and biomass were monitored daily using passive aerial samplers at each of the sites throughout the breeding season. Tree swallows adults (n = 596) and nestlings (n = 1107) from each nest were captured, banded, measured and blood and feather sampled to determine condition and physiological status. In 2014, radio frequency identification (RFID) technology was employed at a subset of nest-boxes to determine adult foraging rates and durations.

Despite strong differences in land use characteristics among sites, insect abundance and biomass varied by year but were similar between heavily cropped and grassland reference sites. Regardless, birds responded to temporal changes in prey abundance and differences were found in measurements of foraging behavior and physiological measures of oxidative stress. Adult foraging rate (number of nest visits/hour) was primarily influenced by wind and nestling age, but

was also positively related to daily insect biomass. Foraging intervals (i.e., length of time spent on each trip) differed between agricultural intensities; birds on agricultural sites spent more time away from the nest box, presumably foraging, suggesting reduced nest attentiveness. Return rates were primarily predicted by body condition and brood size from the previous breeding season, but were also higher on grassland sites, suggesting that agricultural sites may be less favorable. Older adults (based on banding records) and females displayed a higher body condition than did younger individuals and males, respectively. Measures of physiology (i.e. total antioxidant counts and oxidative damage) in both adult and nestling swallows were primarily driven by temporal changes in insect biomass and abundance. Similarly, adult body mass and physiology were related to local insect availability, but not land use (agriculture/grassland). Measures of nestling feather corticosterone were unrelated to any of the explanatory variables. These results provide valuable information pertaining to components of individual quality, foraging behaviour, and return status in response to prey availability under differing agricultural land use regimes, which may help to inform conservation strategies for a variety of insectivorous bird species of conservation concern.

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DEDICATION

I'd like to dedicate this thesis, and all the work that went into it, to my dad, Jeff Stanton, who passed away when I was only a year into my graduate program. He was always extremely proud of me, and was so excited about the research I had the opportunity to be involved in here; I wish he had been able to see its completion. One day, Pops, I'll try to conduct some research on the hummingbirds that you loved so much, in an effort to answer your never-ending questions.

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Chapter 1

Role of Agriculture in Individual and Population Declines of Birds: A Review

1.1 History of agricultural intensification and links to avian declines

There have been many changes in farmland management and operations worldwide over the last few decades, and these changes have affected a variety of wildlife species that depend upon farmland habitat. There has been a shift from diverse mixed-farming systems containing both pasture and arable land, to farms that specialize in one or the other, leading to decreases in habitat heterogeneity (Benton et al. 2003; Ghilain and Belisle 2008). Crop management has changed significantly, as traditional crop rotation cycles have been shortened since the 1970s with the introduction of agrochemicals (Fuller et al. 1995). Other changes include loss of natural habitat (i.e. hedgerows and wetlands), increased mechanization, and changes in the timing of farming activities, with a marked reduction in spring sowing of cereals, as well as earlier planting and harvesting (O'Connor & Shrubbs 1986; Stoate 1996; Chamberlain et al. 2000). These changes in farming practices can be collectively referred to as agricultural intensification, which is defined as “increased production of agricultural commodities per unit area” (Donald et al. 2001).

Globally, large scale changes in agricultural practices began around 1971, coinciding with periods of major avian declines. Data from the Common Bird Census in England and Wales from 1962 to 1996 show that major farmland bird declines began around 1977 (Chamberlain et al. 2000), while Siriwardena et al. (1998) demonstrated that many UK species exhibit noticeable declines from 1974-1976. From the 1960's to 1990's in the UK, farmland bird species experienced a greater reduction in distribution than avian species associated with any other habitat, with 86% (n = 28 species) of farmland species exhibiting reduced distributions and 83%

(n = 18) experiencing declines in abundance; population declines greater than 50% were estimated in seven of these species (Fuller et al. 1995). A follow-up analysis by Donald et al. (2006) demonstrated that this declining trend continued until 2000. Similar trends have been reported for many North American grassland (farmland) birds, which have been experiencing declining populations across the continent for decades (Brennan and Kuvlesky 2005), and with over 75% of grassland birds in mid-continent North America experiencing dramatic declines (average of -1.4% per year) between the years 1966 to 1993 (Herkert 1995). In Canada specifically, 16 of 21 (76%) grassland bird species experienced declines between 1969 and 1998 (Dunn 1998). The temporal overlap between avian declines and intensification of agriculture may signal a causal link.

Studies by the North American Breeding Bird Survey (BBS) determined that grassland birds are experiencing faster declines than birds associated with any other biome (Sauer et al. 2000; Murphy 2003). This pattern of long-term decline is rare in avian species of other habitats, suggesting environment-driven effects as a probable cause (Donald et al. 2006). Other hypotheses for potential causes of farmland and grassland bird declines include climate change, disease, and predation. However, when considering that declines are primarily and most strongly seen in farmland birds, it seems implausible that any of these factors would affect species more strongly in one habitat (Fuller et al. 1995). Habitat loss on the wintering grounds has also been suggested as a contributor to declines (Brooks and Temple 1990; Basili 1997), but few studies have looked into this potential factor (Herkert and Knopf 1998; Vickery et al. 2000). It is also important to acknowledge that there are a few farmland species, most notably corvids, that appear to benefit from increased agriculture (Gregory and Marchant 1996; Barnett et al. 2004).

Some of the most convincing support for a causal link between agricultural intensification and avian declines are results of experiments involving the reversal of intensification through stewardship schemes that promote the farmer's use of environmentally beneficial land management plans (Peach et al. 2001). This process seems to promote a rapid recovery of avian populations that had been in decline during earlier intensification (Aebischer et al. 2000). For example, species that were of high conservation concern, such as the grey partridge (*Perdix perdix*), yellowhammer (*Emberiza citrinella*), tree sparrow (*Spizella arborea*), yellow wagtail (*Motacilla flava*), and others, experienced an average population increase of 30% following 4 years of crop diversification and lowering of pesticide inputs on commercial farmland in the UK (Henderson et al. 2009). The extent of avian declines in individual European countries is also correlated with each country's degree of agricultural intensification (Donald et al. 2001).

1.2 Causal mechanisms for the influence of agricultural intensification on avian populations

The proposed associations between agricultural intensification and avian declines include direct mortality through interference with farming equipment (Crick et al. 1994; Green 1995) and pesticide poisoning (Mineau and Whiteside 2006), as well as indirect effects through loss of nesting habitat (Wilson et al. 1997; Chamberlain et al. 1999) and reduced prey availability (Attwood 2008; Brickle et al. 2000; Campbell et al. 1997; Evans et al. 2007; Potts 1986). Direct mortality from machinery and pesticides typically shows clear negative effects on birds that are immediate and localized. A classic example is the mass mortality of wintering Swainson's hawks (*Buteo swainsoni*) in 1995-96 following agricultural applications of monochrotophos insecticides in Argentina. The pesticide killed thousands of hawks in at least 17/19 mortality incidents which

had a severe negative effect on the population (Goldstein et al. 1999). Indirect effects such as reductions in food supply or sublethal pesticide effects on individuals are inherently much more difficult to quantify. Indirect mechanisms are often subtle, complex and interacting such that effects on birds may be difficult to attribute to agricultural practices. Additionally, a delay in birds' responses to changes in agricultural practices would be expected, as it may take one or more breeding seasons for the indirect effects to be manifested on individual survival and recruitment leading to declines at the population level (Chamberlain et al. 2000

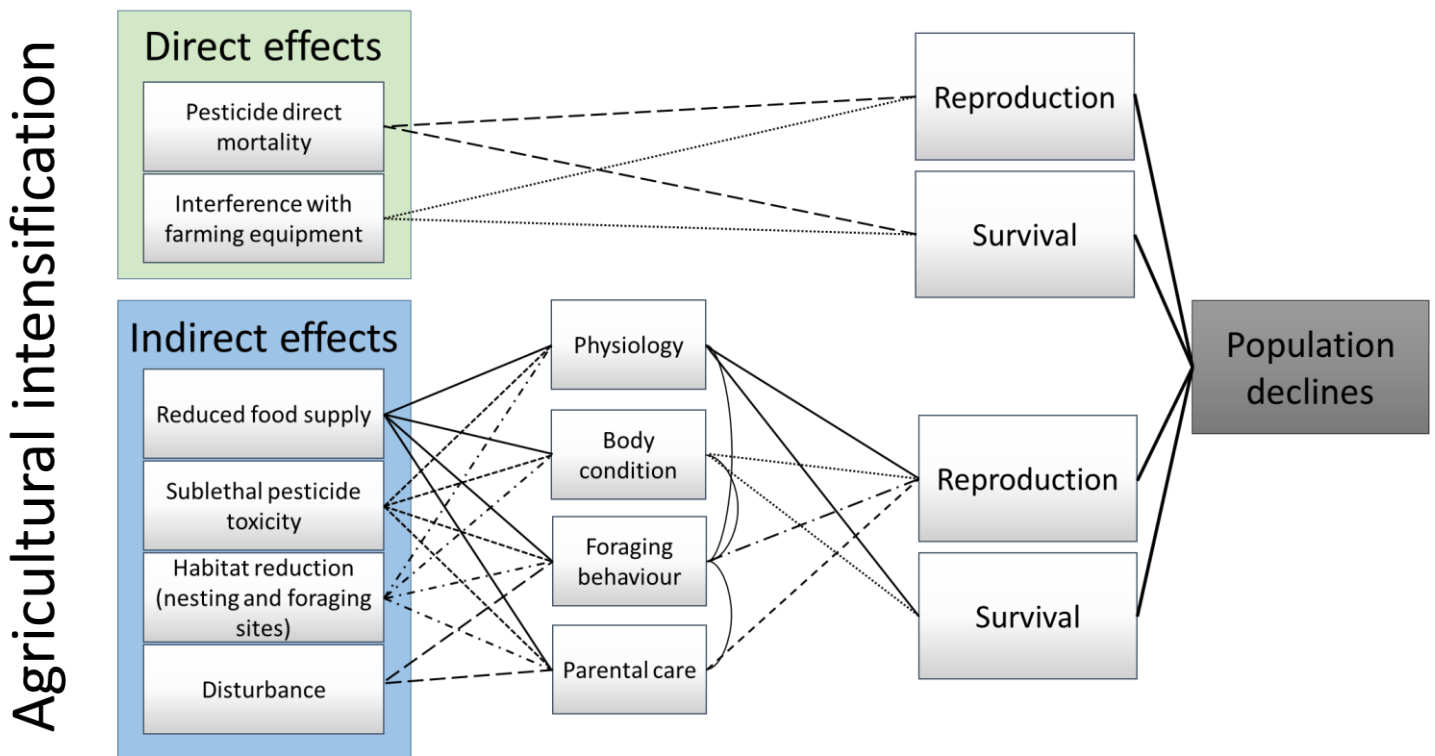


Figure 1.1: Flowchart demonstrating possible direct and indirect effect pathways of agricultural intensification on avian population declines.

1.3 Indirect effects on food supply and diet composition

A reduction in food supply and changes in insect community composition from agricultural intensification are important factors in determining indirect causes of avian declines

(Attwood et al. 2008). Aerial insectivores, which consist of several farmland bird species, including tree swallows, are often considered to be the most steeply declining avian guild in industrialized nations, with strong declines seen in both Europe and North America (Benton et al. 2002; Nebel et al. 2010); it is speculated that insectivory, the common trait of an otherwise ecologically diverse group, and the associated widespread declines in insect abundance, may underpin the common declines across this diverse guild (Nebel et al. 2010; Nocera et al. 2012).

Arthropod abundance decreases as agriculture becomes more intensive (Benton et al. 2002; Gruebler et al. 2008). A meta-analysis by Attwood et al. (2008) determined that arthropod species richness was greater in areas of less intensive agriculture, and richness was significantly greater in native vegetation relative to agricultural land of any intensity, with conventional cropping displaying the lowest richness. The negative relationship between arthropod richness and agricultural intensity was evident across a variety of regions, biomes, and management systems.

Field margins and hedgerows are important habitats for arthropods in an agricultural landscape, as they contain high insect diversity (Mineau and McLaughlin 1996; Wilson et al. 1999). Studies in Europe and North America have demonstrated that areas of vegetation adjacent to cropland can provide essential food and habitat to a variety of insects (Dennis and Fry 1992; Thomas and Wratten 1988). Likewise, Gruebler et al. (2008) determined that aerial insect abundance was higher in areas with trees, hedgerows, and native grassland as compared to areas of cereal crop or arable land (without cereal, root crops, potatoes, or maize). These natural areas are also important for over winter survival of dormant insects, which will determine spring densities, as many insects are unable to survive northern winters in open cropland (Doane 1981).

With increased use and changes in application of pesticides being one of the more recent principal modifications in agriculture, its role in avian declines may have been underrepresented. Although rarely included in ecological risk assessments, there has been growing concern for the potential impact of indirect effects of pesticides on insectivores through food supply reductions (Boatman et al. 2004; Goulson 2014; Sotherland and Holland 2002). In a recent analysis of farmland birds in the Netherlands, Hallman et al. (2014) reported stronger declines of bird populations in areas with higher surface water contamination of imidacloprid (neonicotinoid) insecticides even after controlling for other agricultural land use effects. Even with minute residues of 20 ng/L in surface waters, the authors report average bird declines of 3.5% per year. Similar results from an analysis conducted in the United States by Mineau and Whiteside (2013) suggest that insecticide use provided stronger empirical support for avian declines than the more commonly considered case of agriculturally mediated habitat loss.

The mixedwood plains and prairie ecozones of Canada are hotspots for imperilled species, believed to be due to extensive conversion of native land to agriculture or human settlement. However, Gibbs et al. (2009) determined that species loss is actually more significantly correlated to pesticide use than to agricultural area or human land conversion alone. Likewise, a study investigating 13 components of agricultural intensification found that the use of pesticides, and most notably insecticides and fungicides, resulted in the most consistent negative impacts on species diversity of plants, carabids, and ground-nesting farmland birds (Geiger et al. 2010). Additionally, a study comparing avian grassland declines in the UK versus Denmark found that the decline was much less severe in Denmark, with a notable difference between the habitats being a gradual reduction in agrochemical inputs in the latter (Fox 2004).

Pesticide use has significant effects on both biomass and abundance of a variety of arthropod species, and abundance of aerial invertebrates is 3 times greater in pasture than cereal fields (Evans et al. 2007). Fields treated with insecticides during the avian breeding season have produced significantly lower biomass and abundance of invertebrates relative to untreated fields (Morris et al. 2005). A study investigating yellowhammer (*Emberiza citronella*) chick food supply indicated that fields treated with summer insecticides exhibited decreased abundance of invertebrates compared to those that were treated in winter or left untreated, and counts of available arthropod prey per sample point were further reduced in fields that had been sprayed within the last 20 days (Hart et al. 2006). Common chick food items for corn buntings (*Miliaria calandra*) have also been shown to be negatively correlated with the number of insecticide applications (Brickle et al. 2000).

One order of insects that has been widely studied in terms of their abundance on agricultural systems is the Diptera (true flies). This order comprises 62.5% of the food provided to insectivorous tree swallow nestlings in some regions (Rioux Paquette et al. 2013) and 16-75% of the adult diet (Winkler et al. 2011), and are fundamental to the diet of an array of other wildlife, including waterfowl, wetland birds, fish, amphibians, reptiles, and mammals (Murkin and Batt 1987). Rioux Paquette et al. (2013) reported that dipteran abundance, though not biomass, is negatively influenced by the proportion of intensive agriculture within 500 meters of the sampling point. Dipteran abundance was almost twice as high in fields that did not receive insecticides during the swallow breeding season as those that did, and furthermore, in fields without insecticides, dipteran abundance was positively correlated with the presence of nearby rivers or ditches (Morris et al. 2005). This is an important interaction, as numerous agricultural areas are simultaneously experiencing long-term surface water degradation from agrochemical

use and loss from drainage (e.g. Saskatchewan, Canada).

The abundance and biomass of aerial insect prey will vary throughout the breeding season, due to natural changes in temperature and precipitation which drive emergence patterns. Agricultural practices are known to exacerbate or alter the natural emergence and availability of insect prey throughout this period. For example, Rioux Paquette et al. (2013), found dipteran abundance in early spring to be similar across all sites regardless of agricultural intensity, but as the season progressed, the differences in dipteran abundance and biomass between sites increased, with the more agriculturally intensive sites displaying reduced abundance by the end of July. The timing of this effect may be more critical towards the end of the breeding period, when nestlings are getting older and require a higher daily food intake (McCarty and Winkler 1999a).

1.4 Impacts of reduced prey on foraging behaviour in birds

Aerial insectivores as a guild depend upon consistently high levels of flying insect prey availability to maintain physiological and demographic norms (Bryant 1973), and a decline in insects results in reduced parental care, longer or more frequent absences from the nest-box and, in some cases, altered foraging strategies to locations that are more distant from the nest, but also more reliable (Winkler et al. 2013). In corn buntings (*Emberiza calandra*) chick weight is negatively correlated with parental foraging duration (Brickle et al. 2000), suggesting that the longer the parents are away from the nest collecting prey items, the less food the nestlings will receive.

In insectivorous birds that reside on farmland, typical foraging sites include areas with shorter, low density vegetation, presumably to enhance detection of predators, or areas of high vegetation density if invertebrate abundance is high (Atkinson et al. 2004; Dunn et al. 2010). The

presence of areas such as field margins or tractor tramlines also alter foraging regimes, as these are preferentially selected over cropped land by foraging insectivores (Douglas et al. 2010; Perkins et al. 2002). For example, tree swallows specifically prefer to forage in areas sheltered from the wind where aerial insects will accumulate, such as behind hedgerows (McCarty and Winkler 1999a). Barn swallows (*Hirundo rustica*) are more commonly found foraging at higher densities over areas of pasture than over cereal fields, following the parallel patterns of insect abundances in these habitats (Evans et al. 2007).

Increasing the foraging intensity in resource-poor environments such as agricultural areas may impact both adult and nestling fitness. Barn swallows were found to reduce the energy provided to their nestlings in poor foraging conditions by lowering the feeding rate to the nest (Turner 2006). Increased foraging effort may result in short-term nestling starvation or reductions in clutch or brood size, as well as long-term through reduced survival and fecundity, decreased growth rate, and reduced overwinter survival of both adults and juveniles (Holmes 1995; Siriwardena et al. 2000).

Often the effect of reduced food supply may be more pronounced for parents than nestlings, as parents will sometimes compensate for the sparse supply by altering their foraging strategy in order to maintain chick growth and survival. This phenomenon has been seen in adult blue tits (*Cyanistes caeruleus*) that selectively forage for larger prey items to feed their young when foraging in a resource poor habitat, in order to maintain the same total insect biomass that would be provided in a richer environment (Tremblay et al. 2005). Also, red-backed shrikes (*Lanius collurio*) were able to produce the same clutch sizes in agriculturally intensive landscapes as in low-intensity areas, but nestlings and parents weighed less and parents increased foraging times in the intensive landscape (Leugger-Eggimann 1997).

1.5 Effects of reduced food supply on body condition, reproduction, and survival

Potential responses of parents to changes in foraging conditions include alterations in foraging effort and feeding behavior (Jones 1988; Turner 2006), reductions in body mass (Jones 1987, 1988), and changes in metabolic rate (Speakman et al. 2003; Wiersma et al. 2005). The availability of food resources is one of the most important factors influencing body condition and reproductive success in birds (Lack 1954; Immelmann 1971). Measurements of adult body mass and condition are considered to be important traits through their impacts on components of fitness, such as survival and reproductive success (Blums et al. 2002; Møller and Szep 2002).

Tree swallow clutch size is negatively correlated with agricultural intensification and reduced prey availability (Dunn and Hannon 1992; Dunn et al. 2000; Ghilain and Belisle 2008), and the presence of extensive agriculture (i.e., more pasture and hayfields) increased the probability of fledging in tree swallows (Ghilain and Belisle 2008). More specifically, food abundance during the laying period has the largest influence on reproductive success in female swallows (Dunn and Hannon 1992) and explains 85% of the variation in mean clutch size (Hussell and Quinney 1987).

