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Interacting effects of cold snaps, rain, and agriculture on the fledging success of a declining aerial insectivore

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Abstract

Climate change predicts the increased frequency, duration, and intensity of inclement weather periods, such as unseasonably low temperatures and prolonged precipitation. Many migratory species have advanced the phenology of important life history stages, and as a result are likely exposed to these periods of inclement spring weather more often, thus risking reduced fitness and population growth. For declining avian species, including aerial insectivores, anthropogenic landscape changes such as agricultural intensification are another driver of population declines. These landscape changes may affect the foraging ability of food provisioning parents, as well as reduce nestling's probability to survive periods of inclement weather, through for example pesticide exposure impairing thermoregulation and punctual anorexia. Breeding in agro-intensive landscapes may thus exacerbate the negative effects of inclement weather under climate change. We used daily temperatures related to significant reductions of insect prey availability (cold snaps), combined with measures of precipitation, and assessed their impact on Tree Swallow (*Tachycineta bicolor*) fledging success, a declining aerial insectivore breeding across a gradient of agricultural intensification. Fledging success decreased with the number of cold snap days experienced by a brood, and this relationship was worsened during periods of prolonged precipitation. We further found the overall negative effects of experiencing periods of inclement weather are exacerbated in more agro-intensive landscapes. Our results indicate that two of the primary hypothesized drivers of many avian population declines may interact to further increase the rate of declines in certain landscape contexts.

Key words: aerial insectivores; agricultural intensification; climate change; cold snap; fledging success; precipitation; *Tachycineta bicolor*; Tree Swallows.

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Introduction

Several avian groups are seeing dramatic population declines (Rosenberg et al. 2019). Population estimates of many North American farmland and grassland birds, including aerial insectivores, suggest declines of over 50% since the 1970s (Stanton et al. 2018, Rosenberg et al. 2019). The spatio-temporal occurrence of these declines has led to the hypothesis that they are driven by a combination of global climate change and large-scale landscape modifications (Stanton et al. 2018, Spiller and Dettmers 2019), and particularly the process of agricultural intensification (Stanton et al. 2018).

In the northern hemisphere, global climate change has resulted in earlier spring temperatures (McCarty 2001). The swift rate of change may lead to migrating species being unable to compensate for changes in thermally suitable habitats through dispersal, plasticity, or evolution (Crick 2004, Visser and Gienapp 2019). The inability of species to respond to such changes may generate or accentuate phenological mismatches between peaks of seasonal food resources and peaks in resource requirements of migratory species, and as a result, cause fitness decreases due to overall mistimed breeding schedules (Visser and Gienapp 2019). Furthermore, global climate change predicts increases in the frequency and intensity of inclement spring weather, such as swift changes in ambient temperature (e.g. cold snaps) and prolonged periods of precipitation (Rahmstorf and Coumou 2011, Wuebbles et al. 2014). Individuals experiencing such periods of inclement weather may be subjected to the reduction of temperature-dependent food resources, as well as to the additional consequence of the direct effects of poor weather on thermoregulation, and may thus incur reductions in annual fitness (Pipoly et al. 2013, Moreno et al. 2015, Arbeiter et al. 2016, Marcelino et al. 2020). Therefore, migrating species adapting to global changes through advancing their spring migration, may be at greater risk of experiencing

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periods of inclement weather (Both et al. 2010, Visser and Gienapp 2019). The phenological advancement of several declining species has recently been observed (Dunn and Winkler 1999, Møller et al. 2006, Townsend et al. 2013, Bourret et al. 2015). For example, two Tree Swallow (*Tachycineta bicolor*) populations located respectively in Ontario, Canada, and New York State, USA, observe both chronic population declines and advanced clutch initiation dates (Dunn and Winkler 1999, Shutler et al. 2012). During the same period of declines, a significant increase in the number of poor weather days (e.g., unseasonably low temperatures or prolonged precipitation) was observed and resulted in elevated nestling mortality associated with these poor weather days (Cox et al. 2019, Shipley et al. 2020).

The declines of farmland and grassland birds are correlated with not only climate change but also with the process of agricultural intensification (Stanton et al. 2018, Spiller and Dettmers 2019). Hypothesized agricultural drivers of declines are divided into direct (e.g., habitat loss, mechanization resulting in nest destruction, or acute pesticide exposure) and indirect effects, principally through the reduction in prey availability or sublethal pesticide exposure (Benton et al. 2003, Stanton et al. 2018). Certain agricultural practices are observed to alter insect populations and communities through changes in abundance, phenology, or species composition and interactions (Grüebler et al. 2008, Pisa et al. 2015, Wagner 2020). Insectivorous birds breeding in modern agricultural landscapes, including aerial insectivores, could thereby be subjected to reduced availability of prey items (Poulin et al. 2010, Nocera et al. 2012, Garrett et al. 2021a).

Agricultural drivers of population declines may also impact the physiology of birds in ways that influence their capacity to respond adaptively to periods of inclement weather. For instance, sublethal exposure to organophosphate and carbamate insecticides may induce short-lived

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hypothermia, likely due to the impairment of thermoregulation (Grue et al. 1997). Moreover, sublethal exposure to neonicotinoid insecticides may result in anorexia (Eng et al. 2019), thereby aggravating reduced thermoregulatory capacity and other challenges posed by reduced prey availability (Garrett et al. 2021a). Birds breeding within more agro-intensive landscapes are at elevated risk of exposing themselves or their offspring to such agents (DiBartolomeis et al. 2019, Malaj et al. 2020, Sigouin et al. 2021) and may subsequently be less likely to survive through periods of poor weather. Furthermore, landscapes dominated by row crop monocultures express landscape simplification in which large swaths of areas are occupied by only a handful of habitats (Benton et al. 2003). This phenomenon may make finding and exploiting suitable food resources more difficult for animals relying upon "residual" marginal habitats, as landscape simplification lowers the functional connectivity of agricultural landscapes (Hinsley 2000, Bélisle 2005, Rainho and Palmeirim 2011). Parents may compensate for poor breeding landscape quality by increasing foraging effort, but such increases may result in reduced body condition (Hinsley 2000, Olsson et al. 2008). Periods of inclement weather may thus exacerbate the added stressors stemming from breeding within more agro-intensive landscapes (Stanton et al. 2016, Staggenborg et al. 2017, Evens et al. 2018, Garrett et al. 2021b). Therefore, given that selection favors earlier breeding events (Sheldon et al. 2003, Porlier et al. 2012, Marrot et al. 2017), it seems imperative to evaluate how the expected increase of inclement weather events may interact with the consequences of breeding within more agro-intensive landscapes.

