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Context-specific "silver-spoon" effects of wetlands, climate, and temperature on lifetime fitness in a short-lived temperate-breeding migratory songbird

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Drivers of global change are creating strongly contrasting early life conditions for developing offspring, which may have carry-over effects on lifetime fitness. We tested for "silver-spoon" effects of natal conditions (environmental conditions and maternal quality) and individual quality (pre-fledging) on the lifetime reproductive success (LRS) of aerial insectivorous adult tree swallows (*Tachycineta bicolor*) hatched in distinct populations with contrasting environments in Saskatchewan and British Columbia, Canada. In both populations, LRS of adults was influenced by environmental conditions they experienced as developing nestlings, but silver-spoon effects were context-dependent, indicating population-specific responses to the local environment. Higher natal temperature in Saskatchewan had positive silver-spoon effects on the LRS of adult swallows, but the opposite was observed in British Columbia, likely because the highest temperatures local recruits experienced as nestlings occurred during heat extremes. In Saskatchewan, where wetter conditions reflect higher wetland abundance and food supply, we detected a negative effect of good natal wetland conditions on adult LRS, contrary to our hypothesis. However, since current breeding wetland conditions are a strong driver of adult fitness, and adults experiencing high natal wetland abundance generally bred when wetland abundance was lower, we suspect any potential benefits of natal wetland abundance on LRS were overridden by wetland conditions during breeding. As hypothesized, wetter natal conditions in British Columbia, which reflect an unfavorable environment for developing nestlings, had negative silver-spoon effects on the LRS of adults. No maternal or pre-fledging quality effects were detected at either site. Therefore, LRS of individuals within distinct populations is influenced, at least in part, by carry-over effects of the natal environment that vary locally. Consequently, natal environmental conditions that affect fitness, with putative population-level consequences, may underly spatially-varying population trends of regionally distinct populations within a species' range.

KEYWORDS

body mass, cohort, early life effect, individual quality, lifetime reproductive success, maternal effect, natal environment, pond abundance

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Introduction

Global changes in land use and climate are currently having negative influences on numerous taxa (Spooner et al., 2018; Northrup et al., 2019; Rosenberg et al., 2019; Halupka et al., 2023), with effects predicted to increase over the next several decades (Visconti et al., 2016; Newbold, 2018; Powers and Jetz, 2019). As animals are exposed to novel environmental conditions caused by the loss of habitat and climate change, it is important to understand the long-term fitness consequences of varying conditions, including those experienced during early life. Studies across diverse taxa have shown that early life conditions, including environmental quality and parental effects (reviewed in Lindström, 1999), can have persistent, or carry-over, effects into adulthood affecting the fitness prospects of entire cohorts of individuals born or hatched in the same year (Ancona and Drummond, 2013; Herfindal et al., 2015; Payo-Payo et al., 2023). Therefore, a better understanding of how varying early life conditions may influence fitness is important for the conservation of numerous taxa, including migratory birds, as it may provide deeper insights into mechanisms underlying spatially-varying population trends of species across their range.

“Good” or “poor” early life conditions that are positively or negatively associated with adult fitness, respectively, are called “silver-spoon effects” (Grafen, 1988). For example, offspring born or hatched in years with “good” environmental conditions, such as favorable weather, high-quality habitats, or plentiful prey availability, are generally higher quality, i.e., heavier or in better body condition (Hamel et al., 2009; Ancona and Drummond, 2013) and may perform better at later life stages regardless of the adult conditions experienced (Reid et al., 2003; van de Pol et al., 2006; Brown et al., 2022; Poli et al., 2022). However, even in years of “good” environmental conditions, it is possible that offspring may experience poor-quality or degraded environmental conditions if food resources or local weather vary temporally or deteriorate seasonally during the breeding season at temperate latitudes (Harriman et al., 2017; Shipley et al., 2020). While studies have demonstrated evidence in support of silver-spoon effects (van de Pol et al., 2006; Spagopoulou et al., 2020; Poli et al., 2022), fitness outcomes of early life conditions may also depend on the environment individuals experience as adults (e.g., environmental matching hypothesis; Monaghan, 2008).

Parental effects, such as the quality of parents themselves and/or decisions about when in a season to breed, may influence the early life conditions experienced by offspring during development (Lindström, 1999; Rödel et al., 2009; Bouwhuis et al., 2010). For instance, parents in good body condition, because they can invest more care or resources, often produce offspring that are heavier or in better condition with greater fitness prospects, regardless of environmental quality (i.e., silver-spoon condition-transfer effects; Bonduriansky and Crean, 2018). Likewise, across taxa, offspring produced earlier in the season are often heavier (Plard et al., 2015), more likely to recruit to the breeding population (Blums et al., 2002), and sometimes have higher fitness as adults (Rödel et al., 2009; Saino et al., 2012). This could be due to having higher quality parents (i.e., older, more experienced, in better condition) or better access to food resources during development (reviewed in Verhulst and Nilsson, 2008). Therefore, in seasonally deteriorating environments there could be interactions between parental quality and environmental conditions. For example, even in years with “good” conditions, offspring may still have lower fitness prospects if they are raised by poor-quality parents and/or later in the season. Alternatively, in “good” conditions, offspring may have high fitness prospects even when raised by parents that are poor quality and/or later in the season, as such parental effects may be more pronounced or only detected in poor-quality environments (Engqvist and Reinhold, 2016).