Food supply is typically considered to be the most vital factor influencing nestling growth, and indeed swallow growth rates are positively associated with insect availability (Ardia 2006; McCarty and Winkler 1999b; Whittingham et al. 2007). This same effect is apparent in yellowhammers, where nestlings had reduced growth and body condition on agricultural sites, linked to the use of pesticides and associated decrease in prey availability (Hart et al. 2006; Morris et al. 2005). Considerable effects have been seen in swallow nestlings that were experimentally food-deprived, with these nestlings exhibiting significantly smaller morphometrics and slower growth rates for wing and tail feathers (Hovorka and Robinson,

2000). Whittingham et al. (2007) also found that nestlings that had experienced more rapid early growth rates displayed better immune function later in the nestling period, which is important on a population scale, as immunity serves as a marker of nestling survival and resistance to disease in altricial birds (Lochmiller et al. 1993).

A reduction in food availability may also reduce survival (Payne and Wilson 1999; Peach et al. 1999; Vickery et al. 2001), with starvation being a central cause of mortality in both adults and nestlings (Lombardo 1986; McCarty 1995; Robertson et al. 1992). Often there is a delay in the effects of diminished food supply, with changes in bird populations being detected in the year following reduced arthropod abundances. This temporal gap would be expected if food availability impacted populations through effects on breeding success or post-breeding and overwinter survival (Benton et al. 2002).

1.6 Effects of reduced food supply on physiology through oxidative stress and corticosterone

One of the important costs associated with increased foraging and flight activity in response to food shortage is the acceleration of oxygen metabolism (Leeuwenburgh & Heinecke 2001; Monaghan et al. 2009). Reactive oxygen species (ROS) are generated as by-products of oxygen consumption (Finkel & Holbrook 2000; Balaban et al. 2005) and have the potential to damage biological macromolecules through the process of oxidative stress (Beckman & Ames 1998; Perez-Campo et al. 1998), which arises when an organism experiences an imbalance of antioxidants and pro-oxidants. An accumulation of oxidative damage over a period of time, along with the associated trade-offs required for the allocation of resources to the antioxidant system (Monaghan et al. 2009; Nussey et al. 2009), may potentially have an effect on life history

characteristics and accelerate the aging process and development of degenerative diseases (Beckman and Ames 1998; Finkel and Holbrook 2000; Furness and Speakman 2008).

A reduction in food supplies in agricultural habitats may also affect organisms' oxidative stress levels in a variety of ways, including direct stress on metabolic organs caused by poor nutrition (Robinson et al. 1997; Morales et al. 2004), increased metabolic activity associated with increased foraging effort (Loft et al. 1994), and a possible psychological effect from food insecurity (Møller et al. 1996). Food reduction or a lack of high quality prey can also affect oxidative stress by influencing diet-derived antioxidants, which play a considerable role in the overall antioxidant system (Vertuani et al. 2004; Catani et al. 2008). Different invertebrate food sources contain varying amounts of dietary antioxidants, and in wild birds circulating levels of exogenously-derived antioxidants are positively correlated with the levels of antioxidants in their diet (Cohen et al. 2009).

A poorer quality habitat, such as an intensively cropped area with lower food quantity and quality, can lead to increased foraging rates and durations for adults, which results in increased oxygen consumption and an elevated generation of ROS (van de Crommenacker et al. 2011). Experimental manipulations with captive animals have demonstrated a positive correlation between oxidative stress and physical activity (Magwere et al. 2006; Larcombe et al. 2008; Monaghan et al. 2009), while greater flight effort in insects and birds increases oxidative stress levels (Costantini et al. 2007; Costantini et al. 2008; Williams et al. 2008). Costantini et al. (2008) found that homing pigeons (*Columba livia*) that flew for 200 km (versus 60 km) had a 54% increase in oxidative damage and a 19% decrease in total antioxidants, which results in an overall 86% increase in oxidative stress. The effects of increased oxidant production from higher foraging effort coupled with a decrease in exogenously-derived antioxidants may result in

serious consequences for birds breeding in poor quality agricultural habitats that lack preferred prey.

Another method of looking at the physiological effects of reduced prey availability in birds is through the measure of glucocorticoid (GC) hormones, the primary of which in birds is corticosterone, or CORT. Many species counteract unpredictable stimuli in their environment via a stress response, which is a collection of physiological, hormonal, and behavioural changes that allow the animal to cope with disturbances (Romero et al. 2004). A variety of disturbances, including sudden changes in weather patterns or famine, may lead to a response and activation of the hypothalamus–pituitary–adrenal (HPA) cortex axis from which the GCs are released (Astheimer et al. 1995; Romero 2000). Acute elevation of GCs can assist an organism in avoiding prolonged stress by producing a variety of behavioural and metabolic responses that suspend activities that are not essential for immediate survival and stimulating those that are – such as deactivation of territorial behaviour, activation of locomotion to aid in leaving the area of disturbance, and mobilization of stored energy reserves (Wingfield et al. 1998).

Food restriction has a direct relationship with secretion of GCs in both laboratory settings and wild birds (Marra and Holberton 1998; Kitaysky et al. 1999; Lynn et al. 2003; Clinchy et al. 2004), and prolonged periods of limited food resources can reduce body mass via depletion of fat and protein reserves for fuelling gluconeogenesis (Wingfield 2003). Long-term elevation of CORT during prenatal development in mammals results in suppression of memory and immune system function and can cause neuronal cell death (Wingfield 1994; Sapolsky et al. 2000). In birds, elevated CORT during egg laying and incubation impairs hatching and fledging success (Kitaysky et al. 2007). Increased CORT levels have also been correlated with reduced feeding rates, and reductions in time spent brooding and guarding chicks (Wingfield et al. 1983;

Wingfield and Ramenofsky 1997; Robin et al. 1998). This may in turn cause negative effects on nestling body condition and survival, as there is a correlation between parental circulating CORT and nestling body mass (Jenni-Eiermann et al. 2008).

Higher CORT levels during early development can have important consequences for later in life. For example, tree swallow nestlings with experimentally-elevated CORT were lighter, and had shorter wings, 9th primary feathers, and head-bill measurements, while nestlings with lower CORT levels experienced higher fledging success (Fairhurst et al. 2013). CORT levels in nestlings can also have important effects on phenotypes, including immunocompetence and growth rates (Dufty et al. 2002; Kitaysky et al. 2003; Butler et al. 2010), as well as recruitment and survival (Blas et al. 2007). While many studies have used CORT levels in the plasma as an indicator of physiological condition, recently the merit of feather corticosterone has also been demonstrated. CORT in feathers has been shown to be correlated with stress-induced plasma CORT, and measurements in feathers allows for an integrated response of CORT over the period of feather growth (Bortolotti et al. 2008).

1.7 Tree Swallows as model study organisms in agricultural landscapes

Tree swallows are the most widely distributed species of their genus, with breeding ranges extending from northern Canada and Alaska to the southern United States. Swallows typically arrive at breeding grounds in south-central Saskatchewan during mid to late April, and then depart for wintering grounds in the southern United States and Central America soon after the end of breeding (July to August). Swallows are secondary cavity nesters (i.e. cavities are occupied after use by primary excavators like woodpeckers). While capable of foraging up to 10 km away from nest sites (Dunn and Whittingham 2005), adults tend to forage within a few

hundred meters of the nest during the period from egg-laying to fledging (Winkler et al. 2011). Tree swallows are “income” breeders, meaning they produce eggs based on current foraging intake, rather than relying on stored nutrients (Winkler and Allen 1996). Their diet consists primarily of Diptera (true flies), Odonata (dragonflies and damselflies), Ephemeroptera (mayflies), and Trichoptera (caddisflies). During peak nestling demand, adults can feed nestlings up to 6000-7000 insects per day (Winkler et al. 2011).

Tree swallows are considered model organisms for a variety of studies including those on the effects of agriculture and food supply as they readily occupy artificial nest-boxes, allowing researchers to set population sizes and standardize nest site characteristics (Jones 2003). Swallows can be repeatedly captured and cope with researcher disturbance without high risk of nest abandonment (Ardia et al. 2003; Winkler and Allen 1996). As they typically forage very close to the nest-box, swallows can provide ecological information about prey for a local and known study area (Elliott et al. 2011). Swallows often return to their previous breeding or natal site, and studies in central Canada and north-eastern United States have shown adult and nestling return rates ranging from 13-51% and 0.8-12%, respectively, which can be useful in providing important survival and life history data (Butler 1988).

1.8 General thesis objectives, hypotheses, and predictions

The broad goal of this study is to investigate two primary objectives; the first of which determines whether there a relationship between intensity of agriculture, food supply, and tree swallow foraging behaviour in the agriculturally dominated region of the Canadian prairies. While agriculture has been shown to affect insect prey in previous studies, uniquely this study evaluates the indirect impact on individual foraging responses. The second objective follows

from the first to determine if putative differences in habitat quality and prey availability can be detected through measurements of physiology, adult body condition, and return rates of swallows nesting in areas with different agricultural intensities.

The first objective is addressed in Chapter 2, which highlights the potential relationship between agricultural intensification and abundance and biomass of aerial insects, as well as the potential effects on aspects of foraging behaviour and return rates. Declines of farmland birds may be related to reductions in preferred aerial insect prey, irrespective of habitat loss. This hypothesis makes two key predictions. First, food abundance and biomass should be lower in areas with more intensive agriculture and, second, swallows should alter their foraging strategy to account for differences in food abundance. If habitat quality is reduced on agricultural sites, and therefore swallows have to work harder, this may also result in differences in annual return rates between the site types.

Chapter 3 emphasizes the impacts of potential reductions in food supply and increased flight activity on swallow physiology and adult body condition. I hypothesized that parents foraging at lower quality sites may exhibit an increased absence from the nest, resulting in reductions in parental care, which can influence nestling physiology and survival. If adults compensate for the reduction in prey availability by increasing foraging effort, then adults may incur costs to themselves and/or their nestlings. This can be confirmed through a lower body condition.

If parents are increasing their foraging rate in response to changes in prey abundance, elevated levels of oxidative damage (via higher oxygen consumption from sustained flight) combined with lower levels of exogenously-derived antioxidants may result in higher levels of oxidative stress. Alternatively, adults may not directly reflect depressed food availability, but

rather effects of reduced food abundance or quality may be passed on to their nestlings. This may result in reduced reproductive output, lower nestling body condition, or both, along with elevated oxidative stress and a difference in levels of circulating corticosterone (CORT) in nestlings between sites. Nestlings may also exhibit an increase in CORT even if supplied with sufficient food, simply from longer absences of parents (due to increased foraging time) from the nest-boxes, which leaves nestlings more exposed to the elements (Romero 2000; Wingfield and Kitaysky 2002).

Chapter 2

Tree swallow foraging strategies and return rates in response to agricultural land use and prey availability

2.1 Introduction

Agricultural intensification, which is formally defined as “increased production of agricultural commodities per unit area” (Donald et al. 2001), includes a variety of changes that have occurred to farmland management and operations worldwide over the last several decades. These changes include increased mechanization, shortening of crop rotation cycles with the increasing reliance on agrochemicals, loss of natural habitat such as field margins and wetlands, and decreases in habitat heterogeneity with fewer mixed-farming systems (O'Connor and Shrubbs 1986; Fuller et al. 1995; Stoate 1996; Chamberlain et al. 2000, Benton et al. 2003; Ghilain and Belisle 2008), all of which have the potential to influence a variety of wildlife species that depend upon farmland habitat (Chapter 1).

Globally, large scale changes in agricultural practices began around 1971, coinciding with periods of major avian declines, potentially signalling a causal link. The bird species associated with agricultural habitats, grassland birds, are currently experiencing declines at a faster rate than birds associated with any other biome (Sauer et al. 2000; Murphy 2003). In Canada specifically, 16 of 21 (76%) grassland bird species experienced declines between the years of 1969 to 1998 (Dunn 1998). Likewise, aerial insectivores, a guild that comprises several farmland bird species, are often considered to be the most steeply declining avian guild (Benton et al. 2002; Nebel et al. 2010). This guild includes tree swallows (*Tachycineta bicolor*), whose populations experienced a 2.8% annual decline in Canada during 1989-2009 (Robillard 2012). It is speculated that aerial insectivory, the common trait of an otherwise ecologically diverse group,

and the associated widespread declines in insect abundance, may be the cause (Nebel et al. 2010; Nocera et al. 2012).

Insect abundance decreases as agriculture becomes more intensive (Benton et al. 2002; Gruebler et al. 2008), and aerial insect abundance in particular tends to be higher in areas with trees, hedgerows, and native grassland as compared to areas composed of cereal crop (wheat, barley) or arable land (without cereal, root crops, potatoes, or maize) (Gruebler et al. 2008). Despite this, Mineau and Whiteside (2013) suggested that insecticide use may offer a more plausible explanation for avian declines than the more commonly considered case of habitat loss associated with agricultural intensification. Similarly, a study comparing grassland bird declines in the UK versus Denmark found that the decline was much less severe in Denmark, where a notable reduction in agrochemical inputs was observed (Fox 2004).

One insect order, the Diptera (true flies), are almost twice as abundant in fields that do not receive insecticides during the swallow breeding season as those that do. This order comprises 62.5% of the food provided to tree swallow nestlings in some regions (Rioux Paquette et al. 2013) and 16-75% of the adult swallows' diet (Winkler et al. 2011). Both the adult and larval stages of dipterans are dietary staples for an array of other wildlife, including waterfowl, wetland birds, fish, amphibians, reptiles, and mammals (Murkin and Batt 1987). Additionally, 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 agricultural areas are frequently experiencing long-term degradation and drainage of surface waters (e.g. Saskatchewan, Canada) (Watmough and Schmoll 2007; Bartzen et al. 2010).

Insectivorous birds, such as swallows, depend upon consistently high levels of invertebrate prey availability, and a decline in food supply can result in reduced parental care

from increased absence from the nest, and in some cases, altered foraging strategies to locations that are more distant from the nest, but also more reliable (Winkler et al. 2013). For example, barn swallows (*Hirundo rustica*) will actively forage in vegetated field boundaries rather than in field centers during periods of bad weather (characterized by colder temperatures, higher wind speeds, and higher probability of rain), although this switch from field centers to boundaries is not seen during good weather (Evans et al. 2003). This suggests that any changes in abundance of aerial insects in fields can affect foraging behaviour and energy balance (Norberg 1990). Ultimately, unfavourable conditions may affect the probability of individual birds returning to a site in subsequent years.

While there has been substantial research conducted on links between agricultural intensification and avian declines in Europe (see Fuller et al. 1995; Chamberlain et al. 2000; Donald et al. 2006; Benton et al. 2002; Evans et al. 2007; Vickery et al. 2001; etc.), there have been relatively few studies investigating the potential relationships between agricultural intensification, prey availability, and insectivorous birds in North America. Tree swallows have been recently used as a model insectivore species to study some of these responses in Eastern Canada where cropping regimes and agricultural practices show some clear negative effects on abundance of dipteran insects, nest-box occupancy, clutch size, and adult immune response (see Ghilain and Bélisle, 2008; Robillard et al. 2012; Pigeon et al. 2012; Rioux Paquette et al. 2013). However, swallow populations in Prairie Canada have not yet been studied with respect to agricultural impacts. Given this is Canada's most important crop production region, as well as the most chemically intensive as far as pesticide usage (Brimble et al. 2005), investigations into the threats from agriculture to declining insectivorous birds are strongly warranted. I hypothesize that a reduction of invertebrates may be an important driver in disrupting food webs in

agricultural landscapes - contributing to altered foraging behaviour and decreased return rates in locally breeding birds. This work is an important step in understanding if a causal mechanism exists between prey availability at agricultural sites and the decline of farmland bird populations, particularly in North America where data are lacking.

2.2 Study Sites and Methods

2.2.1 Study sites

Tree swallows breeding in nest-boxes were studied at five sites (n=3 in 2012, n=4 in 2013, n=5 in 2014) in south-central Saskatchewan: Allan (51° 37'14.27"N, 105° 58'14.16"W; 2014 only), Colonsay (52° 1'38.07"N, 105°55'6.22"W), Burr (51°58'15.53"N, 105° 5'58.89"W), Humboldt (52°12'43.87"N, 105°17'25.12"W; 2013 and 2014 only), and St. Denis (52°12'36.32"N, 106° 4'33.60"W). Allan and St. Denis were primarily characterized as grassland (reference) sites, while Colonsay, Burr and Humboldt were agricultural sites which varied in intensity of agricultural influence (Table 2.1). The Colonsay site was relocated a few kilometers south of the original in 2013 and 2014 to avoid interference from house wrens.

Nest boxes were mounted on metal T-posts about 1.5m above the ground, with the entrance hole facing southeast. At each site, nest-boxes (n=30 in 2012 and 2013, n=32 in 2014) were spaced 30 m apart along gravel roads, with alternating Long-Point and Golondrinas style nest boxes at each site; the numbers of each box type changed annually but the relative numbers of each box type was consistent among sites. For detailed descriptions of Long-Point and Golondrinas boxes, see Hussell (2003) and “Golondrinas – Nest Box Design” (2011), respectively. Daily temperature, precipitation, and wind speed were recorded at all sites, as variation in weather affects aerial insect abundance (McCarty 1995; Gruebler et al. 2008; Rioux Paquette et al. 2013; Winkler et al. 2013) and swallow flight and foraging.

2.2.2 Quantifying agricultural intensification through land use and insect abundance

The level of agricultural intensification at all sites was evaluated through measurements such as surrounding crop type, insect abundance and biomass, and land use analysis. ArcGIS was used to quantify the proportions of each land use type at all sites, which included crop, human use (such as roads and buildings), natural (consisting primarily of grass or dried wetlands), trees and shrubs, and standing water. Additionally, water samples were collected in June of each year at 3-5 wetlands per site, and analyzed for total neonicotinoid concentrations using LC-MS/MS at the National Hydrology Research Centre as part of a larger study on neonicotinoid fate and effects on Prairie Wetlands (Main et al. 2014, 2015).

Total wetland area within a 500 m radius of the nest boxes on each site was determined by mapping (on foot) perimeters of all wetlands at each site with a handheld GPS unit during June 2013 and 2014. All wetlands inside this buffer were mapped, as 500 m is a typical maximum distance from the nest-box that parent tree swallows are assumed to forage (McCarty and Winkler 1999a; Winkler et al. 2011). Land use was characterized using aerial photographs for 8-10 agricultural quarter sections per site, depending on layout of the boxes and thus the number of quarters that overlapped with the 500 m buffer around the nest boxes. ArcGIS was used to delineate the different land use types within these areas.

Insects were sampled using an aerial insect passive sampler (3 samplers 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 hours during the swallow breeding season. The insects were then stored in 70% ethanol until counted for abundance, 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 larger than 13 mm (excluding antennae

and ovipositors) were measured and weighed separately, and excluded from analysis, as insects above this size are considered rare in a tree swallow's diet (Quinney & Ankney 1985; McCarty and Winkler 1999a).

Prior to analysis, all data were first thoroughly examined and plotted to look for errors or unusual patterns, and tested for normality. Land use data collected in ArcGIS were analyzed with a multivariate analysis of variance (MANOVA), with the land use types and total neonicotinoid insecticide concentrations (sum of acetamiprid, imidacloprid, clothianidin and thiamethoxam) as the response variables, and site type (agricultural or grassland) as the explanatory variable to determine if the pre-selected sites types differ in agricultural land use.

Insect biomass was adjusted for sampling duration and average wind speed during the sampling period to derive a biomass index. Abundance estimates were adjusted for sampling duration only. To determine if there were differences in insect abundance and biomass index between agricultural and grassland site types, the sum of abundance and biomass index across all three passive samplers on each site was used. Insect abundance and biomass were compared across the entire season, as well as matched to the breeding periods. The breeding season was divided into adult capture and nestling sampling periods, based upon inspections of histograms of bird sampling dates. In 2012 and 2013, 97 and 95%, respectively, of the adults were captured during Julian days 160-180 (i.e., days since 1 January). In 2014, the adult period was between days 160-175, accounting for 100% of the adults sampled. In 2012 and 2013, the nestling period was defined as days 175-190, accounting for 98 and 87%, respectively. In 2014, the sampling period was again slightly reduced, ranging from days 175-185, and accounting for 100% of the sampled nestlings.