Here we present the results of an 11-year study monitoring the breeding success of a Tree Swallow population experiencing a wide range of spring temperatures and precipitation. This population breeds within a nesting box system placed along a gradient of agricultural intensification in southern Québec, Canada. We first identified a critical temperature in which

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the availability of their main prey, namely Diptera (Bellavance et al. 2018), changed significantly, using an approach similar to Winkler et al. (2013). We then defined days in which ambient temperature fell below this critical temperature as a day representing a cold snap. We then evaluated the interacting roles that cold snaps, prolonged precipitation and the gradient of agricultural intensification had on fledging success within this population. As observed by Cox et al. (2019) and Shipley et al. (2020), we expected cold snaps to reduce fledging success, and the effect size to increase with both the duration of the cold snap and the total amount of precipitation. Finally, we expected the severity of these relationships to increase as breeding landscapes became increasingly composed of agro-intensive cultures.

Methods

Study area and nest box system

Between 2006 and 2016, we monitored breeding attempts of Tree Swallows within 400 nest boxes dispersed across a gradient of agricultural intensification in southern Québec, Canada. Ten nest boxes were spaced approximately 50 m apart along the field margins of 40 farms, located in various agricultural landscape contexts (Figure 1; see Ghilain and Bélisle 2008 for details). The gradient of agricultural intensification was characterized by an east-west shift of agricultural production. The eastern portion of the system was composed primarily of pastures and forage crops (e.g., hay, alfalfa (*Madicago sativa*), and clover (*Trifolium spp.*)), requiring less agricultural inputs and interspersed with large expanses of forest cover. The west was dominated by large-scale row-crop monocultures (principally corn (*Zea mays*), soybean (*Glycine max*) and wheat (*Triticum spp.*)) and was denuded of forest cover (Jobin et al. 2003, Ruiz and Domon 2009). Increased use of monocultures has resulted in a near reliance on fertilizers, pesticides, mechanization and drainage of surface waters and wetlands (Jobin et al. 2003). Between 2011 to

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2019, approximately 100% of the corn and 60% of the soybean were sown as neonicotinoid-coated seeds in our study area (MDDELCC 2015). As a consequence, the rate at which several pesticides were detected above the levels deemed safe for the chronic exposure for aquatic life has increased in the surface waters of this region (Giroux 2019).

Nest box monitoring

We monitored the breeding activity in nest boxes every two days, starting prior to the arrival of Tree Swallows. This detailed monitoring allowed us to estimate the dates of laying, incubation, hatching, and fledging, as well as to record the number of eggs, nestlings, and fledglings of each breeding event. We caught and banded adult females during incubation and adult males during food provisioning. We were 99% and 80% successful, respectively, at capturing targeted adults. We applied an aluminum US Geological Survey (USGS) band containing a unique identification code to adults upon capture and nestlings at 12 days post hatching.

Insect sampling and local prey availability

Throughout the study, 2 insect traps were placed on each of the 40 farms (N=80). Traps were spaced ~ 250 m apart along the central portion of each nest box transect. Trap content was collected every two days throughout each breeding season (see Garrett et al. 2021a for details). The processing of insect samples focused on the period between 1 June and 15 July, covering the nestling rearing period of 96% of the monitored breeding attempts. The content of traps included a wide range of insects stemming from many of the surrounding habitat types, and that over lap significantly the diet of nestlings (Laplante 2013, Bellavance et al. 2018). In this system, 74% of the biomass of the food boluses provided to nestlings were Diptera (Bellavance et al. 2018), a pattern shared with other Tree Swallows study systems (Mengelkoch et al. 2004, Twining et al. 2018). We thus used the biomass of Diptera within each sample as a proxy of local prey

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availability (using the number of Diptera resulted in qualitatively similar results and Diptera was substantially favored over analyses incorporating the biomass of all insect taxa; model selection analyses not shown). Once extracted, Diptera samples were placed in an oven at 60ºC for over 24 hours, ensuring no further change in biomass occurred and were then weighed without delay to the nearest 0.0001 g. The dried biomass of Diptera from these samples (hereafter referred to as Diptera biomass) thus represents an estimate of local prey availability on a specific farm and year over the two days prior to the sample collection.

Landscape composition

Landscape composition (i.e. the relative coverage of habitats composing a given landscape) focused on habitats influential to Tree Swallows and ones composing landscapes throughout our study system (Rendell and Robertson 1989, 1990, Winkler et al. 2020). The relative cover of habitats was calculated within 500 m of nest boxes, a spatial scale in which ~80% of food provisioning adult female Tree Swallows spend their time (Elgin et al. 2020, Garrett et al. 2021b). Tree Swallows are often associated with open bodies of water and will travel distances greater than 500 m to forage over them (Elgin et al. 2020, Garrett et al. 2021b). The relative cover of this habitat within 500 m of nest boxes (0.66% ± 1.07%) and in the agricultural contexts covered by this study is low. Recognizing this habitat as important to Tree Swallows (Berzins et al. 2021), we calculated its relative cover at 3 km from nest boxes following methods presented in Garrett et al. (2021a). Calculations used vector layers acquired from the Canadian National Hydro Network (NHN, 2020) and the sf (Pebesma 2018) and rgeos (Bivand and Rundel 2019) packages in R version 3.6.2 (R Core Team 2019). Characterization within 500 m of nest boxes occurred separately for each farm at the end of each breeding season to facilitate crop identification. Parcels representing different habitats and agricultural fields were first delineated

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using orthophotos (scale 1:40,000) in QGIS (version 3.16) (QGIS 2020), and then characterized *in situ*. We determined which cultures, if any, were in agricultural fields and then reclassified them into forested, corn and soybean, forage fields (including hay, other grasses, alfalfa, clover, and pastures), and cereals (principally wheat, and to a lesser extent, oat (*Avena spp*.) and barley (*Hordeum spp*.)). We then calculated the mean percent cover of these habitats across the 10 nest boxes on each farm and for each year independently.