Early life conditions can have both short- and long-term consequences for fitness-related traits of offspring (Lindström, 1999). Short-term effects of early life conditions on offspring have been well characterized, and shown to affect offspring quality (e.g., pre-fledging body mass or condition) and survival, or probability of recruitment to the breeding population (Ancona et al., 2018; Halliwell et al., 2023). However, short-term effects of early life conditions on offspring are not always detected on fitness components over the long term, i.e., after local recruitment to the breeding population (Nevoux et al., 2010; Cam and Aubry, 2011; Mumme et al., 2015). Nevertheless, evidence of early life conditions having carry-over effects on adult survival after recruitment (Brown et al., 2022; Poli et al., 2022) or lifetime reproductive success (van de Pol et al., 2006; Rödel et al., 2009; Plard et al., 2015) have been demonstrated. For example, red-billed choughs (*Pyrrhocorax pyrrhocorax*) hatched in good environments were more likely to recruit to the breeding population and produced more recruits themselves as adults (Reid et al., 2003). Regardless, the context in which early life conditions carry-over to affect fitness and how they may vary across ecological conditions have not been fully evaluated.

In an aerial insectivore, the tree swallow (*Tachycineta bicolor*), we have previously explored the short-term fitness consequences of variation in early life (natal) conditions at two distinct breeding populations in Canada (Saskatchewan [SK] and British Columbia [BC]) that experience strongly contrasting local environments (Figure 1; Table 1). In SK, located in the Canadian prairies, temperatures during the breeding season are generally warmer and there are few days with temperatures below 18.5°C (Berzins et al., 2020), i.e., “cold snaps” (the critical temperature for insect flight; Winkler et al., 2013). This contrasts the BC site, located in the interior of the province, where temperatures are cooler and cold snaps are more frequent (Griebel and Dawson, 2019). However, warmer temperatures during development at both sites, e.g., ambient temperature (SK) (Berzins et al., 2021) or experimentally heated nest boxes (BC) (Dawson et al., 2005), enhance the pre-fledging body mass of nestlings, and therefore reflect “good” environmental conditions. Wetter natal conditions at the semi-arid SK site are indicative of a “good” environment reflecting a high abundance of ponds (i.e., wetland basins containing water; Weegman et al., 2017; Clark et al., 2018). Abundant ponds during development have positive effects on the quality (i.e., pre-fledging body mass) and apparent first-year survival of offspring (Harriman, 2014; Berzins et al., 2021), presumably because of greater insect food availability or quality. In contrast, wetter natal conditions at the BC site are indicative of a “poor” environment, strongly associated with severe weather, such as cold snaps and precipitation, which negatively affect fledging survival (Berzins

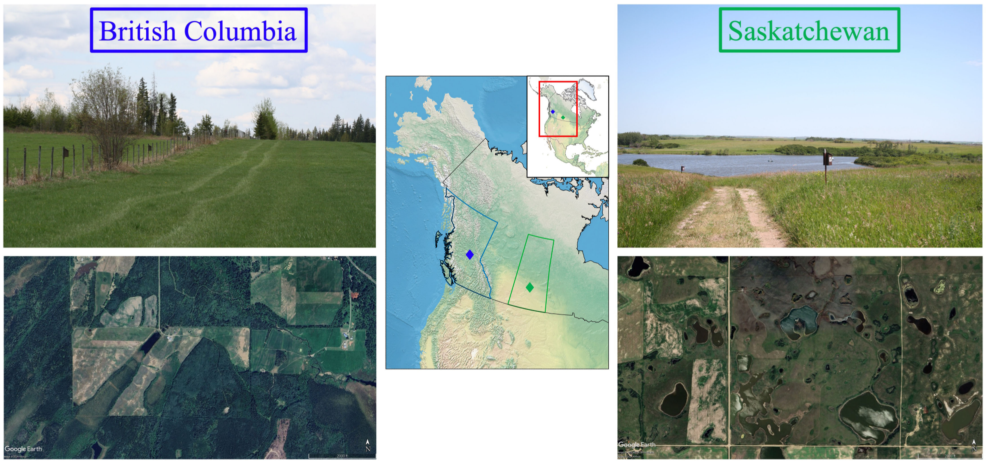

FIGURE 1
Map of North America showing tree swallow (*Tachycineta bicolor*) study sites located in distinct biomes (temperate [evergreen] forest versus temperate prairies) >1200 km apart. The site in British Columbia (left panel; blue) is in the interior of the province, and contains few small permanent wetlands, with stands of deciduous and coniferous trees that are intermixed among open hay fields. The site in Saskatchewan (right panel; green) is in the semi-arid prairies, and contains >100 wetland basins with ponds of varying size and permanency, as well as numerous small groves of trembling aspen (*Populus tremuloides*), cropland, and native and tame grassland. The map of North America was created using map data from Nature Earth (naturalearthdata.com) in QGIS v3.2.6 (QGIS.org, 2024). Photos (top) courtesy of Lisha Berzins, and satellite imagery (bottom) was sourced from Google Earth Pro version 7.3.6.9796, accessed April 2024 [British Columbia. (June 7, 2023). 53°N, 122°W. Eye alt 11682 ft. Terrain layer. Airbus, 2024; Saskatchewan. (June 27, 2023). 52°N, 106°W, Eye alt 11635 ft. Terrain layer. Airbus, Maxar Technologies 2024].

et al., 2020). Overall, the unfavorably cooler and wetter natal conditions likely underly the reported lower fledging success, and lighter nestling body mass prior to fledging, at the BC site compared to SK (Harriman et al., 2017; Weegman et al., 2017).