A linear mixed effects model was used to evaluate whether agricultural and grassland sites differed in terms of insect abundance or biomass indices, and included covariates of date and average temperature and total rainfall for the 48 hours preceding collection. The number of active passive samplers [2 or 3, depending on day] and site identification were included as random effects. Data were log transformed to improve normality. Model results were checked for normality of residuals as well as for patterns of temporal autocorrelation using the `pacf` function in R. Models were run separately for measurements of insect abundance and biomass. Modelling was done in R version 3.0.3 (R Foundation for Statistical Computing 2014) using the `lme` function of the `nlme` package (Pinheiro et al. 2012), and the best model selected by Akaike Information Criterion (AIC), according to Burnham and Anderson (2002).

2.2.3 Swallow population monitoring and capture

Nest building was closely monitored starting in early May to determine the date that the first egg was laid. Nests were observed daily until the clutch was complete and then not checked again until the end of the incubation period (about 12 days). Nests were then checked daily until hatch was completed. The number of eggs that hatched and failed was noted.

Adults were trapped in nest boxes within the first few days of hatch, banded with a metal band (or identified if recapture), and body measurements (wing chord, ninth primary feather, and head-bill lengths, and body mass) taken. 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). Feather and blood samples were collected for all individuals in 2012 and 2013, and a subset of birds in 2014. Blood samples were kept on ice until centrifuged later in the day and then frozen at -80°C. Females were aged as second year or after second year, based on plumage (Hussell 1983a). A body

condition index was established for each adult using the residuals from the regression of mass against the 3 structural measurements for wing, ninth primary, and head-bill lengths such that high residual values indicate better condition, as those birds are heavier for their body size (Schulte-Hostedde et al. 2001).

2.2.4 Foraging behaviour

A randomly-selected sub-sample of adult swallow pairs were monitored through use of radio frequency identification (RFID) technology during the chick-rearing period in 2014 (Bridge and Bonter 2011). This involved temporarily marking both adults at a nest with a unique passive integrated transponder (PIT) by attaching the PIT to the bird's inter-scapular feathers with non-toxic VetBond. A sham RFID antenna made of copper and bronze wire was placed around the nest-box opening at least 24 hours prior to marking to allow swallows to habituate. A subset of swallows was casually observed before and after placement to ensure the use of this technology did not disrupt the typical foraging regime. 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, time and duration of nest visits by each uniquely-tagged male and female, providing information about how often each parent visited the nest and the lengths of absences. The number of nest visits provides a reliable index of food provisioning to nestlings, as swallows have been observed to feed nestlings on 95-98% of their visits to the nest-box (McCarty 2002; Whittingham et al. 2003).

Foraging data were analyzed in two ways: 1) foraging rate, which is the number of nest visits per individual over a fixed time frame (17 hours; 5:00 to 22:00), and 2) foraging interval, which was the time spent foraging between nest box visits. Foraging rate included only trips away from the box with intervals > 12 seconds and < 3600 seconds. Foraging intervals included

all intervals less than 3600 seconds, as periods when the individuals were at the nest-box and not actively foraging are included in this measurement. Foraging rate data were square root transformed prior to analysis to improve normality. Foraging interval was analyzed using all observations (n=8585), as well as using the average interval for each individual, to permit exploration of variable influences. If parents did not enter the nest box for a period longer than 20 seconds, they were assumed to be foraging. General linear mixed effects models (GLMMs) were used to determine whether there were differences in both foraging rate (number of nest visits per hour), and interval between nest-box visits for individual birds at agricultural versus grassland sites. Models included fixed effects such as site type, weather variables, brood size, adult minimum age, box type, body condition, sex, and nestling age, and random effects of nest box ID, site, and date. Modelling was done in R version 3.0.3 (R Foundation for Statistical Computing 2014) using the lme function of the nlme package (Pinheiro et al. 2012), and the best model selected by AIC scores, according to Burnham and Anderson (2002).

2.2.5 Adult swallow return rates

Swallows were monitored through mark-recapture to estimate apparent return rates, defined as the ratio of marked birds that are recaptured on each study site in year $t + 1$ or later relative to the number that were banded in year t . Return rates do not account for recapture failures or permanent dispersal and should not be considered as surrogates for survival. Analysis on the proportion of returning adult individuals was done in relation to characteristics of both the birds (sex, minimum known age, body condition, brood size) and site type using logistic regression.

2.3 Results

2.3.1 Land use and insect abundance and biomass on agricultural and grassland sites

Results from a MANOVA confirmed that the site types (agriculture and grassland sites) differ significantly in agricultural land use intensity (Table 2.1; $F_{1, 21} = 33.4$, $p < 0.0001$). While there was large variation in the total amount of neonicotinoids between wetlands at each site, this was likely related to wetland size and distance from cropland. The main differences between site types were evident in amounts of crop ($t = 11.74$, $p < 0.001$) and neonicotinoids ($t = 2.83$, $p < 0.0001$) which were higher in agricultural sites, while natural land cover ($t = -1.67$, $p < 0.001$), and pasture ($t = -3.25$, $p = 0.005$) were more prevalent on the grassland sites. As the inclusion of neonicotinoids in the analysis reduced the sample size, the MANOVA was repeated without this variable. Results were similar, with land use remaining significantly different between the site types ($F_{1, 44} = 29.2$, $p < 0.0001$), and with an additional trend for more water on the reference sites ($t = -1.94$, $p = 0.06$).

As there were significant date effects for insect abundance and biomass, with insect emergence low at the beginning of the season, insect data was inspected for seasonal peaks by looking at the presence of time quadratics in the models. In 2012, there was a significant peak in insect abundance ($\beta = -0.0007 \pm 0.0003$, $p = 0.02$) and biomass index ($\beta = -0.001 \pm 0.0004$, $p < 0.001$) around day 155 (June 3). In 2013, there was again a significant peak in insect abundance ($\beta = -0.003 \pm 0.0004$, $p < 0.001$) and biomass index ($\beta = -0.07 \pm 0.02$, $p < 0.001$) around days 150-155 (May 28-June 2), but the model for biomass index also included a significant cubic term of date ($\beta = 0.0001 \pm 0.00003$, $p < 0.001$), indicating a second peak, which occurred around day 180 (June 27). In 2014, only insect abundance experienced a significant peak ($\beta = -0.04 \pm 0.02$, $p = 0.04$), occurring around day 155 (June 2), with a second peak ($\beta = 0.0001 \pm 0.00004$, $p = 0.03$) around day 190 (July 9).

When comparing abundance and biomass between site types across the entire season (2012: dates 142-199; 2013: 137-193; 2014: 148-196; ranges of dates were determined based on availability of rain data, as rainfall amount was included in the models), the only difference was found in 2013, with insect abundance being higher on agricultural sites ($\beta = 0.49 \pm 0.10$, $p = 0.003$). Sums of total insect abundance and biomass across the season for each site and each year can be found in Table 2.2.

When separated into adult and nestling periods, insect abundance and biomass appeared similar between the two site types in all time periods and years with only a few exceptions. During the 2012 adult period, abundance was significantly higher on agricultural sites ($\beta = 0.51 \pm 0.16$, $p = 0.04$), with the same trend seen in the biomass index ($\beta = 0.47 \pm 0.18$, $p = 0.05$). The only other difference was the 2013 nestling time period with both abundance ($\beta = 1.12 \pm 0.20$, $p = 0.01$) and biomass index ($\beta = 1.67 \pm 0.35$, $p = 0.02$) being higher on agricultural sites.

2.3.2 Foraging rate and durations between site types

Foraging rate was significantly positively correlated with the wind-corrected, daily insect abundance (Figure 2.4a; $r = 0.45$, $p = 0.002$) and biomass (Figure 2.4b; $r = 0.37$, $p = 0.02$). The best-supported model for foraging rate included variables of nestling age, daily wind speed, and daily insect biomass (Table 2.3), with site and date as random effects. The relationship between foraging rate and nestling age was positive, with foraging rate increasing for older nestlings ($\beta = 0.12 \pm 0.04$, $p = 0.004$; Figure 2.2). Additionally, adults, unexpectedly, increased their foraging rate with higher wind speeds ($\beta = 0.52 \pm 0.14$, $p = 0.002$). There was also a trend for increased foraging rates with higher insect biomass ($\beta = 0.98 \pm 0.51$, $p = 0.08$; Figure 2.3).

Analysis was also done on foraging interval, or the amount of time between PIT detections by the RFID reader, with a total of 8585 observations in the analysis. Males on

agricultural sites spent about 24% of their time at or near the nest box, compared to 70% on grassland sites (Figure 2.5); agricultural females spent 28% of the time at the nest box, compared to 49% on grassland sites (Figure 2.5). The best-supported model included only presence of agriculture as a fixed effect, and nest as a random effect to account for repeated sampling from the same pair. Parents on agricultural sites showed a different distribution of the two “types” of intervals (i.e. staying at or near the nest box versus actively foraging) than those on grassland, by spending more time away from the nest-box and, presumably, actively foraging ($\beta = -0.13 \pm 0.06$, $p = 0.053$).

In order to model the full set of variables in relation to the foraging interval, an average was calculated for each individual. The best-approximating model included fixed effects of agriculture, sex, minimum daily temperature, nestling age, brood size, daily wind speed and precipitation, adult body condition, daily insect biomass, and interactions between agriculture and sex and agriculture and daily insect biomass (Table 2.4). Although the variable set was large, some additional information could be gleaned. For example, males had a significantly shorter foraging interval compared to females ($\beta = -220.5 \pm 79.6$, $p = 0.01$). There was also a significant interaction between presence of agriculture and sex ($p = 0.02$), with average foraging intervals of 397 and 197 seconds for females and males at grassland sites, respectively, and 339 and 382 seconds for females and males at agricultural sites. Average foraging interval was negatively associated with daily wind speed ($\beta = -94.1 \pm 32.5$, $p = 0.01$), precipitation ($\beta = -59.9 \pm 22.9$, $p = 0.03$), and nestling age ($\beta = -33.6 \pm 14.4$, $p = 0.03$). Site type, minimum daily temperature, brood size, adult body condition, daily insect biomass, and the interaction between agriculture and daily insect biomass were not significant in the model output.

2.3.3 Return rates

The respective percentages of returning individuals at the agricultural and grassland sites were 25% and 41% in 2013, and 48% and 37% in 2014. Return rates for each site can be found in Table 2.6. Models to determine factors influencing the probability of returning to the previous capture site were run separately for 2013 and 2014 due to an interaction between site type and year. The top-ranked model for return rates in 2013 included effects of agriculture and date of breeding the previous year (Table 2.5). Return rates were significantly higher on the grassland site compared to the agricultural sites ($\beta = -0.79 \pm 0.40$, $p = 0.048$), while date effects were not significant. The top-ranked model for return rates in 2014 included effects of agriculture, body condition, brood size, and interactions between agriculture and body condition and agriculture and brood size (Table 2.5). Return rates in 2014 were significantly higher on grassland sites over the agricultural sites ($\beta = -4.0 \pm 1.8$, $p = 0.03$), and were also significantly higher in individuals with lower body condition the previous year ($\beta = -0.78 \pm 0.32$, $p = 0.01$). The interaction between agriculture and body condition ($p = 0.03$) however, confounds our interpretation as the relationship with body condition was much stronger on the grassland site (Figure 2.7a). The interaction between agriculture and brood size ($p = 0.02$) was observed as individuals with larger broods were more likely to return on agricultural sites, while the opposite relationship was seen on the grassland site (Figure 2.7b).

2.4 Discussion

2.4.1 Trends in insect abundance and biomass

Although variation in total insect abundance, biomass and timing of peaks were apparent among the individual sites, we were unable to detect any gross differences in mean insect abundance or biomass between the agricultural and grassland site types. Insect abundance and biomass are known to vary within and between seasons (Williams 1961; Goulson et al. 2005;

Dunn et al. 2011), and studies looking specifically at swallow prey availability found large variation throughout the season, at times reaching a sevenfold difference between the minima and maxima of the season (Quinney et al. 1986; Hussell and Quinney 1987; Nooker et al. 2005; Dunn et al. 2011). Previous studies looking at comparisons of insect abundance and biomass in agro-intensive landscapes have found that, at the beginning of the season, these measurements are relatively similar irrespective of land use, but as the season progressed, highly intensive landscapes experienced a reduction in prey (Rioux Paquette et al. 2013). This is often caused by agricultural practices such as insecticide applications, which are not evenly distributed through the swallow breeding season. Therefore, insecticides may only have an effect later in the season following applications as crops continue to grow.

This may partially explain why this difference was not seen in this study system; the pesticides for a majority of prairie crops are commonly applied in the form of seed dressings, and of the 8.5 million ha of seeded cropland in 2012, nearly all used insecticide treated seeds (Statistics Canada 2012; Main et al. 2014). Additionally, one of the oft-cited benefits of seed dressings is that they minimize the need for aerially spraying (Jeschke et al. 2008; Goulson et al 2013). In this case, insecticides would be evenly distributed throughout the season, rather than in pulses of spraying events, which may explain why insect abundance and biomass on the agricultural sites in some years were more stable throughout the season (e.g. 2012 and 2014). Weather variables, such as wind, temperature, and precipitation are also known to influence insect abundance and biomass. However, these are unlikely to explain patterns between sites, as the five study sites were relatively close together, with the furthest distance being around 80 km.

While others have occasionally found that insect abundance and biomass are higher in highly intensive landscapes (Rioux Paquette et al. 2013), this is a unique circumstance and not a

consistent trend (e.g. Møller 2001; Ambrosini et al. 2002; Evans et al. 2007). One of the potential explanations for the tendency toward higher insect abundance on some of the agricultural sites relative to the grassland sites in our study may be the differing topography between the sites, and its influence on the efficiency of the passive insect samplers. The capture rate of the samplers used in this study is known to be influenced by wind (Hussell and Quinney 1987); it is also known that topography and vegetation affect wind speeds (Suárez et al. 1999). The two grassland sites in the study are characterized by a hilly landscape, while the three agricultural sites are comparatively flat. Of necessity, passive samplers were placed on the top of hills. Given that the distribution of insects is known to vary among sites (Hussell and Quinney 1987), and that insects are likely to gather in areas near valleys or trees to avoid wind, I acknowledge that the passive insect samplers may not be the best tool for inter-site comparisons of insect abundance and biomass.

2.4.2 Foraging strategy on differing landscapes

Our novel approach for assessing foraging behaviour of tree swallows using RFID technology successfully recorded more frequent feeding trips as nestlings aged but also during periods of higher prey availability. This is consistent with the expected patterns for swallows to respond to energetic needs of growing chicks (Leonard and Horn 1996; Rose 2009). Tagged birds also responded positively to prey availability to increase their provisioning of nestlings when conditions were favourable. Interestingly, the increase in foraging rate with higher prey biomass was most pronounced in birds occupying grassland sites while responses at agricultural sites were somewhat dampened. This was further reflected in the pattern of foraging intervals which indicated birds, particularly males, at agricultural sites spent more time away from the nest, presumably to locate sufficient or desired prey.

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. Although we did not find evidence here that food supply was higher at grassland reference sites, these sites had greater percentage of pasture and natural areas than the agricultural sites that may have favoured improved foraging opportunities. The presence of hills and valleys at the grassland sites may have contributed to the differences in foraging strategy, assuming insect availability is equivalent across sites types. If insects tend to congregate in low areas between hills or in areas of dense natural vegetation, it may be easier for swallows on grassland sites to find and collect prey, reducing lengths of foraging trips, compared to the agricultural sites. In addition, the grassland sites on average had more trees, possibly creating foraging opportunities for swallows in areas where insects gather to avoid wind.

Our results suggested that the sexes were responding differently in regards to foraging behaviour. In particular, at agricultural sites, males generally spent more time away from the nest, presumably foraging. Interestingly, although swallows generally increased their foraging rate and provisioning of nestlings in response to increasing insect biomass, the response was much weaker at agricultural sites, and those agricultural males were not responding to differences in food supply. While equal feeding rates between the sexes have been reported in some systems (Quinney 1986; Dunn and Robertson 1992), swallows generally show female-biased parental care; which is often related to quality of foraging conditions.

Alternatively, previous studies (Jones 1988, Bryant & Tatner 1991, Turner 2006) have suggested that the positive relationship often seen 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 decreased when conditions were poor. Under favourable conditions, parents experience a lower cost per unit food item, as well as are able to increase their own intake to compensate for energy loss and can therefore forage more intensively. It is thought that this type of strategy may have evolved in response to the short-term fluctuations in food availability due to changes in weather that swallows commonly experience (Gruebler et al. 2008). If foraging conditions are generally more favourable on grassland sites due to some component of habitat quality, this may explain the steeper increase in foraging rate in response to insect abundance on these sites. In contrast, birds (particularly males) at agricultural sites may be optimizing their own energy expenditure by reducing their parental care to compensate for lower food availability.

2.4.3 Return rates on agricultural and grassland sites

The probability of an adult bird returning to a site the following year ranged from 16% to 57%, but was generally higher in 2014 than 2013. Return rates were higher on average for birds on the grassland site compared to agricultural sites in both years after controlling for prior breeding season effects of date, brood size, and body condition. Surprisingly, there was also a general trend that birds with lower body condition during the previous breeding season were more likely to return the next year. This trend was primarily driven by the lower condition of birds on the grassland site where returns were higher. However, this could be an artefact that this grassland site is part of a much larger and well-established colony at the St. Denis National Wildlife Area. I speculate that the higher quality, higher body condition birds from our reference study site are returning to the same general area, but redistributing to the central colony. Overall, there was very little dispersal detected between more distant sites, with one bird from the grassland site moving to an agricultural site in 2013, and two in 2014.

We also found that on agricultural sites, brood size of the previous season predicted return rates, with individuals with larger and ultimately successful broods being more likely to return. This relationship with brood size would be expected, as individuals with larger broods are generally higher quality birds, and therefore would have a higher chance of survival (Houston et al. 1983; Goodburn 1991; Møller and Szep 2002; Blums et al. 2002). Additional years of study on the agricultural sites, as well as the additional grassland site established in 2014, will be needed. The current analysis, however, suggests that the agricultural sites may be somewhat less favourable.

2.4.4 Conclusion

While aerial insectivore declines probably result from multiple causes, understanding the relative influence of potential components can help in better understanding the mechanism for declines, and provide valuable information for developing conservation strategies. Our main findings suggest that subtle differences in prey availability, quality, or composition between sites produce shifts in the parental foraging behavior. Additional work is required to more completely understand the indirect effects of aerial insect abundance and biomass on agricultural sites compared to areas dominated by grassland, and how this may influence aerial insectivores. Indirect habitat effects are often overlooked in ecological risk assessments, but incorporating these considerations into agricultural management strategies may provide a promising strategy for conservation of birds associated with this habitat.

TABLES AND FIGURES

Table 2.1: Summary of site and land use characteristics for grassland (gray) and agricultural (white) sites monitored at 6 study sites in south-central Saskatchewan 2012-2014. Land use is displayed as 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 over each year of the study.

	% Crop¹	% Human use²	% Natural³	% Pasture⁴	% Trees⁵	% Water⁶	Neonic pesticides⁷
Allan (2014)	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)	0.1 (0.1)
St. Denis (2012-2014)	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)
Burr (2012-2014)	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)
Colonsay 1 (2012)	74.2 (49.8 – 83.2)	2.6 (0 – 5.3)	10.0 (1.4 – 31.0)	0.0 (0)	10.5 (2.9 – 18.5)	4.6 (2.0 – 9.2)	13.6 (2.3 – 31.9)
Colonsay 2 (2013-2014)	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)
Humboldt (2013-2014)	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)
<i>p-value</i>	<i><0.001</i>	<i>0.32</i>	<i><0.001</i>	<i>0.005</i>	<i>0.15</i>	<i>0.49</i>	<i><0.001</i>

¹land under cultivation; ²buildings, roads, other human structures; ³grass, dried wetlands; ⁴pasture area for livestock; ⁵trees or shrubs; ⁶surface water; ⁷mean concentration (ng/L) of total neonicotinoids detected in wetlands from 2012-2014.