To obtain an integrative measure of the percent cover of habitat groups, defined as the landscape context, we used a robust principal components analysis (PCA) for compositional data (Filzmoser et al. 2009) to assign "site scores" to each of the farms during each year. Site scores were the values along the first two components of the resulting compositional PCA of each farm during each year. PCAs were fitted using the robCompositions package (Templ et al. 2011) in R, resulting in the calculation of 440 different landscape contexts (i.e. 40 farms x 11 years). Site scores were assigned to each breeding attempt and insect sample and used in all subsequent analyses.

The PCA's first component (Comp.1) explained 80.34% of the variance in landcover, correlating positively with corn and soybean and negatively with both forage fields and forest cover. The second component (Comp.2) explained 14.69% and correlated negatively with forage fields and positively with forest cover (Figure 2). To avoid overly complex models, we included only these two components to represent the landscape context. Landscapes expressed by minimizing Comp.1 and Comp.2 values represent ones for which there is an abundance of forage fields and above average forest cover and are referred to as forage landscapes.

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Weather variables

We monitored hourly temperature with iButtons (model DS1922L; Embedded Data Systems, Lawrenceburg, Kentucky, USA) attached to the underside of a single nest box on each farm. Temperatures were recorded throughout each breeding season and started prior to the spring arrival of Tree Swallows. We derived daily summaries of the minimum, mean, and maximum daily temperatures between daytime hours (05:00 to 20:00). We measured total farm-specific precipitation every two days throughout the breeding season using a single pluviometer placed on each farm and recorded measurements to the nearest 0.5 ml during each farm visit.

Statistical analyses

Cold-snap days

Cold snap values were grounded in the functional response of local prey availability to maximum daily temperature, as we expected insects to require a threshold temperature before they are active (Williams 1961, Grüebler et al. 2008). We calculated the mean maximum daily temperature between the day of and the day prior to sample collection (mean maximum daily temperature). We then used a similar approach to that of Winkler et al. (2013) using generalized additive mixed effects models (GAMMs) to model the relationship between Diptera biomass and mean maximum daily temperature to determine the temperature at which the instantaneous rate of biomass change was greatest. The cold snap threshold temperature was thus calculated as the temperature corresponding to the maximum of the first derivative of the relationship between Diptera biomass and mean maximum daily temperature. Peak rate in change was chosen because temperatures around this critical threshold likely result in dramatic differences in prey availability (Williams 1961). We undertook an extensive modeling exercise to determine the treatment of the functional relationship between these variables, including evaluating the

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hypothesis that the critical threshold temperature varies along the agricultural intensification gradient (full details in Appendix S2). Modeling used the "bam" function from the mgcv package in R (Wood 2015). Diptera biomass was modeled with a Gamma distribution with a log link function. The influence of mean maximum daily temperature was treated as a tensor product smooth, and in order to evaluate overall trends, we kept the basis dimension of this predictor low (k=10). In all models, we included the effect of Julian date of sample collection and precipitation as a tensor product smooth to account for phenological variations in biomass. We further included the year and farm as random effects to control for the hierarchical structure of the sampling design (Pedersen et al. 2019).

Fledging success

We limited analyses of fledging success to first breeding attempts (90% of all attempts and ranging between 80% and 95% across years), as reproductive success varies greatly between first and second attempts, and second attempts occur near exclusively following the failure of a nest during laying or incubation (Robertson and Rendell 2001). Fledging success was modeled as the proportion of a brood that fledged (i.e., number of successes over trials) via generalized linear mixed effects models (GLMMs) with a binomial distribution and logit link function. The year, farm, and nest box IDs were included as random factors to account for the hierarchical structure of the dataset (i.e., nest box nested within farm nested within year).

Model covariate summaries can be found in Table 1 and were averaged across a 12-day window post-hatching. This period is when Tree Swallow nestlings become homeothermic, reach peak body mass, and experience the greatest nestling mortality, thus representing the period where resource availability is presumably most crucial (McCarty and Winkler 1999, Houle et al. 2020). Cold temperatures and precipitation may act both directly on nestlings through thermoregulation

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and indirectly through a reduction in resource availability. To control for trophic mediated indirect effects of weather on fledging success, we desired estimates of local prey availability during the nestling rearing period of each breeding attempt. Prey availability was represented by predictions from generalized additive models (GAMs) in which raw values of Diptera biomass were regressed against the Julian date of sample collection for each farm and year separately. Modeled Diptera availability captures its general phenology throughout each season, avoiding biases caused by more punctual or local disturbances or phenomena such as the capture of an insect swarm. From these predictions, we calculated an estimate of the mean prey availability during the respective 12-day window of each breeding attempt. GAMs were fitted as a tensor product smoother using the mgcv package in R and an identical degree of smoothness (k=10).

We took an information theoretic and multimodel approach to assess how weather influenced fledging success and if its effect varied with landscape context (Burnham and Anderson 2002). We compared a set of competing models, including a Null model with only random effects. These data were previously used to determine the combined influence of prey availability and landscape context within our study area on fledging success, and as a result a most predictive and parsimonious model had then been determined (Garrett et al. 2021a). We thus compared all subsequent models to this base model (Base). This model included the age of the breeding female [second year (SY) vs. after second year (ASY); (Robertson and Rendell 2001)], hatching date, brood size, percent cover of open water within 3 km of the breeding attempt, and the interaction between site scores (Comp.1 and Comp.2) and prey availability estimates. To these variables we also added the number of cold snaps and the mean daily precipitation during the 12 days following hatching, including the interaction between these variables, as these factors are identified as influential to Tree Swallows from other study systems (Cox et al. 2019, Shipley et

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al. 2020). All model terms within Base were included in all subsequent models of the candidate set. Principal interests were in the interactive effects of cold snaps, precipitation, and the gradient of agricultural intensification on fledging success. We included models with interaction terms between Comp.1 and the number of cold snaps (Base + Land*Snap), between Comp.1 and the mean precipitation (Base + Land*Rain), or both of these interaction terms (Base + Land*Snap + Land*Rain). We further predicted these factors may interact with one another and included a model with a three-way interaction between these three variables (Base + Land*Snap*Rain).