Maternal effects, such as timing of egg laying within a season, can also have short-term benefits for nestlings, with those hatching from nests initiated earlier both in SK and BC being more likely to recruit locally (Shutler et al., 2006; Harriman, 2014). The quality of

TABLE 1 Mean ± standard deviation (SD) of variables characterizing natal conditions experienced by locally recruited tree swallows (*Tachycineta bicolor*) as nestlings hatched in Saskatchewan (1991–2014) and British Columbia (2001–2014), Canada.

Environmental conditions	Saskatchewan			British Columbia		
	Mean ± SD	Range	n	Mean ± SD	Range	n
T_{max} (°C)	22.3 ± 2.1	17.4 – 30.6	494	20.7 ± 2.4	16.3 – 27.5	214
Pond abundance	64.6 ± 35.5	2 – 107	23[a]	—	—	—
PDSI	—	—	—	1.1 ± 0.9	-0.3 – 3.3	14
Maternal effects						
Maternal body mass (g)	21.8 ± 1.6	17 – 27	494	19.7 ± 1.3	16.5 – 23.0	214
Maternal wing length (mm)	115.4 ± 3.2	104 – 125.5	494	116.1 ± 2.7	108 – 122	214
Maternal body condition	0.00 ± 1.5	-5.1 – 5.4	494	0.00 ± 1.1	-3.6 – 2.9	214
Hatch date	5.2 ± 4.7	1 – 35	494	5.3 ± 4.8	1 – 37	214
Individual quality						
Pre-fledging body mass (g)	23.5 ± 1.9	17.0 – 28.0	494	22.1 ± 1.9	16.0 – 26.1	214
Pre-fledging body mass (g)[b]	23.7 ± 1.9	17.0 – 28.0	362	22.1 ± 1.9	16.0 – 26.1	204
Pre-fledging wing length (mm)	56.1 ± 6.9	34.5 – 82.0	494	—	—	—
Pre-fledging ninth primary length (mm)	—	—	—	28.3 ± 6.5	11.0 – 52.0	214

Maximum temperature (T_{max}) reflects the daily maximum temperature (°C) during nestling development. Pond abundance is the annual number of ponds, while Palmer drought severity index (PDSI) is annual PDSI averaged for the months of June and July. Refer to Supplementary Table S1 for description of variables characterizing natal conditions.

[a] Cohort sample size is 23 years (instead of 24 years) because no recruits were produced in 1993 due to extreme weather-related nestling mortality (Supplementary Table S6; see Shutler and Clark, 2003 for further details).

[b] Pre-fledging body mass of local recruits measured exclusively at 12 days old.

the female parent, i.e., body condition, age class (second-year [SY] or after-second-year [ASY]), or breeding site experience (previously banded or unbanded when captured), also appear to benefit nestlings in the short-term, although the patterns appear site-and/or possibly year-dependent. Specifically, Harriman et al. (2017) reported that in SK, females in better body condition produced nestlings with better body condition prior to fledging (see also Griebel et al., 2019), but this was not observed at the BC site, although other studies in BC have shown that the age class of females can influence nestling body mass (Bitton and Dawson, 2017). Maternal breeding site experience was also found to be a predictor of apparent first-year survival of offspring in SK, but not at the BC site (Harriman, 2014). Finally, Lombardo et al. (2020) reported that the influence of maternal quality traits on the recruitment potential of nestling tree swallows in Michigan, USA, varied annually but were not found to be influential when the data were pooled over a 12-year time series.

In the current study, we tested whether natal conditions, i.e., environmental conditions, maternal effects, or pre-fledging quality, influenced the lifetime reproductive success (LRS) of locally recruited adult tree swallows. Local recruits are defined as nestlings hatched at our study sites that returned to breed in subsequent years. Given that nestlings which permanently emigrated from our study sites were rarely detected, we hereafter use "apparent LRS" (LRS_a; see Berzins et al., 2020). Based on the short-term benefits of "good" natal conditions in these study systems, we hypothesized (Supplementary Table S1) that local recruits experiencing warmer temperatures during development (SK/BC) or hatched in years with abundant ponds (SK) or relatively drier conditions (i.e., lower Palmer drought severity index (PDSI); BC) would have higher LRS_a (environmental conditions), consistent with the silver-spoon hypothesis. Furthermore, we hypothesized that LRS_a of local recruits would be higher if reared by mothers in better body condition or that bred earlier in the breeding season (maternal effects), and that these effects on LRS_a may depend on environmental conditions in the natal year (maternal effect*environmental condition interactions). For instance, LRS_a of local recruits may be (1) lower if reared by mothers in poor body condition or later in the season even when environmental conditions are good, i.e., warmer temperatures, or higher pond abundance (SK) or relatively drier PDSI (BC); or (2) higher if reared by mothers in better body condition or breeding earlier in the season when temperatures are cooler, or pond abundance is lower (SK) or PDSI is relatively wet (BC). Lastly, while natal environmental conditions may have direct effects on long-term fitness (van de Pol et al., 2006; Spagopoulou et al., 2020), some studies have shown that natal environmental conditions can affect fitness indirectly via their effects on juvenile or yearling body mass which persist into adulthood (Plard et al., 2015; Brown et al., 2022). We hypothesized that local recruits fledging with heavier body mass, and therefore being higher quality individuals, would achieve greater LRS_a as adults. Again, positive effects of pre-fledging body mass may be more pronounced if local recruits were hatched earlier within the season or reared by mothers in better body condition (pre-fledging body mass*maternal effects interactions).