Table 2.2: Summary of cumulative total insect abundance and biomass index (corrected for wind and time) throughout the swallow breeding season on 2 grassland (grey) and 3 agricultural (white) sites in south-central Saskatchewan, 2012-2014. The sampling period was defined as Julian dates 142-199 [day 1 is 1 January] in 2012, 137-193 in 2013, and 148-196 in 2014.

Site	2012 (57 days)		2013 (56 days)		2014 (48 days)	
	Σ abundance	Σ biomass	Σ abundance	Σ biomass	Σ abundance	Σ biomass
Allan	na	na	na	na	3935	637.9
St. Denis	3121	365.6	8318	3945.2	8279	1445.7
Burr	3685	436.1	8065	1700.5	3961	531.5
Colonsay	3532	443.4	9755	3129.5	19567	5467.7
Humboldt	na	na	10004	2467.3	15050	1950.9

Table 2.3: Model selection results for linear mixed effects models developed to explain variation in foraging rates of tree swallows monitored on agricultural and grassland sites in south-central Saskatchewan in 2014. The full (global) model included 8 fixed terms to account for environmental and nest status during the sampling period, plus all models had random effects of date and site. ΔAIC_c is the difference between the AIC_c of the best-approximating model and other models in the candidate set. Also shown are number of parameters (K), AIC_c weights and model deviance.

Model	K	AIC_c weight	Deviance	ΔAIC_c
nestling.age + wind + insect.biomass	7	0.21	73.4	0.0
nestling.age + wind + insect.biomass + insect.biomass ²	8	0.20	70.5	0.1
min.temp + wind + insect.biomass	7	0.18	73.8	0.4
nestling.age + wind	6	0.12	77.4	1.2
brood + wind + insect.biomass	7	0.08	75.3	1.9
brood + insect.biomass	6	0.08	78.3	2.0
Ag + wind + insect.biomass	7	0.07	75.7	2.3
Intercept-only (null)	4	0.05	84.4	2.9
Ag+ nestling.age + wind + insect.biomass + Ag*insect.biomass	9	0.02	71.5	4.4
Ag + Sex + Brood + min.age + nestling.age + min.temp + wind + precipitation + insect.biomass (global)	13	0.0	79.4	27.3

Ag: agricultural or grassland site type

brood: nestling brood size

insect.biomass: wind-corrected daily biomass of insects collected on the day of behavioural monitoring

min.age: minimum known age for adults

min.temp: daily minimum temperature on the day of monitoring

nestling.age: age of the nestlings on the day of the foraging measurements

wind: average daily wind speed on the day of monitoring

Table 2.4: Model selection results for linear mixed effects models developed to explain variation in average foraging interval (time spent on each foraging trip) of tree swallows monitored in south-central Saskatchewan in 2014. All models included random effects of date and site. ΔAIC_c is the difference between the AIC_c of the best-approximating model and other models in the candidate set. Also shown are number of parameters (K) and model deviance.

Model	K	AIC_c weight	Deviance	ΔAIC_c
Ag + BC + Brood + insect.biomass + min.temp + nestling.age + precipitation + Sex + wind + Ag*Sex + Ag*insect.biomass	15	0.66	422.8	0.0
Ag + BC + Brood + insect.biomass + nestling.age + precipitation + Sex + wind + Ag*Sex + Ag*insect.biomass	14	0.16	430.3	2.8
Ag + BC + insect.biomass + min.temp + nestling.age + precipitation + Sex + wind + Ag*Sex + Ag*insect.biomass	14	0.07	432.1	4.5
Ag + BC + Brood + insect.biomass + min.temp + precipitation + Sex + wind + Ag*Sex + Ag*insect.biomass	14	0.03	433.6	6.1
Ag + Brood + insect.biomass + min.temp + nestling.age + precipitation + Sex + wind + Ag*Sex + Ag*insect.biomass	14	0.02	434.2	6.7
Ag + BC + insect.biomass + nestling.age + precipitation + Sex + wind + Ag*Sex + Ag*insect.biomass	13	0.01	439.7	7.8
Ag + BC + Brood + insect.biomass + min.temp + nestling.age + precipitation + Sex + wind + Ag*Sex	14	0.01	436.6	9.1
Ag + BC + Brood + insect.biomass + min.temp + nestling.age + Sex + wind + Ag*Sex + Ag*insect.biomass	14	0.01	436.6	9.1
Ag + Brood + insect.biomass + nestling.age + precipitation + Sex + wind + Ag*Sex + Ag*insect.biomass	13	0.01	441.6	9.7
Ag + BC + Brood + insect.biomass + min.temp + nestling.age + precipitation + Sex + Ag*Sex + Ag*insect.biomass	14	0.01	437.3	9.7
Ag + BC + insect.biomass + min.temp + precipitation + Sex + wind + Ag*Sex + Ag*insect.biomass	13	0.0	442.9	11.0
Intercept-only (null)	4	0.0	549.1	87.6

Ag: agricultural or grassland site type

BC: adult body condition

brood: nestling brood size

insect.biomass: wind-corrected daily biomass of insects collected on the day of behavioural monitoring

min.temp: daily minimum temperature on the day of monitoring

nestling.age: age of the nestlings on the day of the foraging measurements

precipitation: daily rainfall on the day of monitoring

wind: average daily wind speed on the day of monitoring

Table 2.5: Model selection results for models developed to explain variation in return rates in swallows nesting on grassland and agricultural sites in south-central Saskatchewan, 2012-2014. Models were run separately for 2013 and 2013 due to an interaction between site type and year. ΔAIC_c is the difference between the AIC_c of the best-approximating model and other models in the candidate set. Also shown are number of parameters (K), AIC_c weight, and model deviance.

2013	K	AIC_c weight	Deviance	ΔAIC_c
Ag + Date	3	0.14	148.3	0.0
Ag	2	0.13	150.5	0.2
Date	2	0.06	152.3	0.9
Intercept-only (null)	1	0.05	154.4	2.0
Ag + Date + Min.age	4	0.05	148.2	2.1
Ag + Date + Sex	4	0.05	148.2	2.1
2014				
Ag + BC + Brood + Ag*BC + Ag*Brood	6	0.23	209.9	0.0
Ag + BC + Brood + Min.age + Ag*BC + Ag*Brood	7	0.15	208.6	0.9
Ag + BC + Brood + Date + Ag*BC + Ag*Brood	7	0.10	209.4	1.7
Ag + BC + Brood + Sex + Ag*BC + Ag*Brood	7	0.09	209.7	1.9
Ag + BC + Brood + Date + Min.age + Ag*BC + Ag*Brood	8	0.07	208.1	2.6
Intercept-only (null)	1	0.0	229.5	9.0

Ag: agricultural or grassland site type
 BC: adult body condition
 brood: nestling brood size
 min.age: minimum adult age (based on banding records)

Table 2.6: Return rates (\pm SE) of adult tree swallows nesting on agricultural (white) and grassland (gray) sites in south-central Saskatchewan from 2013-2014 that were recaptured at each site when sites were >1 year old.

Site	Number banded in t (2012)	Returned in t + 1 or 2 (2013 or 2014)*	Number banded in t (2013)	Returned in t+1 (2014)
Burr	29	10 (34%)	46	23 (50%)
Colonsay	38	6 (16%)	41	15 (37%)
Humboldt	--	--	21	12 (57%)
St. Denis	58	24 (41%)	59	22 (37%)

*3 grassland and 2 agricultural birds from 2012 returned in 2014 only.

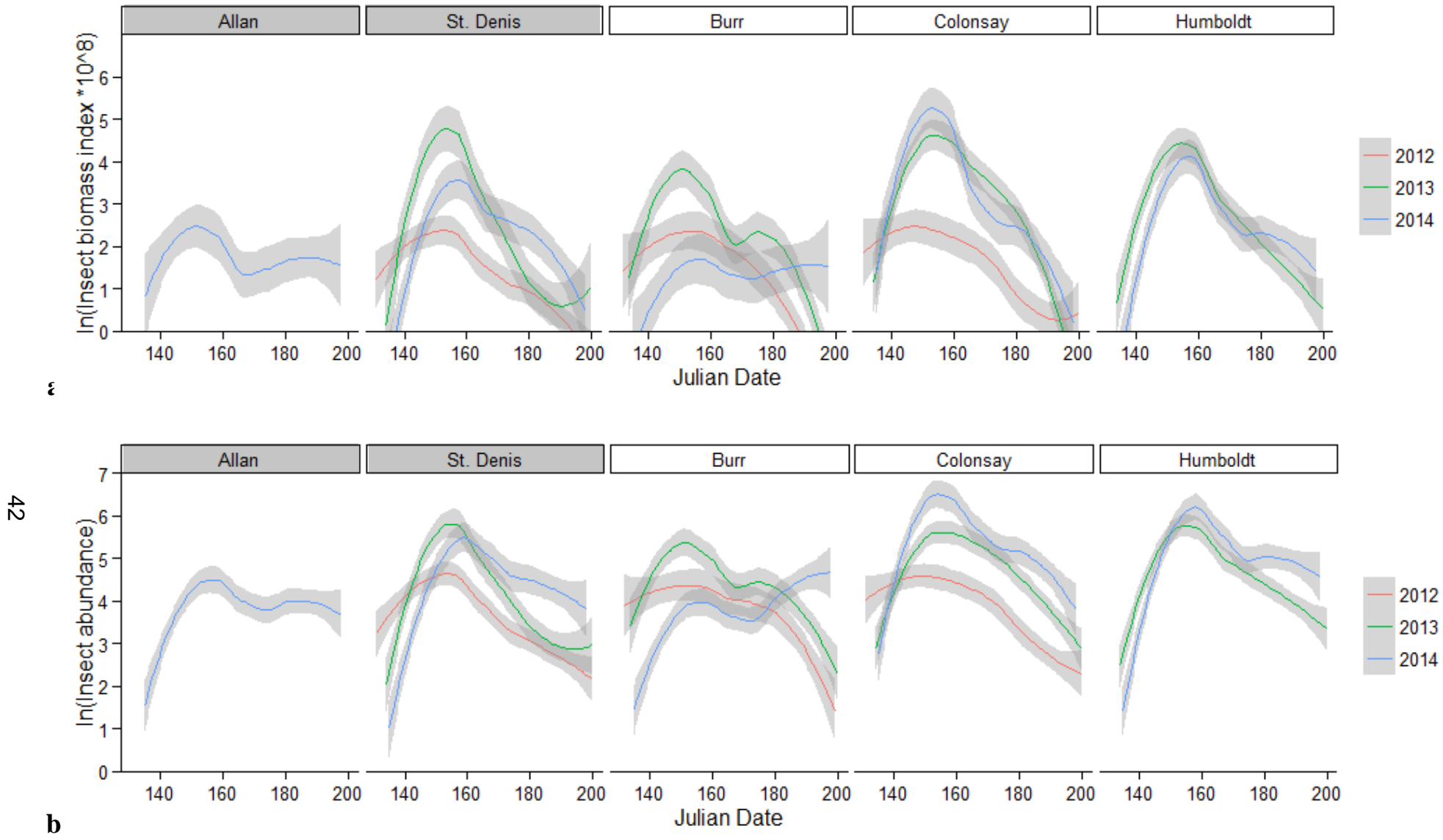


Figure 2.1: Aerial insect biomass (a) and abundance (b) by date across the grassland (gray) and agricultural (white) sites in 2012, 2013, and 2014 (solid lines) with Loess smoother and 95% confidence intervals (shaded area).

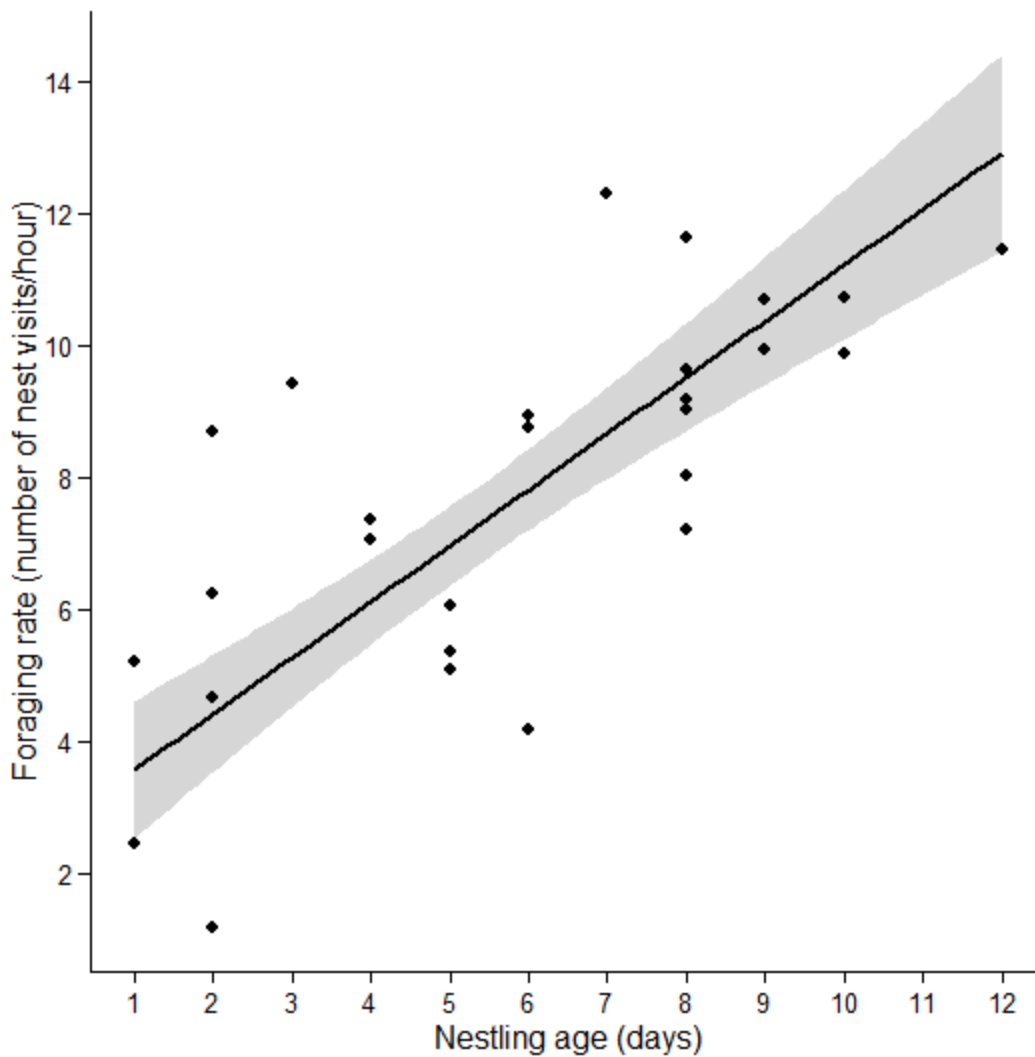


Figure 2.2: Model-predicted relationship between adult tree swallow foraging rate (number of nest visits per hour) and age of nestlings (in days) sampled in south-central Saskatchewan in 2014. Shaded area represents 95% confidence intervals.

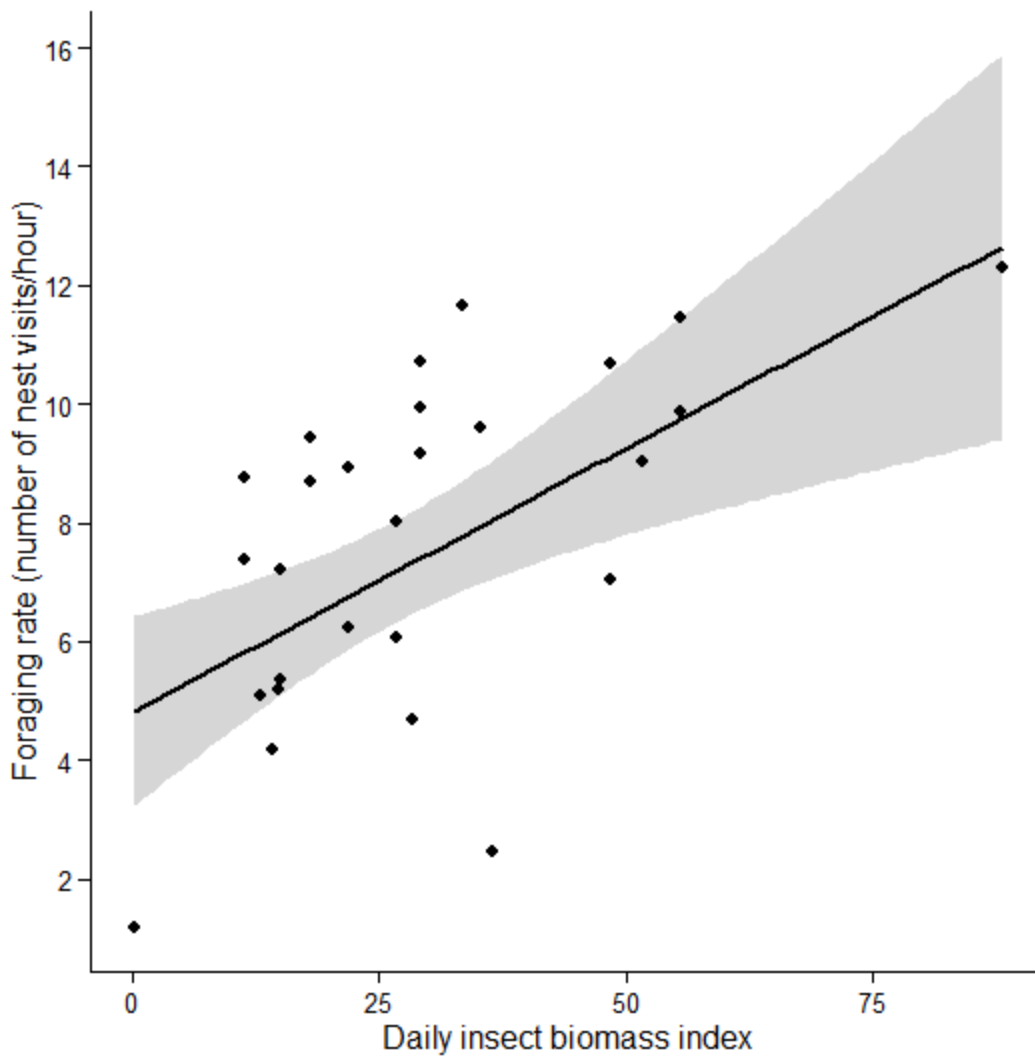


Figure 2.3: Model-predicted relationship between adult tree swallow foraging rate (number of nest visits per hour) and daily insect biomass at sites sampled in south-central Saskatchewan in 2014. Shaded area represents 95% confidence intervals.