The effects of key individual variables, including interactions, were estimated via multi-model inference whereby predictions were calculated by model-averaging with shrinkage and shown with their 95% unconditional confidence intervals (Burnham and Anderson 2002). All quantitative covariates were z-transformed, *R*-squares calculated following Nakagawa and Schielzeth (2013), and analyses performed in R using the glmmTMB (Brooks et al. 2017) and AICcmodavg (Mazerolle 2020) packages. Model validation, including evaluation of normally distributed residuals (simulated), heteroskedasticity, and collinearity checks with variance inflation factors (VIFs), followed Zuur et al. (2009) and used the DHARMa package (Hartig 2020).

Results

Effects of temperature on local prey availability

We collected and processed 15,916 insect samples from 8,614 farm visits. Mean Diptera biomass (± SD) was 0.030 ± 0.044 g (per trap), ranging between 0.019 g and 0.037 g across years. Overall mean maximum daily temperature (± SD) was 25.7°C ± 4.1 ranging between 24.1°C and 26.6°C across years. The greatest instantaneous rate of change in Diptera biomass occurred at 18.2°C (Figure 3, A and B). Around this critical threshold, a two degree decrease or increase in

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maximum daily temperature led to a 13.4% drop or 15.1% rise in Diptera biomass, respectively. Based on this threshold, 8.2% of farm visits followed at least one cold snap (Appendix S1: Figure S1).

Effects of inclement weather on fledging success

We monitored the breeding activity of 1,897 nests across the 40 farms and 11 breeding seasons. Overall mean fledging success (± SD) was 0.74 ± 0.38, varying between 0.63 and 0.88 among years. Overall mean number of cold snap days (± SD) experienced by a brood during its first 12 days was 0.9 ± 1.1 days and varied between 0.2 and 2.3 days between years (Figure 4). At least 52% of broods experienced at least one cold snap day throughout the duration of the study; 24%, 11% and 4% of broods experienced at least 2, 3 and 4 cold snap days, respectively. Mean daily precipitation during the first 12 days (± SD) was 3.4 ± 2.3 ml, ranging between 1.2 and 6.8 ml across years. The correlation between the number of cold snap days and mean daily precipitation experienced by a brood was relatively low (r=0.08; Figure 4).

Models incorporating an interaction between Comp.1 and the number of cold snap days (combined AICc w > 0.99) were substantially supported over Base (ΔAICc > 14.11, Appendix S1: Table S1). Fledging success decreased with the number of cold snap days (Figure 5). Fledging success was on average 40.8% lower when broods experienced four cold snap days in their first 12 days instead of none. Increasing precipitation had a negative effect on fledging success, especially when broods were subjected to both several cold snap days and high daily amounts of precipitation (Figure 5). Broods subjected to four cold snap days versus none showed up to a 45.2% reduction in fledging success if exposed to the 95th percentile of observed values for mean daily precipitation. The effects of weather varied with landscape context (Figure 6). During periods of either increased cold snap days or precipitation, higher levels of agro-intensive

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cover were associated to further reductions in fledging success (Figure 6). Without any cold snap days and under mean daily precipitation, fledging success was 4.8% greater in the most agro-intensive landscapes compared to forage landscapes. Yet, fledging success decreased by 44.2% along the agricultural intensification gradient when broods experienced four cold snap days and average precipitation. The synergistic negative effect of the number of cold snap days and high amount of precipitation on fledging success was, however, far greater in agro-intensive than in forage landscapes: in the absence of precipitation, the negative effect of increasing cold snap days was substantial only in agro-intensive landscapes, but similarly detrimental over the entire intensification gradient under high precipitation levels (Figure 6). Lastly, fledging success increased with local prey availability and percent cover of surface water within 3 km, it decreased with increasing hatching day and brood size, and was lower for SY than ASY females (Figure 5).

Discussion

An outcome of climate change is the increased frequency and duration of weather events potentially reducing the availability of thermally sensitive prey resources (Rahmstorf and Coumou 2011, Wuebbles et al. 2014). These reductions, when occurring during critical life history stages (e.g. nestling periods), reduce the fitness of avian aerial insectivores (Pipoly et al. 2013, Moreno et al. 2015, Arbeiter et al. 2016). Though climate change influences a vast array of species and their interactions, another large-scale continued threat to biodiversity is anthropogenic reductions in habitat amounts and quality, notably through forestry and agriculture (Maxwell et al. 2016). We contended that the use of certain habitats may pose a risk to an animal's ability to breed or survive through periods of reduced food availability and/or poor weather. We provide evidence that the negative impact of weather conditions expected from

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climate change on the annual breeding success of an aerial insectivore are exacerbated in habitats created by agricultural intensification.

The relationship between prey availability and mean maximum temperature, between the day of and day prior to sample collection, revealed the rate of change in prey availability was maximized at a temperature (18.2°C) similar to that deemed critical in past works (18.5°C; Winkler et al. 2013, Cox et al. 2019, Shipley et al. 2020). Such similarity may highlight a generality to temperatures impactful to Tree Swallows and their prey. We further found that this temperature threshold did not vary across the large-scale gradient of agricultural intensification studied here.

In accordance with previous studies, the appearance and frequency of cold snaps during the 12-day post hatching period of each brood led to reduced fledging success of Tree Swallows. This effect increased when cold snaps coincided with periods of prolonged rain. Most notably, the negative effect of poor weather was worse for breeding attempts in more agro-intensive landscapes. Such a result suggests features associated to these landscapes exacerbate the consequences of broods experiencing poor weather.