Materials and methods

Study species

Tree swallows are aerial insectivores, which are birds characterized by their reliance on flying insects. As a guild, aerial insectivores have experienced steep population declines in North America since the 1970's (Rosenberg et al., 2019). Across their breeding distribution in northern North America, tree swallows produce a single clutch per season that generally contains ~4–7 eggs (Winkler et al., 2020). The lifespan of tree swallows is ~ 2.7 years on average (Winkler et al., 2020), and ~50 to 60% of individuals breed only once (Lombardo and Thorpe, 2010; Berzins et al., 2020). Tree swallows are migratory birds that overwinter in the southern United States, Mexico, and the Caribbean (Knight et al., 2018). Apparent survival estimates indicate that adult survival is ~50% (Weegman et al., 2017; Clark et al., 2018), while juvenile survival is ~5–6% at the BC and SK sites (Weegman et al., 2017).

Study areas

Tree swallows were studied at two sites in Canada: Saskatchewan (SK) from 1991–2017, and British Columbia (BC) from 2001–2017. The SK site is located in the Canadian prairies, 40 km east of Saskatoon (52°N, 106°W) at the St. Denis National Wildlife Area. This site has >100 wetland basins containing ponds of varying permanency (Berzins et al., 2021), numerous small groves of trembling aspen (*Populus tremuloides*), cropland, and native and tame grassland (Figure 1). The BC site is in the interior sub-boreal forest and consists of three sub-sites within the vicinity of Prince George (53°N, 123°W). This area is characterized by a few small permanent wetlands, stands of deciduous and coniferous trees that are intermixed among hay fields (Figure 1).

At both sites, nest boxes are mounted ~1.5 m above the ground on metal or wooden posts in lines or grids and spaced ~30 m apart (see Shutler and Clark, 2003; Harriman et al., 2017). Nest boxes used in this study were constructed of plywood (10 mm thickness) similar to the "Long Point" nest box design (Hussell, 2003), i.e., ~38 mm diameter entrance hole centered ~155 mm above the floor of the box, and an interior floor measuring ~140 x 140 mm (Griebel et al., 2020). The number of nest boxes available varied annually at sites, ranging from 75 to >200 (SK) and 196 to >300 (BC) (Harriman, 2014). Nest box occupancy rates are nearly 100% annually at the SK site, but range from ~30 to 60% at the BC site (Shutler et al., 2012).

General field methods

Study sites were monitored from May to August to record data on annual reproductive success and individual quality. At both sites, tree swallows begin egg-laying in May, eggs hatch in June, and the nestling rearing period extends from June into July. Starting in May, nest boxes were visited every 1–2 days to record nest building, dates of clutch initiation and completion, and clutch size. Clutches were presumed complete, and incubation had begun, when the number of eggs was unchanged for three consecutive days and eggs were warm. Approximately 12 days after clutch completion, we monitored nests daily to determine the hatching date (the day the first egg within a clutch hatched = nestling age of day 0; Dawson, 2008). Eggs within a clutch hatch asynchronously, with the hatching of the first- and last-laid eggs usually occurring within a 24 hr period (Bitton et al., 2006), although some nests can take up to three days for all eggs to hatch (Winkler et al., 2020).

Adult tree swallows were captured in nest boxes and their sex was determined based on the presence of a cloacal protuberance (male) or brood patch (female) (Pyle, 1997). Adults were banded with an aluminum band if newly captured or band numbers were recorded if captured previously, weighed with a spring scale to the nearest 0.5 g and wing length was measured with a ruler to the nearest 0.5 mm. Nestlings were weighed, measured, and banded as described above for adults, with a few exceptions due to site-specific field protocols. First, nestlings were weighed with a spring scale to the nearest 0.25 g in SK and 0.125 g in BC. Second, wing length was measured in SK, whereas the ninth primary length was measured in BC. Since wing length is more or less determined by ninth primary length (the outermost feather) both provide similar estimates of structure size. Most nestlings (73% SK, 95% BC) were measured on day 12, but in some cases, they were measured on a different day (i.e., day 11 or a day from 13 to 16 days old). Starting on day 22, we checked nest boxes daily until all nestlings fledged, and recorded band number(s) of those that did not fledge due to mortality.

Apparent lifetime reproductive success

The number of local recruits hatched at our study sites in plywood nest boxes between 1991–2014 (SK) and 2001–2014 (BC) that returned to breed in subsequent years was 678 and 278, respectively. LRS_a was estimated for local recruits until the 2017 breeding season which allowed for up to two breeding seasons to recapture recruiting offspring of birds hatched in 2014. The majority of recruits, 81% (SK) and 96% (BC), are captured breeding in nest boxes 1–2 years after hatching (Supplementary Figure S1), and previous capture-mark-recapture analyses at our study sites indicate that recapture rates of adult swallows are high (Weegman et al., 2017; Clark et al., 2018). LRS_a reflects whether a local recruit produced no recruits (0) or produced at least one recruit detected as a breeding adult (1), and is expressed as a binary outcome since a low percentage (30% [SK] and 19% [BC]) of individuals produced more than one recruit in their lifetime (Berzins et al., 2020; Supplementary Table S2). That the majority of tree swallows produce no recruits in their lifetime (Berzins et al., 2020) is a pattern reported across taxa (e.g., tufted duck, *Aythya fuligula*; Blums and Clark, 2004; elephant seals, *Mirounga angustirostris*; Le Boeuf et al., 2019). Our measure of LRS_a is based on all offspring local recruits raised that recruited, regardless of whether they were biologically related due to egg or nestling swaps between nests (e.g., Shutler et al., 2006; Harriman et al., 2017), which occurred in approximately 15% (SK) and 12% (BC) of nests, or for males specifically, because rates of extra-pair paternity are high (e.g., >70% at the BC site; Berzins and Dawson, 2020).