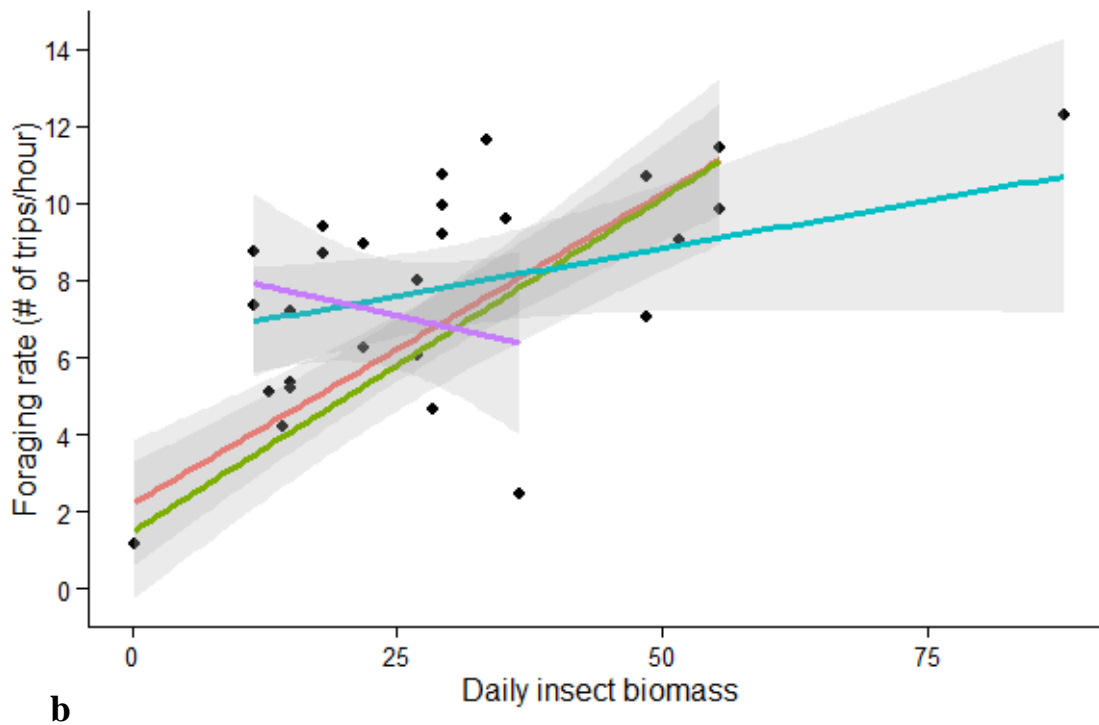
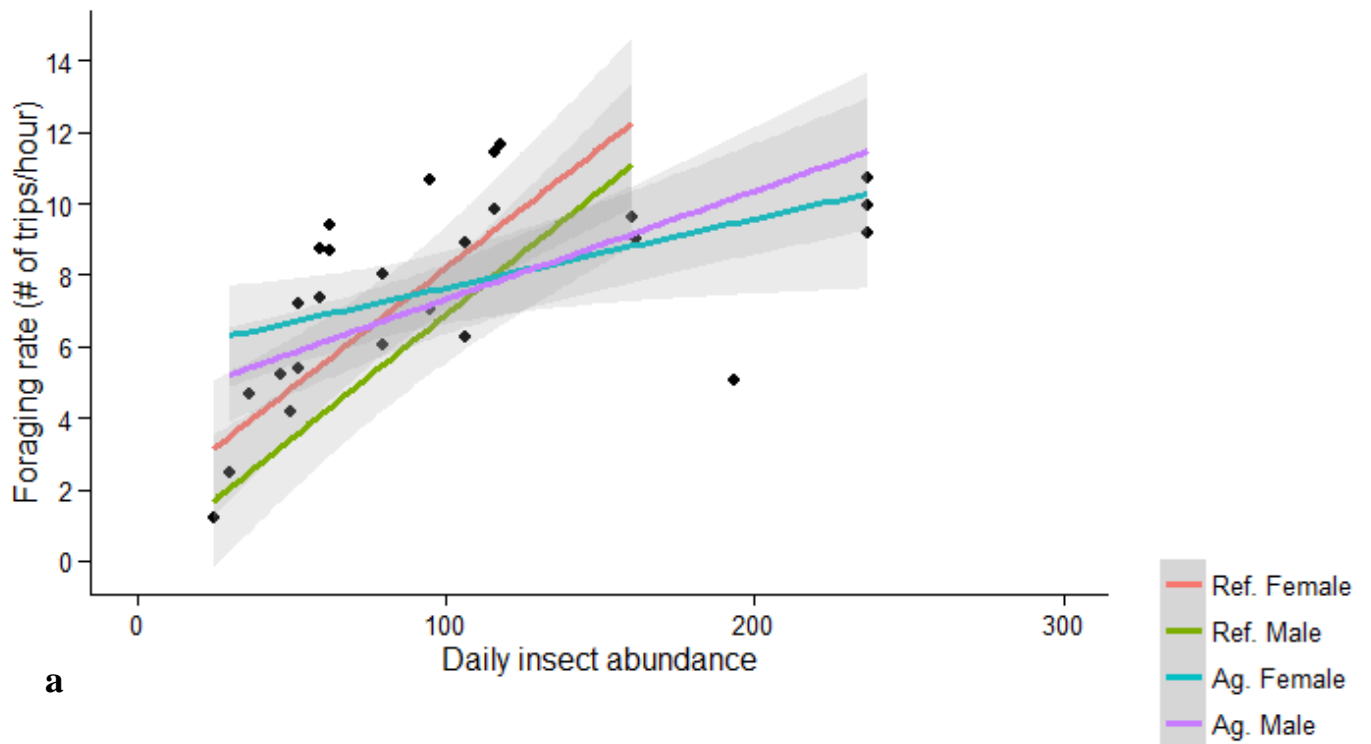


Figure 2.4: Model-predicted relationship between tree swallow foraging rate and wind-corrected daily insect abundance (a; $r = 0.45$, $p = 0.002$) and biomass (b; $r = 0.37$, $p = 0.02$) monitored across 5 agricultural (Ag) and grassland (Ref) sites in south-central Saskatchewan in 2014. Lines indicate best-fit linear trends and 85% confidence intervals (shaded area).

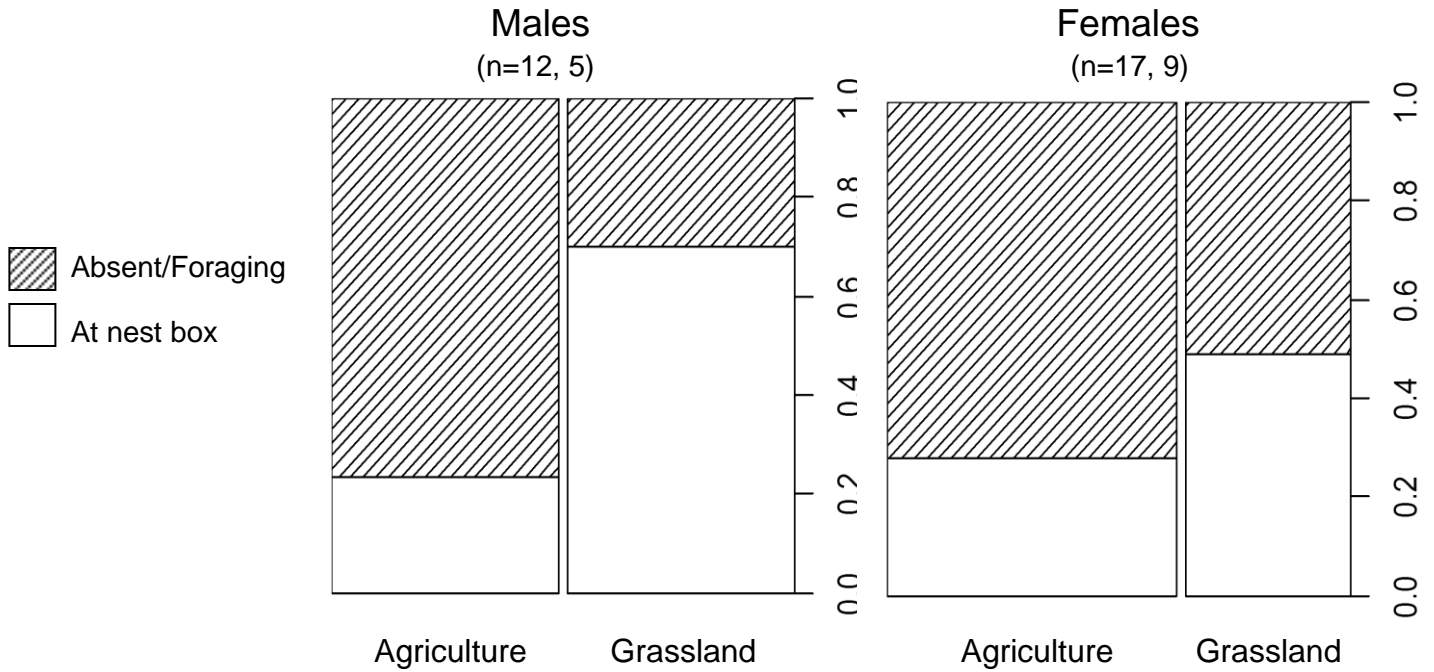
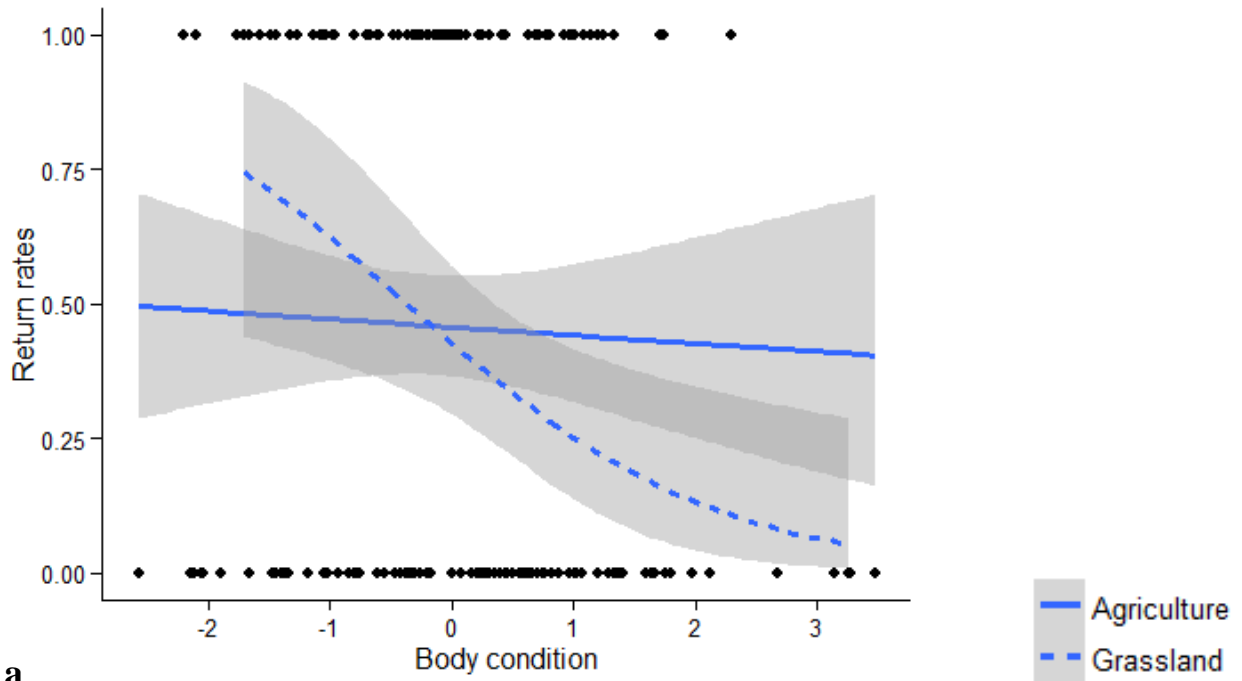
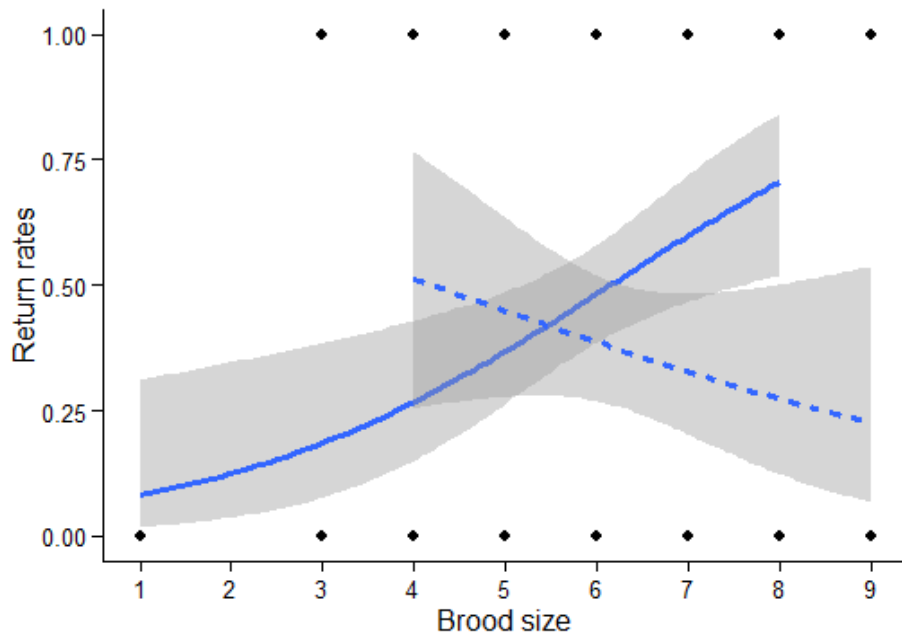


Figure 2.5: Proportion of time spent at the nest-box (interval ≤ 20 seconds) or absent/foraging (interval >20 seconds) for male and female tree swallows on agricultural and grassland sites in south-central Saskatchewan in 2014. Sample size is shown in parenthesis (n = agriculture, reference/grassland).



a



b

Figure 2.6: Logistic regression plot showing the relationship between return rates and body condition (a) and brood size (b) of adult tree swallows nesting on agricultural (solid line) and grassland sites (dashed line) in south-central Saskatchewan in 2014. Shaded area represents 95% confidence intervals.

Chapter 3

Influence of intensive agriculture and seasonal shifts in insect prey availability on body condition and physiology of tree swallows

3.1 Introduction

Over the last several decades agricultural practices worldwide have undergone drastic changes, with increased mechanization, introductions of new agrochemicals, and loss or degradation of remnant natural habitats such as field margins and wetlands (O'Connor & Shrubbs 1986; Fuller et al. 1995; Stoate 1996; Chamberlain et al. 2000, Benton et al. 2003; Ghilain and Belisle 2008). These changes may influence a variety of wildlife species that depend upon farmland habitat. Grassland birds associated with agricultural habitats, are currently experiencing declines more severe than birds associated with any other biome (Sauer et al. 2000; Murphy 2003). Likewise, aerial insectivores, a group that comprises several farmland bird species, including tree swallows (*Tachycineta bicolor*), are often considered to be the most steeply declining avian guild (Benton et al. 2002; Nebel et al. 2010). For example, the tree swallow population in Canada experienced a decline of 2.8% annually during 1989-2009 (Robillard 2012). It is speculated that the strict reliance on aerial insects as prey, and the trends in declining insect abundance and diversity along with changes in agriculture, may be involved (Nebel et al. 2010; Nocera et al. 2012).

Arthropod abundance typically decreases as agriculture becomes more intensive (Benton et al. 2002; Gruebler et al. 2008), and aerial insect abundance in particular is higher in areas with trees, hedgerows, and native grassland as compared to areas of cereal crop or arable land (without cereal, root crops, potatoes, or maize; Gruebler et al. 2008). Tree swallows depend on consistently high levels of aerial insect availability, and a decline in their preferred food supply

can reduce parental care resulting from longer absences from the nest-box, and in some cases, altered foraging strategies to more profitable locations that are more distant from the nest (see Chapter 2; Winkler et al. 2013). Each has potential consequences for affecting both physiology and fitness of individual adults and nestlings.

There are many potential responses of parents to changes in foraging conditions, including modified foraging behavior (Turner 2006; Jones 1988), reductions in body mass (Jones 1987; 1988), and changes in metabolic rate (Speakman et al. 2003; Wiersma et al. 2005). The availability of food resources is one of the most important factors influencing body condition and reproductive success in birds (Lack 1954; Immelmann 1971; Harriman et al. 2014). Females with poorer body condition often produce smaller clutches (Houston et al. 1983; Goodburn 1991) and fledge fewer young (Reid and Boersma 1990; Wendeln and Becker 1999), which then tend to exhibit poorer body condition themselves (Schluter and Gustafsson, 1993). If parents experience lower body condition as a result of reduced prey availability, this may in turn affect nestlings. A reduction in food availability may also reduce survival (Payne and Wilson 1999; Peach et al. 1999; Vickery et al. 2001), with starvation being a central cause of mortality in both adults and nestlings (Lombardo 1986; Robertson et al. 1992; McCarty 1995).

One of the important costs associated with increased foraging effort and flight activity is the acceleration of oxygen metabolism (Leeuwenburgh and Heinecke 2001; Monaghan et al. 2009). Reactive oxygen species (ROS) are generated as by-products of oxygen consumption (Finkel and Holbrook 2000; Balaban et al. 2005) and have the potential to damage biological macromolecules (Beckman and Ames 1998; Perez-Campo et al. 1998) through the process of oxidative stress. Oxidative stress arises when an organism experiences an imbalance of antioxidants and pro-oxidants. Damage to biomolecules caused by pro-oxidants is referred to as

oxidative damage (Halliwell & Gutteridge 2007). An accumulation of oxidative damage over a period of time, along with the associated trade-offs required for the allocation of resources to the antioxidant system (Monaghan et al. 2009; Nussey et al. 2009), may potentially accelerate the aging process and development of degenerative diseases (Beckman and Ames 1998; Finkel and Holbrook 2000; Furness and Speakman 2008). The interaction of oxidative stress and life history traits has been observed in barn swallows, where a high total antioxidant count predicted long term survival (Saino et al. 2011). Similarly, alpine swift (*Apus melba*) males with greater resistance to oxidative stress were more likely to survive to the following breeding season, and females with higher resistance laid larger clutches (Bize et al. 2008).

Reductions in food supplies could increase foraging rates in adults, produce higher oxygen consumption and elevate the generation of reactive oxygen species (van de Crommenacker et al. 2011). Experimental manipulations with captive animals have demonstrated a positive correlation between oxidative stress and physical activity (Magwere et al. 2006; Larcombe et al. 2008; Monaghan et al. 2009), while greater flight effort in insects and birds increases oxidative stress levels (Costantini et al. 2007; Costantini et al. 2008; Williams et al. 2008). Increased production of reactive oxygen species from higher foraging effort coupled with a decrease in food-derived antioxidants may result in serious consequences for swallows breeding in poorer quality habitats.

Another method of looking at the physiological effects of reduced prey availability in birds involves measuring glucocorticoid (GC) hormones, the primary GC in birds being corticosterone, or CORT. Many species counteract unpredictable stimuli in their environment via a stress response, which is a collection of physiological, hormonal, and behavioral changes that allow the animal to cope with disturbances (Romero 2004).

Food restriction has a direct relationship with secretion of GCs in both laboratory settings and wild birds (Marra and Holberton 1998; Kitaysky et al. 1999; Lynn et al. 2003; Clinchy et al. 2004) and prolonged periods of limited food resources can reduce body mass via depletion of fat and protein reserves for fuelling gluconeogenesis (Wingfield 2003). Food restriction in nestlings of several species can lead to elevated baseline and acute stress-induced CORT levels as compared to nestlings on a normal diet (Kitaysky et al. 2003), and fat reserves and body mass are typically negatively correlated with GC secretion in nestlings (Heath and Dufty 1998; Kitaysky et al. 2001). In contrast, nestlings of some species have exhibited suppression of CORT in response to nutritional stress, allowing them to maintain their protein and fat stores, but leading to possible reductions in immunity or growth rates (Sears and Hatch 2008; Fairhurst et al. 2011).

While there has been advances in research to determine connections between agricultural intensification and avian population declines in Europe and North America (see Fuller et al. 1995; Chamberlain et al. 2000; Donald et al. 2006; Benton et al. 2002; Evans et al. 2007; Vickery et al. 2001; Ghilain and Bélisle 2008; Robillard et al. 2012; Pigeon et al. 2012; Rioux Paquette et al. 2013), there have been relatively few studies investigating the potential mechanistic underpinnings. Therefore, the objective of this study extends this work to determine how agriculturally-driven landscape differences and food supply can impact body condition, oxidative status, and CORT in breeding tree swallows.