We propose two non-mutually exclusive mechanisms for such a finding: the structural characteristics of agro-intensive landscapes and the likelihood of exposure to agrochemical agents. Successfully acquiring food during periods of poor weather potentially result in greater costs for food provisioning parents, inasmuch as the increased foraging effort needed to overcome the reduced availability of prey likely results in reduced body condition (Hinsley 2000, Evens et al. 2018). Parents may possibly forgo foraging during poor weather periods in order to brood nestlings and provide food at greater rates once poor weather has subsided (Cox et al. 2019). Given the homogeneity of intensively-managed agricultural landscapes, prey patches may

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be fewer or farther apart therein (Benton et al. 2003, Fahrig et al. 2011). Increased foraging efforts following poor weather events may come at greater costs to foragers breeding in agro-intensive landscapes where energetic gain rates are already lower (Stanton et al. 2016, Garrett et al. 2021b). Furthermore, agro-intensive landscapes tend to be denuded of structural habitats (e.g. woodlots and hedgerows) (Figure 1; Benton et al. 2003, Fahrig et al. 2011). In addition to being prey habitat, these features may block wind, and their removal may limit prey aggregation (Evans et al. 2003, Grüebler et al. 2008) and facilitate heat dissipation of nests (Heenan 2013). Moreover, the likelihood of a brood to encounter a cold snap was greater within less agro-intensive landscapes (Appendix S3), suggesting we underestimate the consequences of rearing young within agro-intensive landscapes.

Evidence suggest several commonly used agrochemical agents can alter avian physiology, potentially hindering their response to poor weather (Mayne et al. 2005, Mineau and Palmer 2013, Lopez-Antia et al. 2015, Gibbons et al. 2015), most notably through a reduction in thermoregulatory capacity (Grue et al. 1997). These same agents may also influence the ability for food provisioning parents to optimize foraging strategies, by inducing anorexia and impairing locomotor function and navigational capacity (Eng et al. 2019). These factors illustrate that within more agro-intensive landscapes, food provisioning parents may present longer foraging bouts, potentially at a cost to their own body condition, while also reducing the time spent brooding nestlings.

Our conclusions, as well as predicted impacts of climate change on aerial insectivores, assume food provisioning adults are unable or less capable to forage during periods of poor weather. However, fine scale movements of small passerines are becoming less difficult to monitor (Elgin et al. 2020, Garrett et al. 2021b), understanding such movements may further elucidate the

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combined roles of breeding habitat quality and predictions of climate change on animal behavior. For instance, the increased food provisioning of nestlings by adults, following periods of poor weather (Cox et al. 2019), may be facilitated by foraging in more profitable habitat patches (Elgin et al. 2020, Geary et al. 2020, Garrett et al. 2021b). In the context of climate change, the combined roles of poor weather and landscape structure on foraging responses is still unknown. Validation of these assumptions will be imperative as the effectiveness of food provisioning, during periods of poor weather, likely varies across a gradient of breeding landscape quality. Finally, a focus here was on the effects of cold snaps, yet another growing concern of climate change are periods of high ambient temperature [i.e., heat waves; (Perkins-Kirkpatrick and Lewis 2020)]. The energetic expenditure of food provisioning Tree Swallows is potentially constrained by an upper thermal limit (Tapper et al. 2020). Moreover, prey availability decreased sharply above 30ºC in our study system (Figure 3A). Food provisioning parents may thus be hindered and the effects of breeding within more agro-intensive landscapes may further be exacerbated during heat waves. Future work should focus on evaluating this hypothesis, as reduced food provisioning potentially results in reduced nestling growth and survival (Cox et al. 2019, Garrett et al. 2021b).

Aerial insectivore populations are witnessing significant reductions in several parts of their North American and European breeding grounds (Spiller and Dettmers 2019, Rosenberg et al. 2019, Bowler et al. 2019), and we provide evidence that two of the primary hypotheses explaining reductions may interact to further intensify these declines. We propose that future work investigating aerial insectivore declines should explicitly focus not only on climate change or anthropogenic reductions or alterations of breeding habitats, but also on how these factors may interact with one another.

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Tables and figures

Table 1: Mean (±SD) of covariates used to model fledging success of 1,897 Tree Swallow broods between 2006 and 2016. Covariates were averaged over a 12-day period after hatching. Variable groups identify which covariates were present within models found in Appendix S1: Table S1.

Covariate	Acronym	Unit	Mean ± SD	Variable group
Site score Comp.1	Comp.1	-	0.20 ± (1.80)	Base/Land
Site score Comp.2	Comp.2	-	-0.18 ± (0.91)	Base/Land
Cold snap days	CSD	(day)	0.91 ± (1.12)	Base/Snap
Precipitation	RN	(ml)	6.81 ± (4.51)	Base/Rain
Open water	WT	(%)	0.01 ± (0.01)	Base
Prey availability	PA	(g)	0.03 ± (0.02)	Base
Hatching day	HD	(Julian day)	159.91 ± (5.76)	Base
Brood size	NN	(nestlings)	4.83 ± (1.27)	Base