Quantifying natal conditions

Definitions of variables characterizing natal conditions (environmental conditions and maternal effects) and pre-fledging quality, and the predicted relationships to LRS_a of local recruits, are provided in Supplementary Table S1. Means and standard deviations (SD) for variables describing the natal conditions are provided in Table 1.

Environmental conditions

Based on our current knowledge of tree swallows at the study sites (Berzins et al., 2020, 2021; see also Cox et al., 2019), we selected two variables to characterize the natal environment: maximum temperature (T_{max}) and moisture conditions represented by pond abundance (SK) or Palmer drought severity index (PDSI; BC). Scatter plots showing variation between annual pond abundance or PDSI and seasonal T_{max} are provided in Supplementary Figure S2.

Maximum temperature (T_{max}) is a nest-level variable reflecting the average daily maximum temperature (°C) local recruits experienced as nestlings aged 2 to 12 days old (Berzins et al., 2021), and ranged from 17.4 to 30.6°C (SK) and 16.3 to 27.5°C (BC). T_{max} data were retrieved from weather stations operated by Environment and Climate Change Canada at the airports in Saskatoon (~42 km from the SK site) and Prince George (~15 to 24 km from the BC sub-sites). Nestlings fledged at heavier masses in SK when daily T_{max} was warmer (Berzins et al., 2021) and in BC when nest boxes were experimentally heated (Dawson et al., 2005) during growth. We therefore predicted that local recruits reared when temperatures were higher, reflecting good natal conditions, would have higher LRS_a.

Pond abundance is a cohort-level variable reflecting the number of wetland basins flooded with water at the SK site (Berzins et al., 2020). The number of ponds was recorded annually in the month of May preceding the hatching of local recruits (Clark et al., 2018). Pond numbers recorded in May and July in sub-set of years were positively correlated (Rotella et al., 2003), which suggests that our measure of pond abundance should provide a good estimate of moisture conditions during nestling rearing (Berzins et al., 2021). In this region, climate extremes drive annual fluctuations in the number of ponds during wet-dry cycles (Johnson et al., 2004), and pond numbers at the SK site annually ranged from 2 to 107 (Berzins et al., 2021). We considered pond abundance as a categorical variable, where low and high categories represent the extremes, by dividing years into three groups: <41 ponds representing "low" pond abundance, 52 to 70 ponds as "intermediate" pond abundance, and >80 ponds as "high" pond abundance (Supplementary Figure S3). These categories divide the distribution of pond numbers into roughly thirds, and also take advantage of natural breaks in pond numbers between 41 to 52 and 70 to 80. Our previous work has shown that pond abundance in the natal year is a strong predictor of nestling pre-fledging body mass and recruitment potential (Berzins et al., 2021). Therefore, we predicted that local recruits hatched in years of intermediate to high pond abundances would have greater LRS_a than those hatched in years of low pond numbers, if the benefits of good pond conditions in the natal year carry-over into adulthood.

The BC site has few permanent wetlands, in contrast to SK, so we instead used PDSI as a cohort-level variable characterizing local moisture conditions (Harriman, 2014; Berzins et al., 2020). Values of PDSI reflect the average for the months of June to July (Berzins et al., 2020), which overlap with the nestling rearing period. In general, negative and positive PDSI values represent drier and wetter conditions, respectively, but while PDSI values ranged from -0.26 to 3.33, there was only a single year with a negative PDSI value at the BC site (Supplementary Figure S4). To represent PDSI variability, we divided values into categories such that <0.5 represented relatively "dry" conditions, 0.5 to 1.5 "intermediate" conditions, and >1.5 relatively "wet" conditions. Data for PDSI were obtained from Agriculture and Agri-Food Canada (station #1096453). Wetter PDSI conditions are positively correlated with precipitation during the nestling period (Spearman correlation: $r_s = 0.71$, $p < 0.001$, $n = 14$ years), and these inclement weather conditions presumably reduce the activity and availability of insect prey (Cox et al., 2019), resulting in a "poor" natal environment. Therefore, we predicted that local recruits hatched in relatively wetter years would have lower LRS_a if negative effects of being raised in wetter conditions carry-over into adulthood.

Maternal effects

Early life rearing conditions experienced by local recruits as nestlings may vary as a result of maternal quality or decisions about when to initiate breeding. Two variables were selected to characterize variation in natal conditions due to maternal quality effects: maternal body condition and hatching date within a season.

Maternal body condition is a nest-level variable reflecting body mass corrected for structural size and stage of the breeding season. Body condition was calculated as the residual from linear models that regressed the body mass of local recruits' mothers (response variable) against their wing length (structural size) and the number of days prior to or after hatching of nestlings (O'Brien and Dawson, 2013), which ranged from before hatch to 16-days old (Supplementary Table S3). Because the body mass of local recruits' mothers was higher at the SK site (Table 1), we used linear models to calculate maternal body condition for each site separately. Maternal body condition was used as a variable to characterize maternal effects in this system because it reflects differences in the age class and/or breeding experience of female tree swallows (Harriman, 2014; Bitton and Dawson, 2017). Additionally, females in higher body condition may produce offspring with higher body condition that are better able to convert resources into traits that enhance fitness (i.e., silver-spoon condition-transfer effects; Bonduriansky and Crean, 2018). Therefore, we predicted that local recruits reared by mothers in higher body condition would achieve higher LRS_a. Additionally, we predicted that benefits of maternal effects provided to offspring may depend on the quality of the natal environment (maternal body condition*environment interactions): (1) lower LRS_a for local recruits may be expected if reared by mothers in poor body condition even when environmental conditions are good; or (2) local recruits may only achieve high LRS_a if reared by mothers in better body condition in years with poor environmental conditions.