3.2 Methodology

3.2.1 Study sites

Tree swallows breeding in nest-boxes were studied at five sites ($n = 3$ in 2012, $n = 4$ in 2013, $n = 5$ in 2014) in south-central Saskatchewan: Allan ($51^{\circ} 37'14.27''\text{N}$, $105^{\circ} 58'14.16''\text{W}$; 2014 only); Colonsay ($52^{\circ} 1'38.07''\text{N}$, $105^{\circ}55'6.22''\text{W}$); Burr ($51^{\circ}58'15.53''\text{N}$, $105^{\circ} 5'58.89''\text{W}$);

Humboldt (52°12'43.87"N, 105°17'25.12"W; 2013 and 2014 only); and St. Denis (52°12'36.32"N, 106° 4'33.60"W). Allan and St. Denis were primarily characterized as grassland (reference) sites, while Colonsay, Burr and Humboldt were agricultural sites (details below).

Nest boxes were mounted on metal t-posts about 1.5m above the ground, with the entrance hole facing southeast. At each site, nest-boxes (n = 30 in 2012 and 2013, n = 32 in 2014) were spaced 30 m apart along gravel roads, alternating the deployment of Long-Point and Golondrinas style nest-boxes, with the number of each box type differing among years but the ratio of each box type being the same on all sites each year. For detailed descriptions of Long-Point and Golondrinas boxes, see Hussell (2003) and “Golondrinas – Nest Box Design” (2011), respectively. Daily temperature, precipitation, and wind speed were recorded at all sites, as variation in weather affects aerial insect abundance and foraging behaviour of swallows (McCarty 1995; Gruebler et al. 2008; Rioux Paquette et al. 2013; Winkler et al. 2013).

3.2.2 Quantifying agricultural intensification through land use and insect abundance

The level of agricultural intensification at all sites was evaluated through measurements such as surrounding crop type, insect abundance and biomass, and land use analysis. ArcGIS was used to quantify the proportions of land use categories at all sites, including crop, roads and buildings, natural vegetation (consisting primarily of grass or dried wetlands), trees and shrubs, and water.

Total wetland area within a 500 m radius of the nest boxes on each site was determined by mapping perimeters of all wetlands at each site during June 2013 and 2014, by walking wetland perimeters with a handheld GPS unit. All wetlands inside this buffer were mapped, as 500 m is a typical maximum distance from the nest-box that parent tree swallows are assumed to forage (McCarty and Winkler 1999a; Winkler et al. 2011). Land use was characterized in 8-10

quarter sections surrounding the nest-boxes at each site. Depending on layout of the boxes, the number of quarters that overlapped with the 500 m buffer around the nest boxes varied.

Insects were sampled using an aerial insect passive sampler (3 samplers per site), as described in Hussell and Quinney (1987). Glass jars filled with a mixture of 70% ethanol (25% water) and 5% glycerol (to prevent evaporation) were changed out every 24-48 hours throughout the duration of the swallow breeding season. The insects were then stored in 70% ethanol (30% water) until counted for abundance, placed in a drying oven at 95°C until dry, and weighed (nearest 0.00001 g) on an analytical balance to obtain dry biomass. Insects longer than 13mm (excluding antennae and ovipositors) were measured and weighed separately, as arthropods of this size are rare in a tree swallow's typical diet (Quinney & Ankney 1985; McCarty and Winkler 1999a). These insects were excluded from analysis. Insect biomass was adjusted for sampling duration and average wind speed during the sampling period to derive a "biomass index". Abundance estimates were adjusted for sampling duration only. In order to relate temporal changes in food supply to swallow body condition and physiology, a sum was taken of the insect abundance and biomass index in the 48 hours preceding capture and sampling.

3.2.3 Swallow population monitoring and capture

Nest building was closely monitored starting in early May, to determine the date that the first egg was laid. Nests were observed daily until the clutch was complete and then not checked again until near the end of the incubation period (about 12 days). Nests were then checked daily until hatch was completed. The number of eggs that failed to hatch was recorded.

Adults were trapped in nest boxes within the first few days of hatch, banded (if not recaptures), and body measurements (wing, 9th primary, and head-bill lengths, and body mass) taken. Wing and 9th 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 (near 0.5 g). Feather and blood samples were collected for all individuals in 2012 and 2013, and a subset of the birds in 2014. Blood samples were kept on ice until centrifuged later in the day and then frozen at -80°C . Females were aged as second year or after second year, based on plumage (Hussell 1983a).

Nests then remained undisturbed until nestlings were banded at 12 days old and measured for the same morphometrics as adults. Blood and feather samples were collected from 3 nestlings in boxes where adults were sampled. Then, boxes remained undisturbed until 18 days post-hatching, when they were monitored daily to determine fledging success.

3.2.4 Oxidative stress measurements

Measurement of both antioxidants and reactive oxygen species (ROS), rather than just one of these factors, is critical for determining oxidative stress. High levels of ROS do not necessarily result in oxidative damage, for instance, if there are sufficient levels of antioxidant defences to counteract them. Likewise, high levels of antioxidants do not necessarily indicate a better oxidative status, as this will depend also on the levels of ROS that they are required to counteract (Monaghan et al. 2009; Costantini 2008). Levels of oxidative stress were determined for all breeding adults ($n = 368$ for 2012-2014), as well as a sub-sample of nestlings ($n = 30$ per site per year, using 3 nestlings sampled from 10 randomly selected boxes). While handling time was recorded when sampling swallows, garden warblers (*Sylvia borin*) and barn swallows exhibited no significant effects of a 30 minute handling period on levels of either antioxidants or reactive oxygen metabolites (Costantini et al. 2007). Time of day was also recorded, as this can sometimes influence levels of antioxidants and oxidative damage (van de Crommenacker et al. 2011). There was a slight trend for lower levels of both antioxidants ($r^2 = 0.002$) and oxidative

damage ($r^2 = 0.002$) later in the day, but as no significant pattern was observed, time of day was omitted from the analyses.

Oxidative damage was quantified using the d-ROMs test (Diacron, Grosseto, Italy). This test measures the concentrations of reactive oxygen metabolites (ROMs), primarily hydroperoxides (ROOH) in the plasma, which are more stable and easier to detect than reactive oxygen species (van de Crommenacker et al. 2011). ROMs are early markers of oxidative damage, and are produced from the peroxidation of biomolecules, including proteins, lipids, and nucleic acids (Beckman and Ames 1998; Halliwell and Gutteridge 2007). ROMs are considered to be an accurate marker of oxidative damage to lipids and proteins (Alberti et al. 2000; Iamele et al. 2002), and are positively correlated with oxygen consumption in birds (van de Crommenacker et al. 2010).

The d-ROMs assay was conducted following previously used protocols (see Costantini et al. 2011, Guindre-Parker et al. 2013) with minor modifications. Plasma (15 μ l) was diluted in 300 μ l of a 1:100 mixture of alkylamine solution (which serves as the chromagen) and acetic acid/sodium acetate buffer (pH 4.8). The mixture was incubated for 75 minutes at 37°C in microcentrifuge tubes. Following incubation, samples were centrifuged at 10,000 rpm for 60 seconds, and the upper 300 μ l was transferred into a second tube to remove precipitates (i.e. lipids). The mixtures were then centrifuged for an additional 30 seconds, and 130 μ l added in duplicate to wells in a 96-well plate. Absorbance was read at 490 nm with a BioTek ELx800 microplate reader. Results are given in mg H₂O₂/dL.

Total plasma antioxidant capacity was determined using the OXY-adsorbent test (Diacron, Grosseto, Italy). This test measures the ability of the plasma antioxidant barrier (OXY) to counter-balance the oxidative action of hypochlorous acid (HOCl), and includes both

exogenous (i.e., flavonoids and tocopherols) and endogenous (i.e., glutathione and bilirubin) antioxidants. Methods followed Guindre-Parker et al. (2013). Plasma was diluted in a 1:100 ratio in distilled water, and then 5 μ l of the diluted plasma was added in triplicate to wells in a 96-well plate with 200 μ l of HOCl solution. The plate was shaken at 450 rpm for 10 seconds, and then incubated for 10 minutes at 37°C. Following incubation, 2 μ l of the chromagen (N,N-diethyl-p-phenylenediamine) was added, the plate shaken again for 30 seconds, and then read with the same microplate reader as described above at 490 nm. Results are given in μ mol of HClO/ml. The total oxidative status of each individual was then evaluated through the ratio between ROMs and OXY, which is considered to be the best indicator of individual OS levels (Finkel and Holbrook 2000, Dotan et al. 2004). Intra-assay coefficients of variation were under 10% for all samples in OXY (triplicate) and d-ROMs (duplicate) analyses. Inter-assay coefficients of variation were calculated for each assay using a control of pooled chicken plasma collected in 2012 (OXY = 13.0%; d-ROMs = 8.1%; Appendix 1).

3.2.5 Feather corticosterone measurements

Corticosterone was measured in the feathers of nestling tree swallows only ($n = 30/\text{site}$, same individuals as used in OS assays), as adult swallows go through their definitive prebasic molt any time between the end of breeding to arrival at wintering grounds (Hussell 1983b), and would not be indicative of the study period or sites. Circulating CORT levels can be quantified through the feathers because feather corticosterone (CORT_f) accurately reflects the levels of stimulated plasma CORT during the period of feather growth (Bortolotti et al. 2008). As nestlings grow feathers in the nest during the period of pre fledging development, CORT_f provides an integrated measurement for this full time period up to date of collection.

CORT_f was extracted from feathers via a methanol-based method previously used with nestling tree swallows (Bortolotti et al. 2008; Fairhurst et al. 2012). Fully grown flank feathers (n = 2-3 per individual) were weighed using an analytical balance and the length of the feather measured. The calamus was cut and removed, and the remaining feather re-weighed and length re-measured. Samples were placed in glass scintillation vials with 10 ml of methanol and sonicated at room temperature for 30 minutes, before incubating overnight in a 50°C water bath. Vacuum filtration was used to separate methanol from the feather parts, and the extracted methanol placed in a fume hood to evaporate. Dried methanol extracts were reconstituted with a small volume of phosphate-buffered solution (PBS, pH 7.6) and frozen at -20°C until assayed for CORT_f via radioimmunoassay (RIA). Extraction efficiency was assessed through the inclusion of additional feather samples that had approximately 5000 CPM of [³H]-labelled corticosterone added during extraction. Greater than 90% of the reactivity was found to be recoverable.

Standard RIA measurements followed Bortolotti et al. (2008). Antiserum (batch number 092M4784) and purified corticosterone for standards were obtained from Sigma-Aldrich, and [³H]-labelled corticosterone from Amersham BioScience. Diluted antiserum (200 µl) was incubated overnight at room temperature with extracted samples and standards (100 µl total) and 5000 CPM of [³H]corticosterone (100 µl). A dextran-coated charcoal stripping technique was then used to separate bound and free hormones. Results are given in picogram of CORT per millimeter of feather. All samples were assayed blind, random, and in duplicate. Intra-assay coefficient of variation, based on the ED50 value of the standard curve, was 13.3% (Appendix 1), while all inter-assay CVs were less than 15%. The assays had a mean limit of detection (ED80) of 16.2 pg CORT per µl of reconstituted feather extract, but all values were above this limit.

3.2.6 Statistical analyses

Prior to analysis, all data were first thoroughly examined and plotted to look for outliers or unusual patterns, and tested for normality of distributions. Land use data collected in ArcGIS along with mean neonicotinoid pesticide residues were analyzed with a multivariate analysis of variance (MANOVA), with the land use types as the response variables, and site type (agricultural or grassland) as the explanatory variable. The pre-selected site types differed significantly in their land use, with primary differences seen in amount of crop, pasture, natural area, and neonicotinoid residues (Chapter 2).

A regression analysis of each morphometric measurement (ninth primary feather, wing, and head bill lengths) against body mass determined that a combination of all three structural measures was most predictive of body mass (Ninth: $r^2 = 0.02$, Wing $r^2 = 0.02$, Head-bill $r^2 = 0.097$, Combined: $r^2 = 0.10$). The residuals of this relationship were then used to determine the body condition index. Individuals with high residual values would be considered to be in better condition, as they are heavier for their body size (Schulte-Hostedde et al. 2001).

For analyses of morphometrics, oxidative stress, and $CORT_f$ measurements, generalized linear mixed effects models (GLMMs) were used to determine whether there were differences between individuals at agricultural versus grassland sites by including fixed effects of body condition brood size, recapture status, sex, box type, 48- hour cumulative insect biomass and abundance, and age, depending on the response, and random effects of date, site and year (correlated intercept and slope model) for adults, and nest ID, date, site and year (correlated intercept and slope model) for nestlings. Nestling feather corticosterone had additional random effects of nestling age and assay number. Modelling was done in R version 3.0.3 (R Foundation for Statistical Computing 2014) using the lme function of the nlme package (Pinheiro et al.

2012), and Akaike Information Criterion (AIC) was used in model selection to determine the best-approximating model(s) following the methods of Burnham and Anderson (2002).

3.3 Results

3.3.1 Adult body condition

Adult body condition was analyzed using explanatory variables of agriculture, box type, sex, brood size, minimum age, antioxidant counts (OXY), oxidative damage (ROMs), and 48-hour cumulative insect biomass, with random effects of date, site and year (correlated intercept and slope model). The best-approximating model for adult body condition included fixed effects of minimum age and sex (Table 3.1). There was a positive relationship between minimum age and body condition, where older birds had significantly higher condition ($\beta = 0.21 \pm 0.07$, $p = 0.003$; Figure 3.1). Body condition scores were also lower in males (-0.25 ± 0.08) compared to females (0.23 ± 0.06) ($\beta = -0.26 \pm 0.12$, $p = 0.03$; Figure 3.2a). While neither insect abundance nor biomass were included in best-approximating models for adult body condition, there was a positive correlation between adult mass and previous 48-hour cumulative insect biomass ($r = 0.10$, $p = 0.02$, $n = 591$).

3.3.2 Adult oxidative stress physiology

All measurements of adult physiology were analyzed using explanatory variables of agriculture, box type, sex, brood size, minimum age, body condition, and 48-hour cumulative insect biomass (with the exception of oxidative damage, for which 48-hour cumulative insect abundance was used, as models would not converge using insect biomass), with random effects of date, and site and year (correlated intercept and slope model). The best-approximating model for total antioxidants (OXY) in adults included box type and 48-hour cumulative insect biomass (Table 3.2). Adult OXY was higher in the more open Golondrinas box types compared to Long

Point style nest-boxes ($\beta = -0.56 \pm 0.21$, $p = 0.01$; Figure 3.4a). There was also a trend for higher OXY with greater local (48-hour) insect biomass counts ($\beta = 0.75 \pm 0.48$, $p = 0.12$; Figure 3.3a), with a steeper positive relationship found on the grassland site.

Adult oxidative damage (ROMs) was strongly predicted by sex alone (Table 3.3). Oxidative damage was higher in males (3.3 ± 0.15 H₂O₂/dL) than in females (2.2 ± 0.09 H₂O₂/dL) ($\beta = 0.33 \pm 0.04$, $p < 0.001$; Figure 3.2c). The best-approximating model for adult oxidative stress (OS), which estimates the balance between antioxidant levels and oxidative damage, included effects of site type and sex (Table 3.4). Males again had higher levels of OS than females (Figure 3.2d; $\beta = 0.47 \pm 0.07$, $p < 0.001$), and although site type was supported in the top model, the effect of agriculture was not significant ($p = 0.38$). In addition, according to the second-ranked model ($\Delta AIC_c = 2.6$), there was a negative relationship between OS and 48-hour insect biomass (Figure 3.3c; $\beta = -0.83 \pm 0.37$, $p = 0.03$), suggesting reduced prey may have had an effect on the adult bird's oxidative stress balance.

3.3.3 Nestling oxidative stress physiology

All measurements of nestling oxidative stress physiology were analyzed using explanatory variables of agriculture, box type, brood size, age, body condition, and 48-hour cumulative insect biomass, with random effects of sampling date, nest ID, and site and year (correlated intercept and slope model). The best approximating model for nestling antioxidant counts (OXY) included agriculture, box type, 48-hour cumulative insect biomass, and an interaction between agriculture and insect biomass (Table 3.5). In contrast to the adults, there was a negative relationship between 48-hour insect biomass and nestling OXY ($\beta = 2.5 \pm 0.69$, $p = 0.001$), as well as an interaction between agriculture and insect biomass ($\beta = 2.0 \pm 0.94$, $p = 0.03$; Figure 3.3d), such that nestlings on grassland sites exhibited a stronger decline in

antioxidant counts with increases in insect biomass. Consistent with the adults, nestling OXY was also very strongly related to box type such that OXY was higher in Golondrinas style nest-boxes compared to Long Point boxes ($p = 0.004$; Figure 3.4b).

The best-approximating models for both nestling oxidative damage (ROMs) and oxidative stress (OS) included 48-hour cumulative insect biomass which exhibited a quadratic relationship (insect biomass²) (Tables 3.6 and 3.7). Nestling oxidative damage was negatively related to insect biomass ($\beta = -0.77 \pm 0.23$, $p = 0.001$; Figure 3.3e), with a steeper relationship on the grassland sites. The same negative relationship was observed between insect biomass and nestling OS ($\beta = -1.1 \pm 0.42$, $p = 0.01$; Figure 3.3f).

3.3.3 Nestling feather corticosterone

The best-approximating model for predicting feather corticosterone levels ($CORT_f$) was the intercept-only (null) model (Table 3.8), which included random effects of nest box ID, nestling age, assay ID, sampling date, site and year (correlated intercept and slope model). No variables in the global model improved the fit, including effects of agriculture, box type, brood, body condition, insect biomass, and an interaction between agriculture and biomass. The average \pm SE for $CORT_f$ levels for the agricultural ($n = 156$) and grassland ($n = 85$) sites were 7.24 ± 0.19 pg/mm and 7.19 ± 0.22 pg/mm, respectively.

3.4 Discussion

Agricultural intensification has the potential to influence aerial insectivores such as tree swallows through reductions in prey availability, and an associated increase in foraging effort. If adult swallows on poorer quality sites are required to increase foraging rates or alter their foraging strategy, this may manifest through effects on body condition, or measures of physiology such as oxidative stress and corticosterone. We found that local prey availability (48-

hour insect biomass) was a consistent and sensitive predictor of physiological changes in both adult and nestling swallows. Some of the relationships appear stronger in relation to agricultural site types which may be related to prey availability or other habitat or land use features. Adult body condition was not related to 48-hour insect abundance or biomass, but adult mass was correlated with insect biomass. We speculate that body condition may be more closely related to events occurring over a longer time scale, whereas body mass may fluctuate with short term changes in aerial insect availability.

Differences found in adult body condition were primarily driven by sex and known minimum age. The relationship with age would be expected, as birds in better condition typically have a higher chance of survival (Møller and Szep 2002; Blums et al. 2002); therefore birds in good condition are able to survive to more advanced ages. This relationship also has the potential to influence nestling condition, as older birds are more efficient at foraging and display higher provisioning rates (Wheelright and Schultz 1994; Wilcoxon et al. 2010).

Adult antioxidant levels (OXY) were positively related to 48-hour insect biomass; when food is more abundant, adults should be able to consume more, and increase their dietary antioxidants. There was also a steeper response in OXY to changing biomass on grassland sites compared to the agricultural sites. This may indicate that some aspect of habitat quality, such as the differences in land use or amounts of area containing grass or water, enables birds to more rapidly increase their feeding rates in response to higher insect abundance on grassland sites. In comparison, nestling OXY exhibited the opposite relationship, decreasing with increasing insect biomass, and with a steeper relationship on the grassland sites. One potential explanation for this reverse relationship may be the composition and quality of available insects. Nutritional value can vary between insect orders (Rumpold and Schluter 2013; Matrková and Remeš 2014), and

those lacking in vital antioxidants such as carotenoids or vitamins A and E could result in impaired antioxidant defences for the consumers (Catani et al. 2008). In this instance, it may be that abundance or larger biomass insects provided to the nestlings may carry a lower antioxidant value. During pronounced emergence events, parents may select and provide nestlings with insects that are most common, larger, or easier to obtain, rather than those that provide the greatest nutritional benefit. Analyses of antioxidant content of different insect species found on our study sites could provide additional information for inferring relationships between insect availability and avian antioxidant counts. But additional studies on the same system have shown that adults focus their own diet on aquatic diptera, while nestling diets include a larger proportion of terrestrial diptera (C. Michelson, unpublished data), with potential differences in the nutritional content of each.