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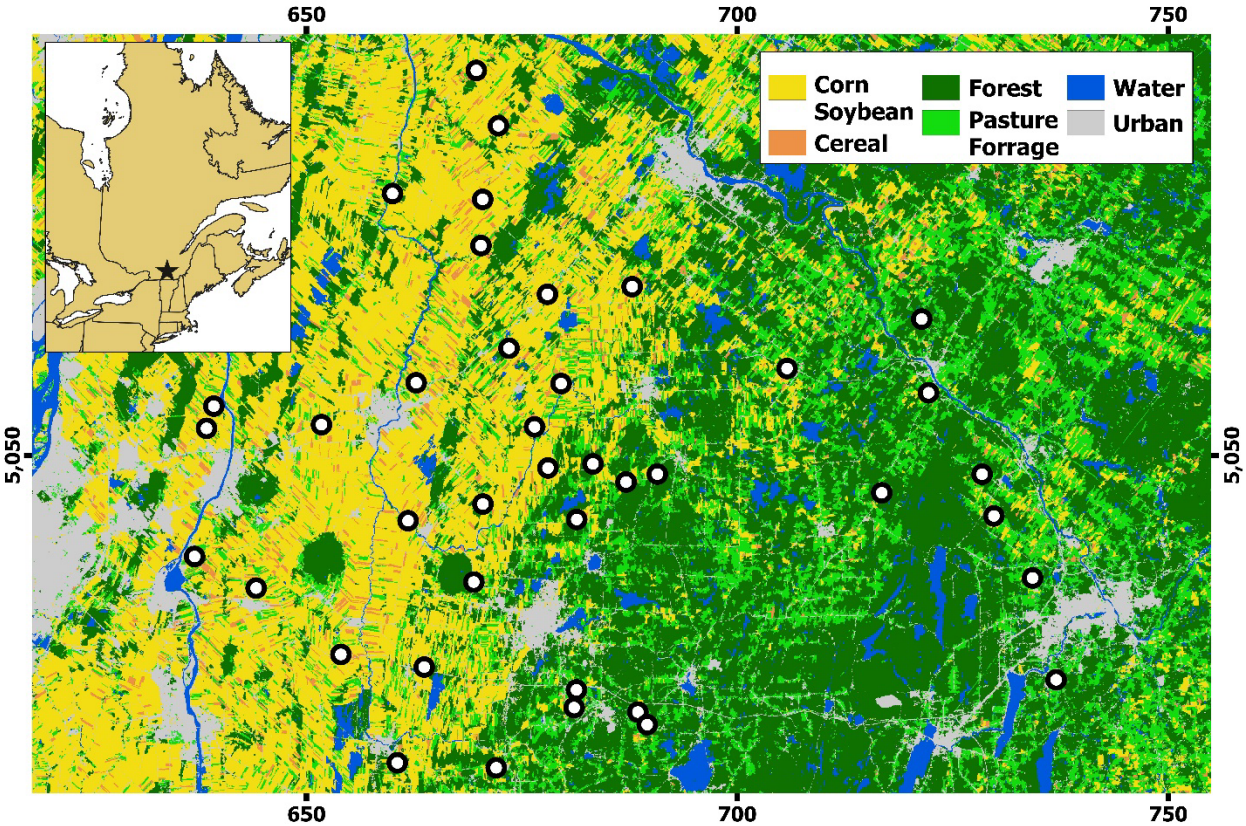

Figure 1: Location of the 40 farms (white dots) monitored across a gradient of agricultural intensification within southern Québec, Canada. Underlying image represents the agricultural gradient derived from the Annual crop inventory of 2013 (AAFC, 2018). Each pixel is either one of the five higher order land cover categories or open water. The star within inset map denotes the centroid of the study system. Projected coordinate reference system is the Universal Transverse Mercator (UTM) zone 18 north and graticules indicate the number of kilometers from some origin.

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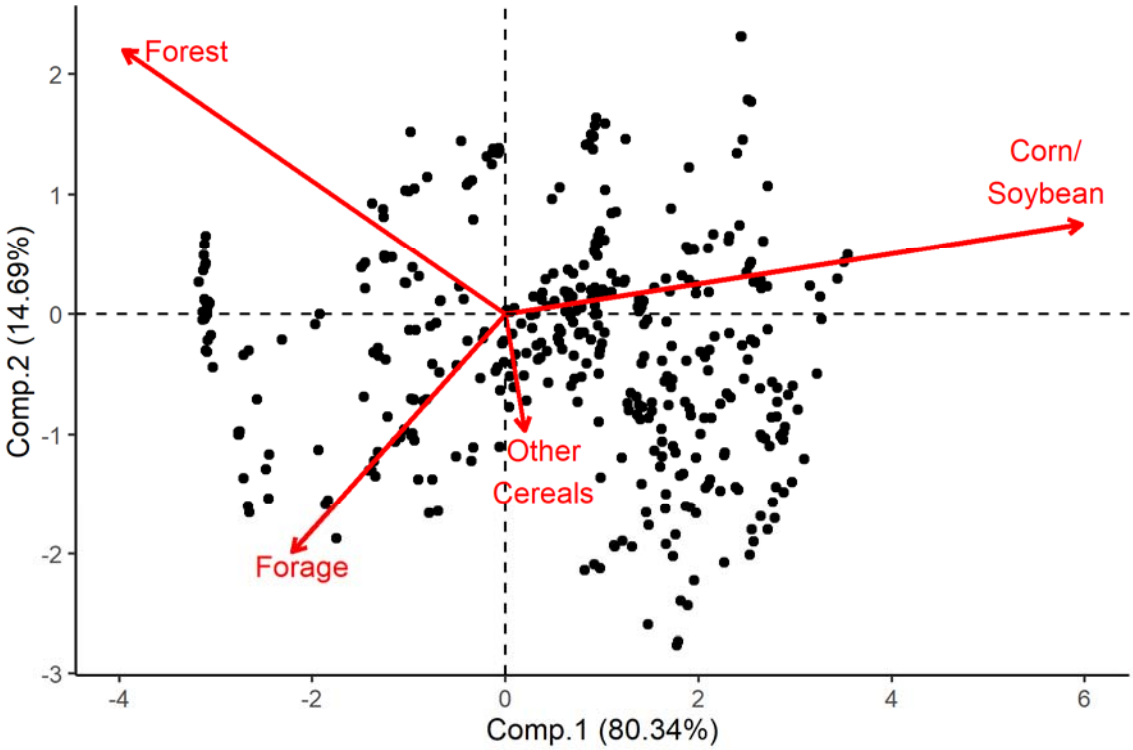

Figure 2: Robust compositional principal components analysis (PCA) of the landscape habitat composition surrounding each of the 40 farms monitored between 2006 and 2016. Arrows indicate the eigenvalue and loadings of each higher order land cover. Points within the background represent the site scores assigned to each farm and year combination and used to define the landscape context within 500 m of nest boxes (N=440 farms*years).