Hatching date is a nest-level variable reflecting the date within a season local recruits hatched relative to all nests. Mean (± SD) hatching date for each site and year are reported in Supplementary Table S4. To standardize hatching dates across years, we subtracted the annual date when 5% of all nests hatched from the hatching date of each nest (Clark et al., 2014). Hatching dates were standardized for each site and year separately. At the BC site, the 5% hatching date was calculated for all three sub-sites combined. At temperate latitudes, offspring hatched early in the season generally have greater fitness prospects (Svensson, 1997), being more likely to recruit (Shutler et al., 2006; Lombardo et al., 2020) and/or having higher LRS_a as adults (Saino et al., 2012), either because they are reared by higher quality parents or experience more abundant food (reviewed in Verhulst and Nilsson, 2008). Therefore, we predicted that locally recruited offspring hatching from early-season nests at both sites would have higher LRS_a. We also predicted this pattern may depend on environmental conditions (hatching date*environment interactions): (1) lower LRS_a for local recruits may be expected if hatched later in the season even when environmental conditions are good; or (2) local recruits may achieve higher LRS_a if hatched early in the season when environmental conditions are poor.

Individual quality

The quality of local recruits was estimated using their body mass as nestlings prior to fledging, which ranged from 17.0 to 28.0 g (SK) and 16.0 to 26.1 g (BC), after controlling for age-corrected structural size (i.e., wing length [SK] or ninth primary length [BC]; Supplementary Table S5). Pre-fledging body mass reflects the culmination of environmental and maternal effects of the developmental environment, where heavier offspring are indicative of good natal conditions (van de Pol et al., 2006; Spagopoulou et al., 2020). In some cases, effects of natal conditions on fitness are mediated indirectly via effects on natal body mass (Plard et al., 2015; Poli et al., 2022). We predicted that local recruits fledging at heavier masses, presumably as higher quality individuals, would thus attain greater LRS_a as adults, especially if hatched earlier in the season or reared by mothers in good body condition (pre-fledging body mass*maternal effects interactions).

Statistical analysis

All statistical analyses were performed using R (version 4.2.2.; R Core Team, 2022). The sample sizes of local recruits that we used to examine silver-spoon effects of natal conditions on LRS_a were 494 in SK (n = 207 females, n = 287 males) and 214 in BC (n = 117 females, n = 97 males) after we excluded those that were: (1) reared by a foster mother after being moved to a different nest (e.g., Shutler et al., 2006; SK: n = 49; BC: n = 21); (2) involved in experiments as a nestling that altered the microclimate of their nest, their hatching date within a season and/or resource competition in the nest (e.g., Dawson et al., 2005; Fairhurst et al., 2012; Berzins and Dawson, 2016; Harriman et al., 2017; Griebel et al., 2020; SK: n = 73; BC: n = 22), as such manipulations can create/prevent "silver-spoon" rearing conditions (Spagopoulou et al., 2020); (3) involved in experiments as adults that could affect their return or survival rates (e.g., geolocators, Gómez et al., 2014; SK = 15); or were (4) missing information on their hatching date (SK: n = 12) and pre-fledging body mass (SK: n = 13) or the body condition of their mother (SK: n = 22; BC: n = 21). Sample sizes of local recruits in each cohort with complete information for all variables are provided in Supplementary Table S6.

To examine whether natal conditions influenced LRS_a of locally recruited tree swallows, we used generalized linear models (GLMs) fit with a binomial error distribution and a probit link function. The dependent variable was LRS_a (binary response variable: 0 = produced no recruit; 1 = produced at least one recruit), and we constructed an *a priori* candidate set of 11 models (see Supplementary Table S7) to disentangle the relative contributions of natal conditions on LRS_a of local recruits at each site separately: environmental factors, maternal effects and/or individual quality. Natal year was not included as a random or fixed effect since it was confounded with cohort-level variables of pond abundance/PDSI, and pre-fledging body mass (e.g., Berzins et al., 2021). Additionally, although 27% (SK) and 25% (BC) of local recruits shared a common mother, and 15% (SK) and 17% (BC) were siblings from the same nest, likelihood ratio tests indicated that models containing random effects of mother identity or natal nest identity were not a better fit to the data than GLMs with no random effects ($p > 0.90$).

For all models, continuous variables (e.g., T_{max}, pre-fledging body mass) were z-score transformed (mean = 0, SD = 1) so standardized parameter estimates (relative effect sizes) could be directly compared, even in the presence of interactions (Schielzeth, 2010). Extreme values of variables, such as hatching date, were truncated by pooling with less extreme values to improve the fit of data to models (Clark et al., 2014). We assessed the fit of competing models via Q-Q and residual plots produced using the "DHARMa" package (Hartig, 2022). Generalized variance inflation factor values computed using the "car" package (Fox and Weisberg, 2019) were <2 indicating low collinearity among variables in models. Model selection was performed by generating Akaike's information criterion corrected for sample size (AIC_c) values using the package "AICcmodavg" (Mazerolle, 2023). We considered the model with the lowest AIC_c value to be the most parsimonious, although models within 2 AIC_c units were considered equivalent (Burnham and Anderson, 2002). Standardized parameter estimates (β) for variables in best-supported model(s) are reported with the lower and upper 95% confidence intervals (CI), and were considered informative when 95% CI did not overlap zero (Arnold, 2010). Model predictions from the best-supported model (s) were calculated using the package "ggeffects" (Lüdecke, 2018).