The dominant influence on oxidative damage in adult swallows was sex, such that males displayed significantly higher levels of oxidative damage. Breeding chronology could play a role in this distinction, because most adult blood samples were collected immediately post-hatch. For the previous 12-14 days, females spent ~70% of their time incubating eggs. In contrast, males were at the nest about 50% of the time, frequently involving energetically demanding activities such as territory and nest defense (Ardia et al. 2009; Ros et al., 2006; Finerty et al., 2009). Higher activity levels in males, and an associated increase in oxygen consumption, could elevate reactive oxygen species involved in oxidative damage (Larcombe et al. 2008; Monaghan et al. 2009). The considerable differences in male and female levels of oxidative damage may average out later in the nestling period, when both parents then spend about 80% of their time in flight (Ricklefs 1971).

The differences observed in oxidative damage appear to parallel differences in overall oxidative stress levels of adults and nestlings. In adults, sex was the primary influence. As predicted, oxidative stress was also negatively related to 48-hour cumulative insect biomass for both adults and nestlings, indicating changes in the abundance of food has a direct influence on the oxidative status of breeding and nestling birds.

Additionally, in both adults and nestlings, antioxidant levels were higher in birds occupying the more open Golondrinas style nest boxes. These boxes typically are cooler and exhibit less variation in temperature than the Long-Point style nest boxes (Appendix 2). As colder temperatures lead to an increase in metabolic rate, this may lead to an upregulation of antioxidant levels and enzymes as a response (Selman et al. 2000; Cohen et al. 2008). Zebra finches (*Taeniopygia guttata*) in experimentally cooled enclosures have demonstrated a mobilization of dietary antioxidants in response to temperature challenges (Eraud et al. 2007). Swallows in this study may be similarly upregulating their antioxidants in response to the cooler and more variable temperatures in the Golondrinas style nest-boxes.

Overall, despite a lack of overt difference in food abundance and biomass between agricultural and grassland site types (Chapter 2), it appears that both swallow body mass and measurements of oxidative stress physiology are influenced by short-term changes in insect availability. Although no differences were detected between the site types for overall population averages of body condition or physiology, conditions influencing food supply, such as agricultural pesticide use, marginal habitat degradation and loss of wetlands, are likely capable of affecting individual swallow physiology with potential consequences for long-term survival (Saino et al. 2011).

The lack of response seen in measures of feather CORT is able to provide value as well. These results demonstrate that perhaps potential differences in food availability, microclimate, or parental care were not strong enough to lead to changes in nestling CORT levels. Additionally, the study area in the Prairie Pothole Region is marked by 5-10 year cycles in water availability (Murkin et al. 2000). Each year of this study was relatively wet and characterized by good to excellent wetland conditions, and subsequently a likelihood of higher overall seasonal insect biomasses. It is plausible that during a drier climate phase, possibly when fewer aerial insects are naturally available, stronger physiological costs may be incurred for breeding and nestlings swallows, particularly at agricultural sites. Longer term studies are warranted to understand the complexity of how local declines in food abundance from agricultural intensification at the breeding site and their subsequent effects on body condition and physiology translate into key fitness parameters such as survival and reproduction.

TABLES AND FIGURES

Table 3.1: Model selection results for linear mixed effects models developed to explain variation in body condition of adult tree swallows nesting in agricultural and grassland sites in south-central Saskatchewan, 2012-2014. AIC_c refers to Akaike's Information Criterion corrected for sample size, and ΔAIC_c is the difference between the AIC_c of the best-approximating model and other models in the candidate set. Also shown are number of parameters (K), model weight and model deviance All models had random effects of date, and site and year.

Model	K	AIC_c weight	Deviance	ΔAIC_c
Min.age + Sex	8	0.21	990.3	0
Min.age	7	0.18	992.8	0.5
Boxtype + Min.age + Sex	9	0.14	989.0	0.9
Boxtype + Min.age	8	0.14	991.2	0.9
Ag + Min.age + Sex	9	0.05	991.0	2.9
Min.age + Sex + 48biomass	9	0.05	991.1	2.9
Sex	7	0.04	995.7	3.3
Min.age + 48biomass	8	0.04	993.7	3.4
Intercept-only (null)	6	0.0	1006.6	12.1
Ag + Boxtype + Brood + Min.age + Sex + 48biomass (global)	12	0.0	994.6	12.8

Ag: agriculture or grassland site type

Boxtype: Long-point or Golondrinas style nest-box

Brood: nestling brood size

Min.age: minimum known age for adults (based on banding records)

48biomass: cumulative insect biomass for the 48 hours prior to sample collection

Table 3.2: Model selection results for linear mixed effects models developed to explain variation in antioxidant counts (OXY) of adult tree swallows nesting in agricultural and grassland sites in south-central Saskatchewan, 2012-2014. AIC_c refers to Akaike's Information Criterion corrected for sample size, and ΔAIC_c is the difference between the AIC_c of the best-approximating model and other models in the candidate set. Also shown are number of parameters (K), model weight and model deviance. All models had random effects of date, and site and year (correlated intercept and slope model).

Model	K	AIC_c weight	Deviance	ΔAIC_c
BoxType + 48biomass	8	0.21	1445.5	0.0
Ag + BoxType + 48biomass + Ag*48biomass	10	0.17	1441.8	0.5
BoxType	7	0.15	1448.3	0.7
Ag + BoxType + 48biomass	9	0.15	1444.1	0.7
Ag + BoxType	8	0.12	1446.7	1.2
48biomass	7	0.04	1451.1	3.5
Ag + 48biomass + Ag*48biomass	9	0.04	1446.9	3.5
BoxType + Sex + 48biomass	9	0.04	1447.0	3.6
BoxType + Brood + 48biomass	9	0.03	1447.1	3.7
Ag + 48biomass	8	0.03	1449.3	3.8
Intercept-only (null)	6	0.03	1453.5	3.8
Ag + BoxType + Sex + Brood + Min.age + BC + 48biomass (global)	13	0.0	1457.1	24.4

Ag: agriculture or grassland site type

BC: adult body condition

Boxtype: Long-point or Golondrinas style nest-box

Brood: nestling brood size

Min.age: minimum known age for adults (based on banding records)

48biomass: cumulative insect biomass for the 48 hours prior to sample collection

Table 3.3: Model selection results for linear mixed effects models developed to explain variation in oxidative damage (ROMs) of adult tree swallows nesting in agricultural and grassland sites in south-central Saskatchewan, 2012-2014. AICc refers to Akaike’s Information Criterion corrected for sample size, and $\Delta AICc$ is the difference between the AICc of the best-approximating model and other models in the candidate set. Also shown are number of parameters (K), model weight and model deviance. Models including 48-hour insect biomass, as has been used previously, were unable to converge, so 48-hour insect abundance was included instead. All models had random effects of date, and site and year (correlated intercept and slope model).

Model	K	AIC_c weight	Deviance	ΔAIC_c
Sex	7	0.89	382.8	0.0
Boxtype + Sex	8	0.04	386.8	6.1
Min.age + Sex	8	0.02	388.0	7.3
BC + Sex	8	0.02	388.7	7.9
Brood + Sex	8	0.02	388.8	8.1
BoxType + Min.age + Sex	9	0.0	392.0	13.4
BC + BoxType + Sex	9	0.0	392.7	14.1
BoxType + Brood + Sex	9	0.0	392.7	14.1
BC + Min.age + Sex	9	0.0	393.9	15.3
Brood + Min.age + Sex	9	0.0	394.0	15.3
Intercept-only (null)	6	0.0	431.8	46.9
Ag + BoxType + Sex + Brood + BC + Min.age + 48abundance (global)	13	0.0	382.78	55.9

Ag: agriculture or grassland site type

BC: adult body condition

Boxtype: Long-point or Golondrinas style nest-box

Brood: nestling brood size

Min.age: minimum known age for adults (based on banding records)

48abundance: cumulative insect abundance for the 48 hours prior to sample collection

Table 3.4: Model selection results for linear mixed effects models developed to explain variation in oxidative stress (OS, or ROMs/OXY) of adult tree swallows nesting in agricultural and grassland sites in south-central Saskatchewan, 2012-2014. AICc refers to Akaike's Information Criterion corrected for sample size, and $\Delta AICc$ is the difference between the AICc of the best-approximating model and other models in the candidate set. Also shown are number of parameters (K), model weight and model deviance. An intercept-only model is not included, as it was unable to converge. All models had random effects of date, and site and year (correlated intercept and slope model).

Model	K	AICc weight	Deviance	$\Delta AICc$
Ag + Sex	8	0.55	673.8	0
Ag + Sex + 48biomass + 48biomass ²	10	0.14	672.2	2.6
Ag + Sex + 48biomass	9	0.13	674.4	2.8
Ag + Sex + 48biomass + Ag*48biomass	10	0.05	674.0	4.5
Ag + BoxType + Sex	9	0.04	677.0	5.4
Ag + Min.age + Sex	9	0.02	678.0	6.3
Ag + BC + Sex	9	0.02	678.2	6.5
Ag + Brood + Sex	9	0.02	678.6	7
Ag + BoxType + Sex + 48biomass	10	0.01	677.7	8.2
Ag + Min.age + Sex + 48biomass	10	0.0	678.7	9.1
Ag + BoxType + Sex + Brood + Min.age + BC + 48biomass + Ag*48biomass + Ag*Sex (global)	16	0.0	698.9	43.4

Ag: agriculture or grassland site type

BC: adult body condition

Boxtype: Long-point or Golondrinas style nest-box

Brood: nestling brood size

Min.age: minimum known age for adults (based on banding records)

48biomass: cumulative insect biomass for the 48 hours prior to sample collection

Table 3.5: Model selection results for linear mixed effects models developed to explain variation in antioxidant counts (OXY) of nestling tree swallows monitored on agricultural and grassland sites in south-central Saskatchewan, 2012-2014. AICc refers to Akaike's Information Criterion corrected for sample size, and $\Delta AICc$ is the difference between the AICc of the best-approximating model and other models in the candidate set. Also shown are number of parameters (K), model weight and model deviance. All models had random effects of date, nest ID (including box and year), and site and year (correlated intercept and slope model).

Model	K	AICc weight	Deviance	$\Delta AICc$
Ag + BoxType + 48biomass + Ag*48biomass	11	0.34	1348.5	0.0
Ag + BoxType + Age + 48biomass + Ag*48biomass	12	0.13	1348.5	2.2
Ag + BoxType + Brood + 48biomass + Ag*48biomass	12	0.12	1348.7	2.3
Ag + BoxType + Brood + 48biomass + Ag*Brood + Ag*48biomass	13	0.09	1347.2	3.1
BoxType + 48biomass	9	0.07	1356.3	3.6
Ag + BoxType + 48biomass	10	0.06	1354.7	4.1
Ag + BoxType + Brood + Age + 48biomass + Ag*48biomass	13	0.05	1348.8	4.6
Ag + BC + BoxType + 48biomass + Ag*48biomass	12	0.04	1351.6	5.2
Ag + BoxType + Brood + Age + 48biomass + Ag*Brood + Ag*48biomass	14	0.04	1347.3	5.4
Ag + 48biomass + Ag*48biomass	10	0.03	1356.1	5.5
BoxType + Age + 48biomass	10	0.03	1356.4	5.8
Ag + BoxType + Brood + BC + Age + 48biomass + Ag*48biomass + Ag*Brood (global)	15	0	1353.9	16.3
Intercept-only (null)	7	0	1375.2	18.3

Ag: agriculture or grassland site type

BC: nestling body condition

Boxtype: Long-point or Golondrinas style nest-box

Brood: nestling brood size

Age: Nestling age (in days)

48biomass: cumulative insect biomass for the 48 hours prior to sample collection

Table 3.6: Model selection results for linear mixed effects models developed to explain variation in oxidative damage (ROMs) of nestling tree swallows monitored on agricultural and grassland sites in south-central Saskatchewan, 2012-2014. AICc refers to Akaike's Information Criterion corrected for sample size, and $\Delta AICc$ is the difference between the AICc of the best-approximating model and other models in the candidate set. Also shown are number of parameters (K), model weight and model deviance. All models had random effects of date, nest ID (including box and year), and site and year (correlated intercept and slope model).

Model	K	AIC _c weight	Deviance	ΔAIC_c
48biomass + 48biomass ²	9	0.49	368.2	0.0
48biomass	8	0.31	371.2	0.9
BoxType + 48biomass	9	0.07	372.1	3.9
Ag + 48biomass	9	0.03	373.6	5.5
Age + 48biomass	9	0.03	373.8	5.6
Ag + 48biomass + Ag*48biomass	10	0.02	372.1	6.1
Intercept-only (null)	7	0.02	378.7	6.3
BoxType	8	0.01	377.9	7.7
BC + 48biomass	9	0.01	376.4	8.3
Brood + 48biomass	9	0.01	376.5	8.3
Ag + BoxType + 48biomass	10	0.0	374.7	8.7
BoxType + Age + 48biomass	10	0.0	374.8	8.8
Ag + BoxType + Brood + BC + Age + 48biomass + Ag*48biomass (global)	14	0.0	390.8	35.6

Ag: agriculture or grassland site type

BC: nestling body condition

Boxtype: Long-point or Golondrinas style nest-box

Brood: nestling brood size

Age: Nestling age (in days)

48biomass: cumulative insect biomass for the 48 hours prior to sample collection

Table 3.7: Model selection results for linear mixed effects models developed to explain variation in oxidative stress (OS, or ROMs/OXY) of nestling tree swallows monitored on agricultural and grassland sites in south-central Saskatchewan, 2012-2014. AICc refers to Akaike's Information Criterion corrected for sample size, and $\Delta AICc$ is the difference between the AICc of the best-approximating model and other models in the candidate set. Also shown are number of parameters (K), model weight and model deviance. All models had random effects of date, nest ID (including box and year), and site and year (correlated intercept and slope model).

Model	K	AIC_c weight	Deviance	ΔAIC_c
48biomass + 48biomass ²	9	0.35	727.2	0.0
48biomass	8	0.33	729.4	0.1
Intercept-only (null)	7	0.11	733.5	2.1
Age + 48biomass	9	0.06	730.2	3.0
Ag + 48biomass	9	0.05	730.5	3.3
Age	8	0.03	733.6	4.3
BoxType + 48biomass	9	0.02	731.8	4.6
Ag + 48biomass + Ag*48biomass	10	0.01	730.8	5.7
Ag	8	0.01	735.3	5.9
Ag + Age + 48biomass	10	0.01	731.1	6.0
Brood + 48biomass	9	0.01	733.3	6.1
BoxType	8	0.01	735.5	6.2
Ag + BoxType + Brood + BC + 48biomass + Ag*48biomass (global)	14	0.0	746.9	32.7

Ag: agriculture or grassland site type

BC: nestling body condition

Boxtype: Long-point or Golondrinas style nest-box

Brood: nestling brood size

Age: Nestling age (in days)

48biomass: cumulative insect biomass for the 48 hours prior to sample collection

Table 3.8: Model selection results for linear mixed effects models developed to explain variation in nestling $CORT_f$ of tree swallows monitored on agricultural and grassland sites in south-central Saskatchewan, 2012-2014. AICc refers to Akaike's Information Criterion corrected for sample size, and $\Delta AICc$ is the difference between the AICc of the best-approximating model and other models in the candidate set. Also shown are number of parameters (K), model weight and model deviance. All models had random effects of date, nest ID (including box and year), assay number, age, and site and year (correlated intercept and slope model).

Model	K	AICc weight	Deviance	$\Delta AICc$
Intercept-only (null)	9	0.72	217.8	0.0
Brood	10	0.07	220.4	4.8
Boxtype	10	0.06	220.5	4.9
Ag	10	0.06	220.5	4.9
5day.biomass	10	0.04	221.3	5.7
BC	10	0.01	223.9	8.3
BoxType + Brood	11	0.01	223.2	9.8
Ag + Brood + BoxType + BC + Date + 5day.biomass (global)	14	0.0	242.2	37.8

Ag: agriculture or grassland site type

BC: nestling body condition

Boxtype: Long-point or Golondrinas style nest-box

Brood: nestling brood size

Age: Nestling age (in days)

5day.biomass: cumulative insect biomass for the 5 days prior to sample collection

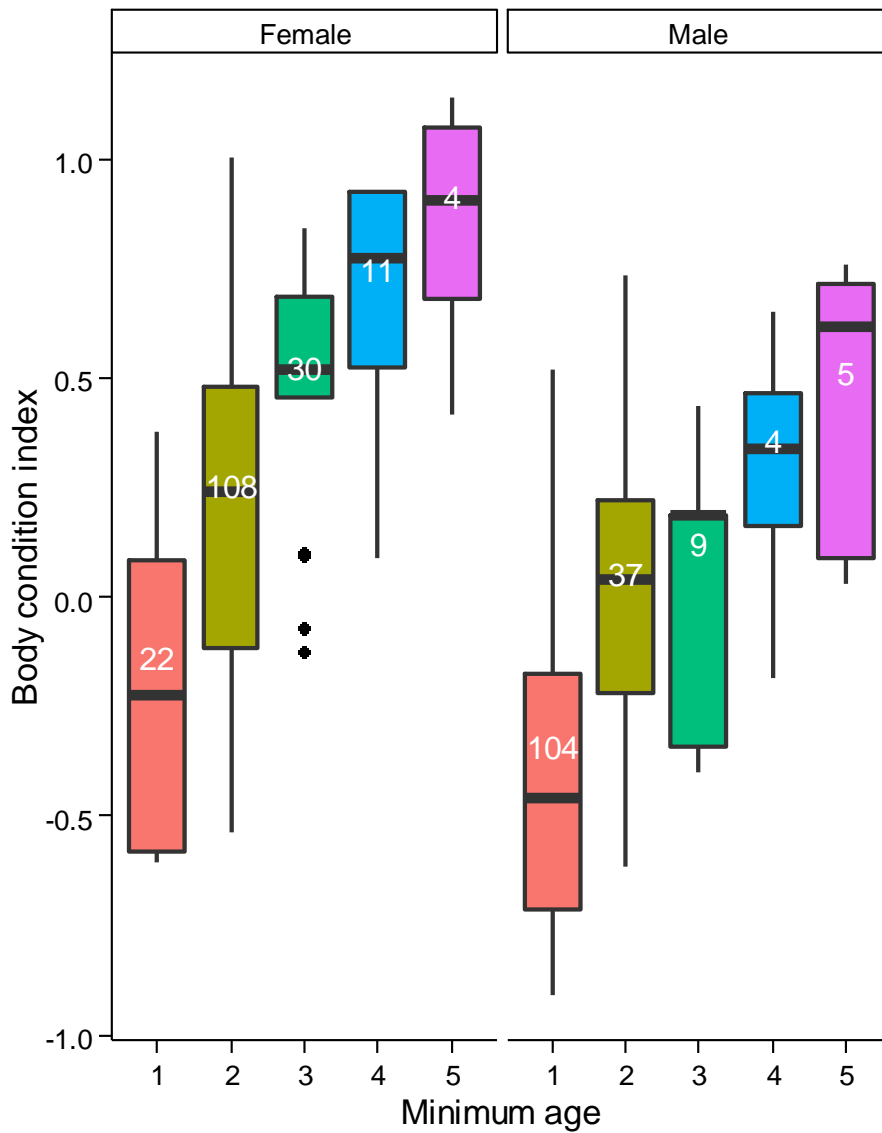


Figure 3.1: Boxplot showing the model-predicted relationship between body condition (residuals from regression of mass vs structural measures for body size) and minimum age (based on banding records) for female and male tree swallows sampled in south-central Saskatchewan, 2012-2014. The line in the middle represents the median, with the first and third quartile as the hinges, and the vertical lines are a 95% confidence interval of the median with black dots as outliers. Sample sizes given in white text.