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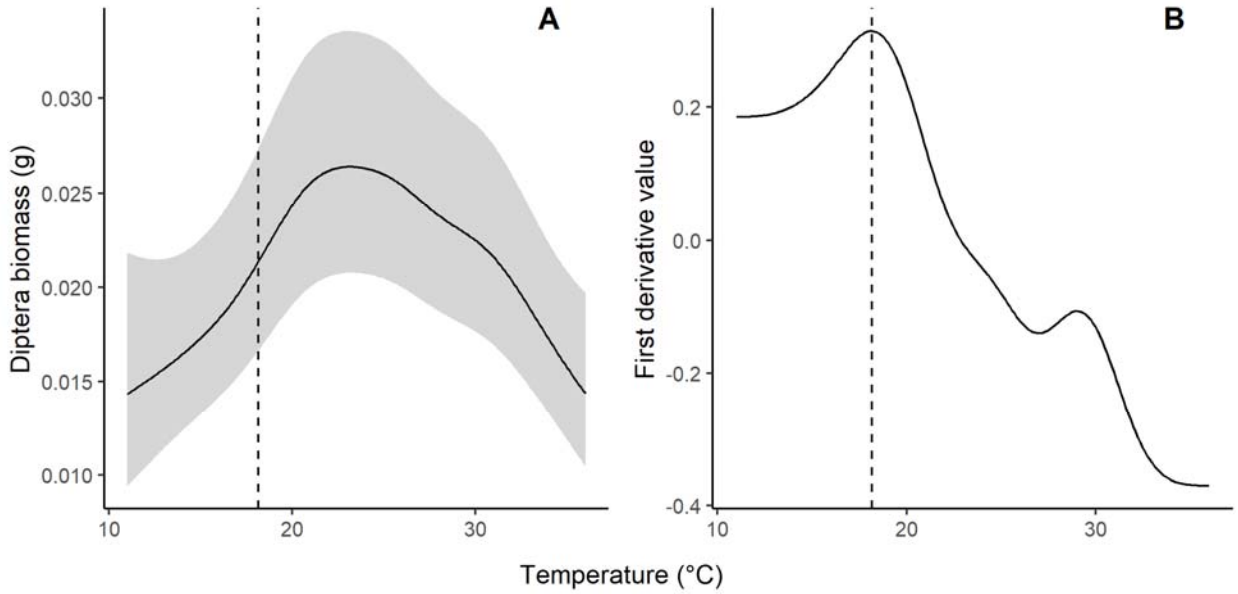

Figure 3: Functional relationship between Diptera biomass and the mean maximum temperature between the day of and day prior to sample collection (A) and the first derivative values of this relationship (B). Diptera biomass was derived with GAMMs using a Gamma distribution and a log link function. Vertical dashed line indicates the temperature at which the maximum of the first derivative was observed. Model controlled for, as tensor product smoothed terms, the Julian date and the interaction between sites score values (Comp.1 * Comp.2), and the total precipitation two days prior to insect collection (N=15,916 samples). Model also included year and farm IDs as random effects.

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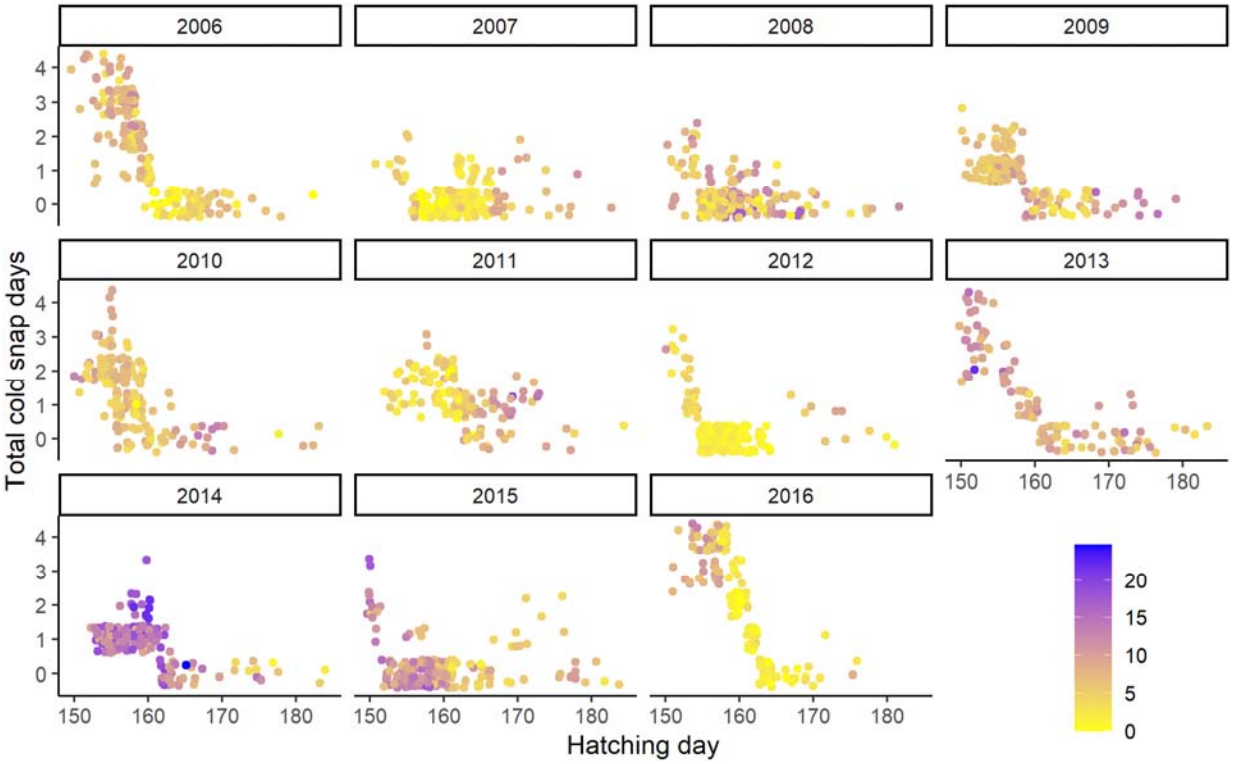

Figure 4: Number of cold snap days (jittered) experienced by Tree Swallow broods (N=1,897) according to their hatching dates between 2006 and 2016. Cold snap days were days on which maximum temperature on the farm did not surpass 18.2°C. Point color represents the mean daily precipitation volumes (ml) that broods experienced over a 12-day period after hatching.