Results

Apparent lifetime reproductive success of local recruits

In SK, 66% of local recruits produced no recruit themselves as breeders, while 34% produced at least one recruit (n = 494). The best-supported model explaining variation in LRS_a of locally recruited offspring was the environmental model (Table 2). The maternal effects and individual quality models, as well as models containing interactions, had $AIC_c > 2$ relative to the model containing only environmental variables that local recruits experienced as nestlings (Table 2). Parameter estimates indicated that the likelihood of local recruits producing a recruit increased with warmer temperatures during development ($\beta_{Tmax} = 0.16 \pm 0.06$, 95% CI = 0.04, 0.27; odds ratio [OR] = 1.17, 95% CI = 1.04, 1.32; Figure 2A). Additionally, local recruits were more likely to produce a recruit themselves when pond abundance in the natal year was intermediate compared to relatively higher ($\beta_{\text{pond abundance: high}} = -0.36 \pm 0.15$, 95% CI = -0.66, -0.05; OR = 0.70, 95% CI = 0.52, 0.95) and possibly lower abundance of ponds ($\beta_{\text{pond abundance: low}} = -0.31 \pm 0.18$, 95% CI = -0.66, 0.03; OR = 0.73, 95% CI = 0.52, 1.03; Figure 3A), although the 95% CI slightly overlapped 0.

In BC, 77% of local recruits produced no recruit themselves as breeding adults, while 23% produced at least one recruit in their lifetime (n = 214). The best-supported model explaining variation in LRS_a of local recruits was the environmental model (Table 3). There was some suggestion that the likelihood of local recruits producing a recruit themselves decreased with warmer temperatures during development ($\beta_{Tmax} = -0.24 \pm 0.13$, 95% CI -0.51, 0.01; OR = 0.78, 95% CI = 0.60, 1.01; Figure 2B), although the 95% CI slightly overlapped 0. Additionally, local recruits hatched in years with intermediate and dry PDSI conditions were as breeders equally likely to produce a recruit themselves ($\beta_{\text{PDSI: dry}} = 0.02 \pm 0.25$, 95% CI = -0.47, 0.52; OR = 1.02, 95% CI = 0.63, 1.68); however, compared to local recruits hatched in years with intermediate PDSI conditions, those that hatched in wetter years were less likely to produce a recruit ($\beta_{\text{PDSI: wet}} = -0.83 \pm 0.30$, 95% CI = -1.44, -0.27; OR = 0.43, 95% CI = 0.24, 0.77; Figure 3B).

Discussion

The quality of natal conditions experienced by offspring is predicted to have carry-over effects on adult lifetime fitness. In a short-lived aerial insectivore, we showed that the best-supported models explaining LRS_a were those containing environmental conditions. Therefore, environmental conditions, specifically T_{max} and/or pond abundance or PDSI, that local recruits experienced as nestlings during development, appear to have long-term effects on LRS_a in tree swallows. These results demonstrating consequences of variation in the natal environment on adult fitness are consistent with silver-spoon effects reported previously in diverse taxa (Reid et al., 2003; van de Pol et al., 2006; Plard et al., 2015). However, while evaluating two geographically distinct populations with contrasting environments on the breeding grounds, we also show that silver-spoon effects were context-specific depending on the populations' response to the local environment. Maternal effects and pre-fledging quality models, including those containing interactions with environmental conditions, were not supported. As a consequence, we found no evidence that the maternal effects variables we studied, i.e., mother body condition or timing of breeding, or pre-fledging quality of local recruits influenced LRS_a. This suggests that the benefits to offspring of maternal effects or

TABLE 2 Summary of model selection results of generalized linear models examining the effect of natal conditions on apparent lifetime reproductive success (LRS_a; binomial = produced at least one recruit, produced no recruits) of locally recruited tree swallows (*Tachycineta bicolor*) hatched in Saskatchewan (1991–2014; n = 494), Canada.

Model structure	K[a]	ΔAIC_c[b]	AIC_c weight[c]	Log- likelihood[d]
Pond abundance + T_{max}	4	0.00	0.68	-308.84
T_{max} * hatching date	4	2.98	0.15	-310.33
Pond abundance + T_{max} + maternal body condition + hatching date + pre-fledging body mass + pre-fledging structural size	8	4.36	0.08	-306.92
T_{max} * maternal body condition	4	5.02	0.06	-311.35
Pond abundance * maternal body condition	6	7.60	0.02	-310.60
Null	1	8.30	0.01	-316.03
Pond abundance * hatching date	6	8.88	0.01	-311.24
Pre-fledging body mass + pre-fledging structural size	3	10.66	0.00	-315.19
Maternal body condition + hatching date	3	12.27	0.00	-315.99
Pre-fledging body mass * hatching date + pre-fledging structural size	5	14.31	0.00	-314.98
Pre-fledging body mass * maternal body condition + pre-fledging structural size	5	14.45	0.00	-315.05

Maximum temperature (°C) is denoted as T_{max}. Where interaction terms are shown, main effects were included in models. Refer to Supplementary Table S1 for description of variables characterizing natal conditions.