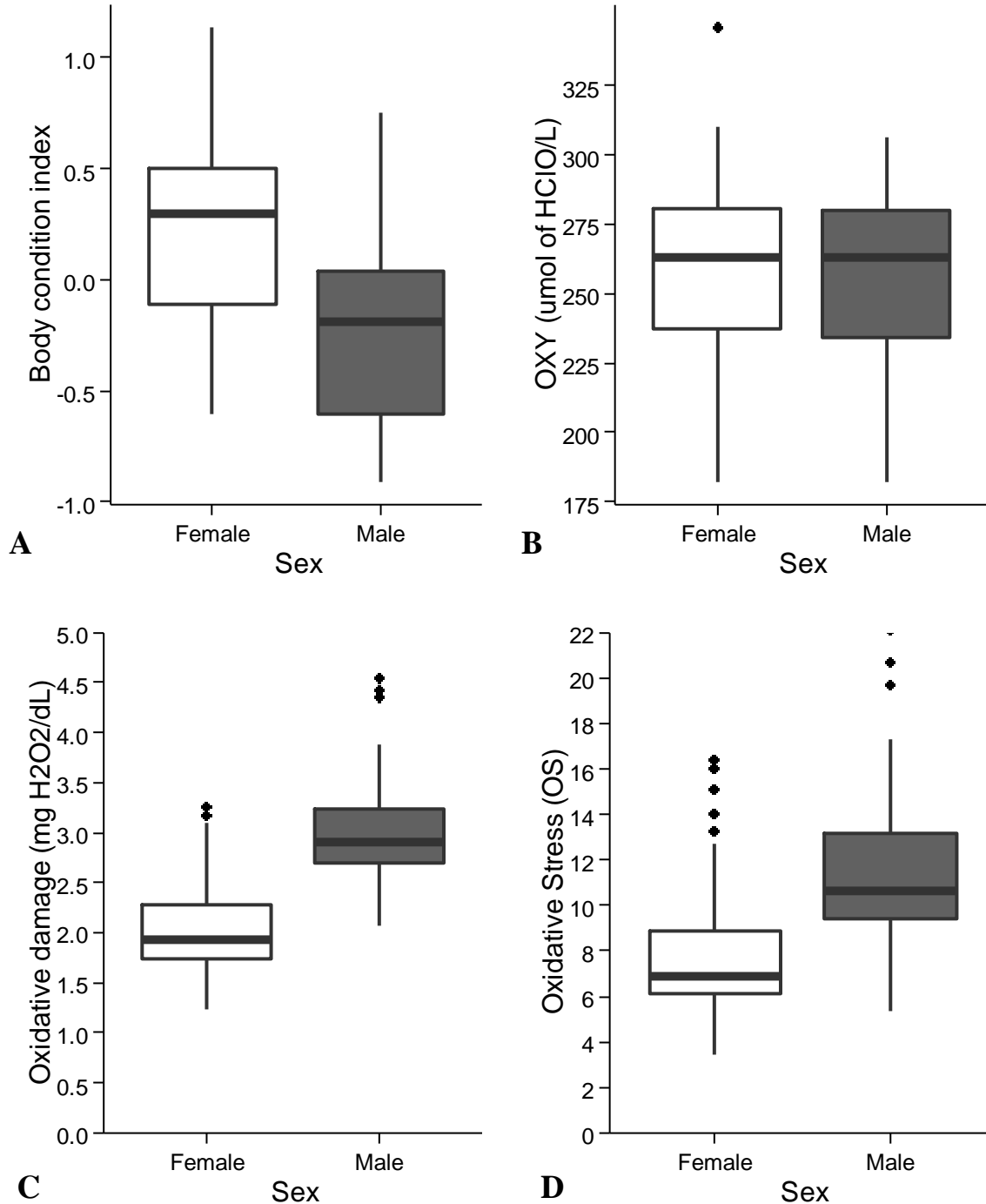


Figure 3.2: Boxplot showing sex model-predicted body condition index (A; residuals from regression of mass vs structural measures for body size), antioxidant counts (B; OXY in $\mu\text{mol of HClO/L}$), oxidative damage (C; ROMs in $\text{mg H}_2\text{O}_2/\text{dL}$), and oxidative stress (D; ROMs/OXY) for female and male tree swallows sampled in south-central Saskatchewan, 2012-2014. The line in the middle represents the median, with the first and third quartile as the hinges, and the vertical lines are a 95% confidence interval of the median with black dots as outliers

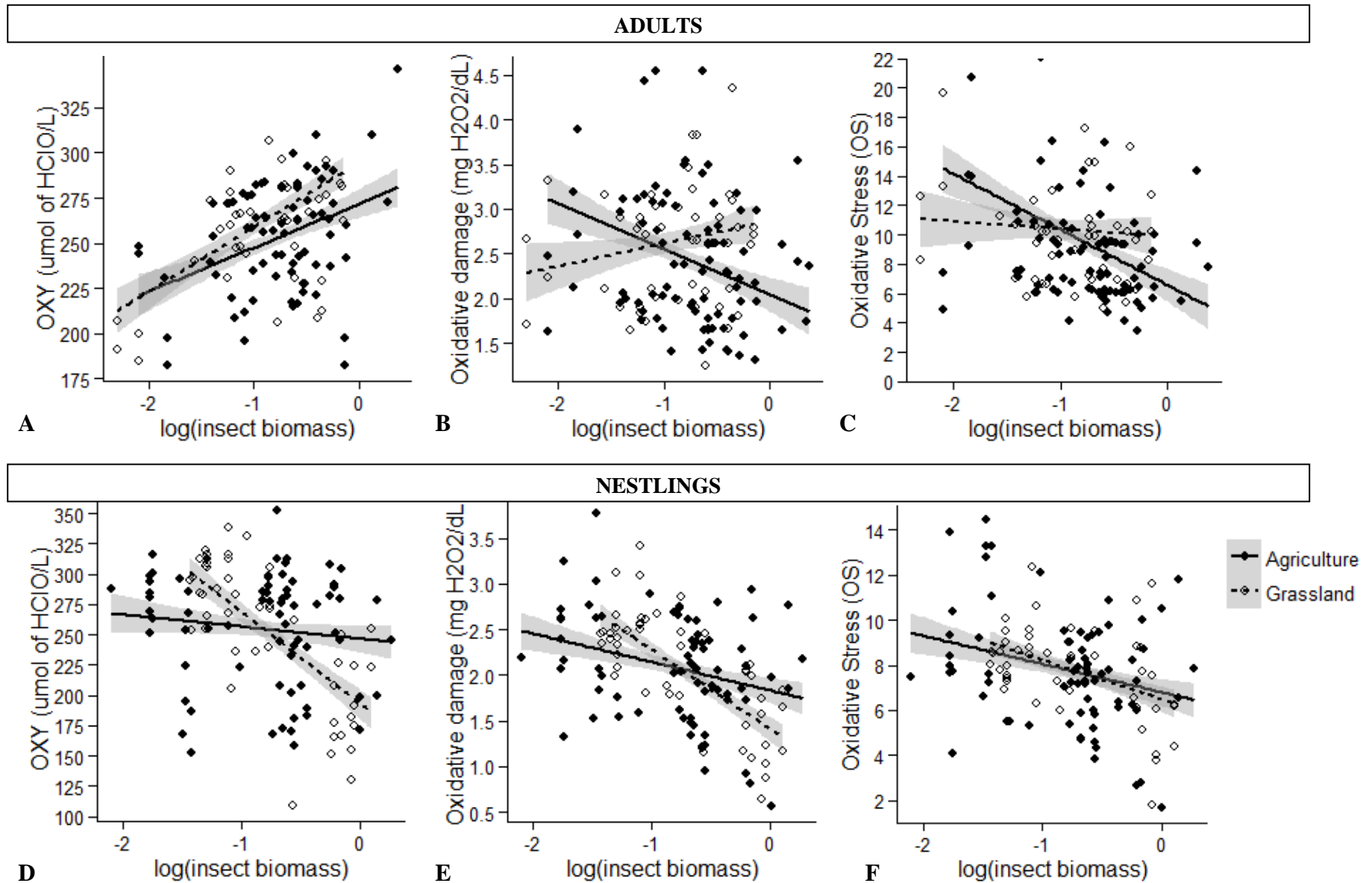


Figure 3.3: Model-predicted relationships between antioxidant counts (OXY in μmol of HClO/L), oxidative damage (ROMs in $\text{mg H}_2\text{O}_2/\text{dL}$), and oxidative stress (ROMs/OXY) and 48-hour cumulative insect biomass index for adult (A-C) and nestling (D-F) tree swallows on sites in south-central Saskatchewan, 2012- 2014. Shaded area represents 95% confidence intervals. The x-axis shows the 48-hour cumulative insect biomass.

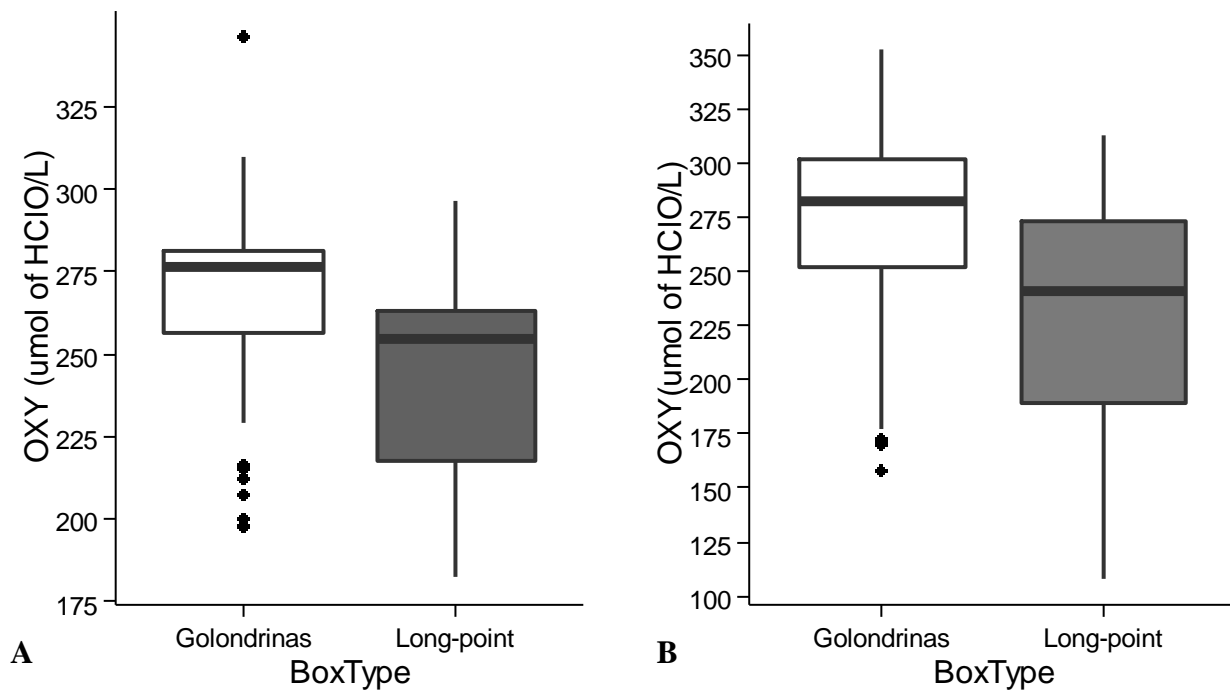


Figure 3.4: Boxplot showing model-predicted antioxidant counts (OXY in μmol of HClO/L) for adult (A) and nestling (B) tree swallows between the two nest-box types used in the study, Golondrinas and Long-Point, measured on agricultural and grassland sites in south-central Saskatchewan, 2012-2014. The line in the middle represents the median, with the first and third quartile as the hinges, and the vertical lines are a 95% confidence interval of the median with black dots as outliers.

Chapter 4

Conclusions and recommendations for future research

The broad goal of this study was to determine the mechanistic links for indirect effects of agricultural intensification on tree swallows, a species which has experienced significant annual declines in Canada over the past 30 years (Robillard, 2012). I investigated two primary questions; the first asks if insect abundance and biomass in the Canadian Prairies are affected by agriculture, and if so, how does this influence swallows' foraging behaviour? I attempted to address this in the Prairie landscape, which has a history of widespread agricultural expansion, high pesticide use, and high density wetland (Prairie potholes) landscapes. The second question follows from the first; are presumed differences in habitat quality detected through measurements of swallow physiology, return rates, and adult body condition in differing landscapes? The use of sensitive eco-physiological measurements of individuals can provide greater insight into the subtleties of habitat effects experienced by birds in agricultural environments.

It is widely accepted that monitoring and quantifying insect abundance in this wetland-dominated region has significant challenges. Here, I found no gross differences in insect abundance and biomass between agricultural and grassland sites. However, birds still showed responses that were linked to differences in site types. A common factor that predicted many of the tree swallow response variables was short term changes in insect biomass or abundance, often with a steeper response on the grassland sites. A response was seen in measures of foraging rate, nest visit intervals and oxidative stress physiology in both adult and nestling swallows, as well as adult mass. In short, swallows were responding to fluctuations in the abundance and biomass of insects. These results verify that, although questionable for between site

comparisons, the application of the passive insect samplers within each site holds merit, as well as demonstrate that changes in food supply can influence swallow physiology with potential effects on fitness. Data on the return rates further hinted that the agricultural sites were somewhat less favourable.

Despite the lack of observed effects on insect abundance and biomass between the different site types as measured by the passive samplers, several lines of evidence suggest that there may be differences in actual insect availability or habitat quality between the agricultural and grassland sites used in this study. Birds at grassland reference sites responded positively to the increases in food availability by increasing their foraging and nest provisioning, whereas those at agricultural sites were less responsive to changes in insect biomass. In addition, physiological responses to changes in insect biomass or abundance were also typically steeper on the grassland sites, hinting at a higher quality habitat.

The primary limitation of this research and my main recommendation for future work is a need for new or additional methods to better characterize and compare inter-site insect abundance and biomass. As demonstrated by the results, the passive insect samplers that were used here are reliable for detecting seasonal and temporal trends in insect biomass *within* each site; but there are many concerns raised over their reliability *between* sites. Some other methods include the use of sweep sampling, emergence or sticky traps standardized on or near wetlands or field margins at each site, providing more accurate comparisons in the aquatic insect emergence between agricultural and grassland site types and a better understanding of the prey availability.

The second recommendation would be to extend this work to conduct longer-term studies. The continuance of such a study over different climatic cycles may result in a more pronounced difference in site quality experienced under drought conditions. A drier season

would likely result in a decrease in insect availability across all sites that may exacerbate swallow responses to agriculture. As I have demonstrated, swallow physiology is indeed responding to fluctuations in prey availability, so this environmental change may potentially push the physiological boundaries of swallows on one site type more than the other. Alternatively, the use of brood manipulations may also help to tease apart differences in physiological responses across the two site types.

The final recommendation would be to pursue the influence of carry over effects through measures of feather CORT in adults, as well as obtain data on migratory and wintering locations via stable isotope analysis or new tracking methods for small birds. Swallows undergo body and flight feather molt directly following breeding, and continuing until they reach the wintering grounds in October or November (Stutchbury and Rohwer 1990). The use of stable isotopes would be useful to inform on the migratory routes and wintering locations of swallows by tracking progress through sequentially molted feathers, with primary feather molt undergoing a slow progression from P1 to P9. In addition, feathers grown on the wintering grounds can be used for CORT analysis, and to investigate whether birds experiencing higher CORT over winter are associated with a particular habitat or condition upon arrival at the breeding grounds. Miniaturized tracking devices such as geolocators have recently revealed wintering locations and migration routes. The effects of agriculture could be investigated for potential delayed impacts on migration (routes and timing), survival, and recruitment of offspring.

While tree swallows are not currently of serious conservation concern in the Prairie region, many other grassland and aerial insectivore species are experiencing even more dramatic declines (e.g. barn swallows or chimney swifts) across North America. Other species are less amenable for similar large-scale studies and will yield considerably smaller sample sizes, as

there are few avian species as well adapted for a role as a model study organism as the tree swallow. Regardless, the information obtained from responses in tree swallow provided by this work should hopefully be broadly applicable to other similar insectivorous species of conservation concern. Our conclusion that subtle changes in food availability in agricultural landscapes play a key role in swallow foraging ecology and physiology should inform the management of agricultural landscapes and the similar insectivorous birds that use these farmland habitats.

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APPENDIX 1: OXIDATIVE STRESS AND RADIOIMMUNOASSAY QA/QC DATA

Table A1.1: Coefficient of variation calculated from pooled chicken plasma samples that were used in all assays for measuring antioxidant counts (OXY-adsorbent) and oxidative damage (dROMs).

Assay	# of assays	CV
OXY-adsorbent	31	13.0%
dROMs	68	8.1%

Table A1.2: Radioimmunoassay parameters for the 9 assays used to measure CORT levels in feathers of tree swallow nestlings monitored on agricultural and grassland sites in south-central Saskatchewan, 2012-2014. TC are total count values (in CPMs). ED20, ED50, and ED80 are CORT levels in pg/100µL at 3 points on the standard curve: 20% bound, 50% bound, and 80% bound. Average SIS is the average value obtained for three steroid internal standards included in each assay.

Assay number	TC	% binding	%NSB	ED20	ED50	ED80	Average SIS	# samples
1	3988	26.9	4.0	318.9	85.1	26.2	121.8	6
2	5058	20.7	2.8	260.6	55.6	11.9	97.3	43
3	4848	23.1	3.6	288.9	65.3	14.5	125.9	36
4	4468	22.3	3.3	302.1	62.9	13.1	108.9	37
5	4226	20.3	3.2	338.7	72.9	14.3	91.6	42
6	4399	23.4	5.2	262.0	70.9	19.1	91.8	26
7	4811	20.4	5.3	268.9	61.3	13.7	113.7	42
8	4729	20.7	4.7	315.2	66.9	14.9	100.6	35
9	4691	23.7	5.4	346.8	79.2	18.1	92.1	7

APPENDIX 2: MICROCLIMATE DATA

Table A2.1: Microclimate in two different nest-box styles (G: Golondrinas, and LP: Long-Point) was monitored in tree swallow nest-boxes at 5 sites in south-central Saskatchewan, 2014.

Temperature data was collected using iButtons, small temperature loggers, over a 4 day period during nestling rearing. Two iButtons were placed in each box, one on the nest-box wall above the nest, and the other in the nest cup itself.

Box	Box Type	Nest-box wall		Nest cup	
		mean	SD	mean	SD
A11	G	18.91	3.84	34.13	2.54
A26	G	19.17	3.84	37.19	2.82
B2	G	18.46	3.45	38.17	1.28
B28	G	18.63	4.02	38.91	0.98
C18	G	19.19	3.85	35.83	3.26
C24	G	18.43	3.35	31.29	4.85
E14	G	19.51	4.56	38.45	2.67
E18	G	20.15	4.18	36.13	3.14
H13	G	18.95	3.50	38.10	2.12
H28	G	18.47	3.61	32.48	3.32
mean		18.99	3.82	36.07	2.70
A10	LP	21.25	5.77	NA	NA
A16	LP	19.38	4.74	NA	NA
B1	LP	20.43	4.94	38.57	0.88
B9	LP	19.54	3.99	38.33	0.94
C10	LP	19.98	4.60	35.56	3.74
C25	LP	20.52	5.13	36.27	2.41
H14	LP	20.89	5.14	37.00	1.96
H17	LP	22.96	5.87	32.80	4.33
E13	LP	NA	NA	37.62	3.14
mean		20.62	5.02	36.60	2.49