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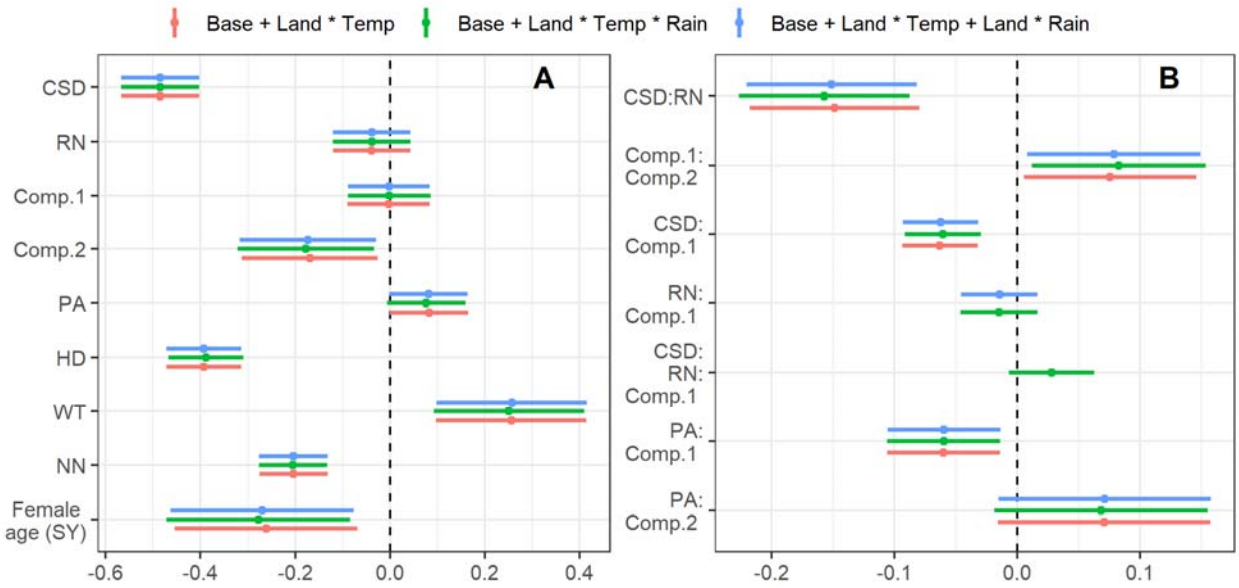

Figure 5. Standardized coefficient estimates and 95% confidence intervals of the three top ranking models, with combined $w > 0.99$ and max ΔAICc = 1.2. Models quantified the effect of covariates on the fledging success of Tree Swallow broods (N=1,897) raised across a gradient of agricultural intensification within southern Québec, Canada, between 2006 and 2016. See Table 1 for acronyms and summary statistics of fixed effects and Appendix S1: Table S1 for outcome of model selection. The GLMM with binomial response and logit link function included year, farm, and nest box IDs as random effects.

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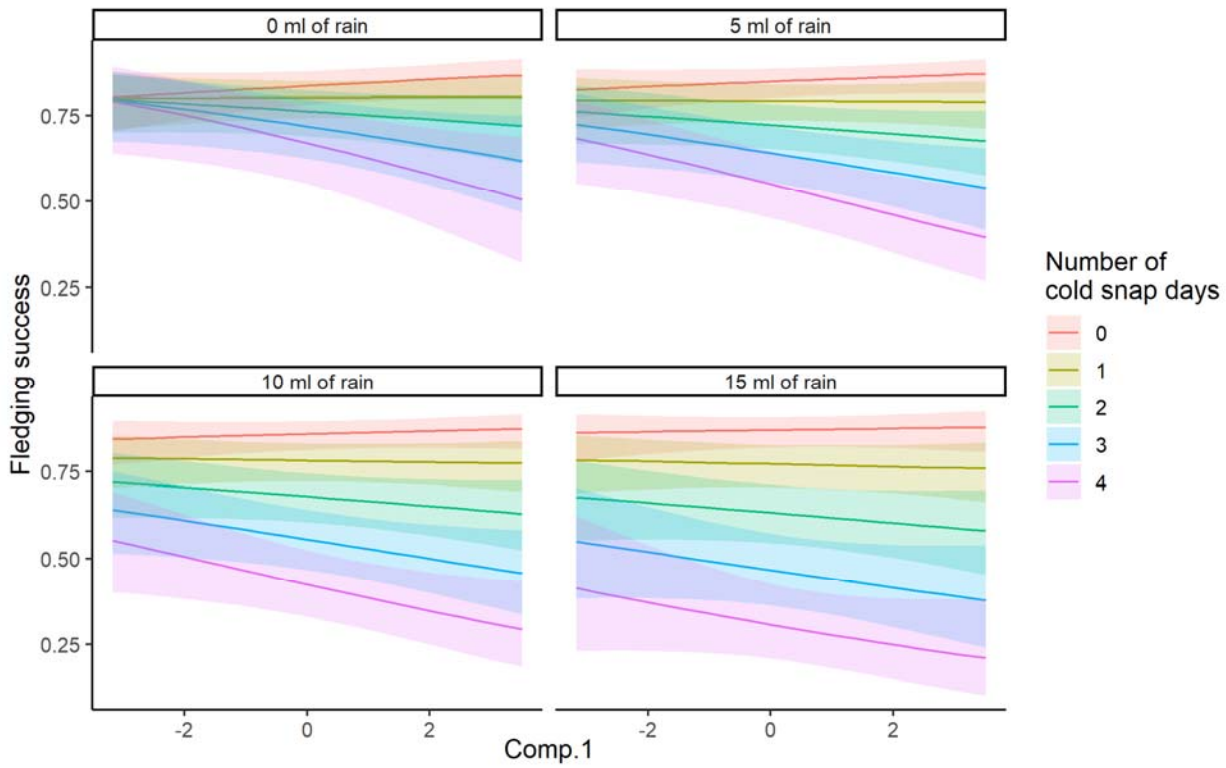

Figure 6: Unconditional model predictions (including unconditional 95% confidence intervals) of the effect of landscape context (Comp.1 in Figure 2) on the fledging success of Tree Swallow broods (N=1,897) exposed to different numbers of cold snap days (days which maximum temperature < 18.2°C) and, in each panel, the mean daily precipitation volumes (ml) over 12 days post hatching. Predictions were made keeping all other covariates at their mean.