[a] Number of parameters estimated in the model.

[b] Difference between AIC_c of each model and minimum AICc.

[c] Weight of evidence for a model being the best-supported.

[d] Log-likelihood of each model.

heavier pre-fledging body mass previously detected in this species (Harriman, 2014; Berzins et al., 2021) may (1) not extend beyond initial recruitment to the breeding population (Nevoux et al., 2010; Mumme et al., 2015) and therefore provide only short-term benefits, and/or (2) be less influential, or outweighed by, the stronger effect of the environmental conditions (Verhulst et al., 1995; Pärt et al., 2017) that we observed on LRS_a. Overall, results indicate that variation in LRS_a of locally recruited adult tree swallows is shaped, at least in part, by the local environment they experienced as developing nestlings.

Maternal traits and environmental factors we measured to characterize natal conditions can be important determinants of nestling quality and recruitment in tree swallows, yet not all variables were related to LRS_a. For instance, while maternal decisions on when to breed within a season are strongly related to the fitness prospects of nestlings (Verhulst et al., 1995; Verhulst and Nilsson, 2008), we did not find that an earlier hatching date within a season enhanced LRS_a. This finding contrasts with a study in another aerial insectivore, the barn swallow (*Hirundo rustica*; Saino et al., 2012), where recruits from nests hatched early had higher LRS than recruits hatched later in the season. It is possible that these contrasting results are due to the differing proxies of lifetime reproductive success, i.e., probability of producing a recruit (sexes pooled; this study) versus total eggs (males only; Saino et al., 2012), which may differ in their ability to reliably predict fitness (Alif et al., 2022). Indeed, a previous study in song sparrows (*Melospiza melodia*) using a proxy similar to ours, i.e., number of offspring surviving to independence, also reported no effect of maternal laying date on LRS of local recruits (Tarwater et al., 2018). However, in some species, it is the first-hatched nestlings within a brood that achieve higher LRS than their later hatched siblings (Martínez-Padilla et al., 2017; Song et al., 2019). We recognize that tree swallow clutches hatch asynchronously (Bitton et al., 2006), but do not have long-term data on hatching sequence to explore this possibility further.

Previous studies in tree swallows have shown that nestlings hatched from early-season nests and/or those that are heavier prior to fledging are more likely to recruit locally (Shutler et al., 2006; Harriman, 2014; Lombardo et al., 2020). Thus, it is possible that we did not detect carry-over effects of these variables on LRS_a because our sample of birds are mainly those early hatched and/or heavier nestlings, as reported in Shutler et al. (2006) and Harriman (2014), and are of relatively higher quality compared to non-recruiting offspring. In other species, higher quality individuals attain better breeding territories (van de Pol et al., 2006), and so lower quality individuals may have been outcompeted (e.g., Mumme et al., 2015), at least in SK where competition for nest boxes is high (Shutler et al., 2012). Alternatively, this pattern may also arise because of the selective disappearance of lower quality offspring prior to becoming a breeder (Nevoux et al., 2010; Payo-Payo et al., 2016). While the underlying mechanism is unknown, that local recruits may be relatively high quality is supported by two lines of evidence. First, a decrease in the proportion of local recruits with advancing hatching date suggests that more high-quality individuals were hatched earlier than later in the season (Supplementary Figure S5). Second, the reported negative effects of later hatching date (SK/BC), lower pond abundance (SK), and lower temperature (SK/BC) on pre-fledging body mass of nestlings (Berzins et al., 2021) are no longer detected on body mass of local recruits as adults (Supplementary Tables S8, S9; Supplementary Figures S6, S7).

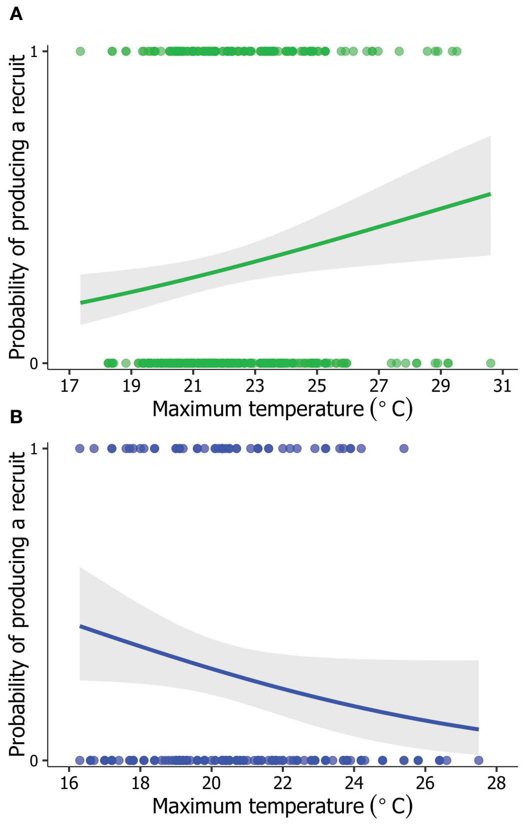

FIGURE 2
Model-predicted probability that locally recruited tree swallows (*Tachycineta bicolor*) hatched in **(A)** Saskatchewan (1991–2014; n = 494; green circles) and **(B)** British Columbia (2001–2014; n = 214; blue circles), Canada, would produce a recruit themselves as breeders in relation to maximum temperature, averaged from days 2 to 12 of nestling development. Model predicted values (line) and 95% confidence intervals (grey shaded area) are based on the top-supported model in Tables 2, 3.

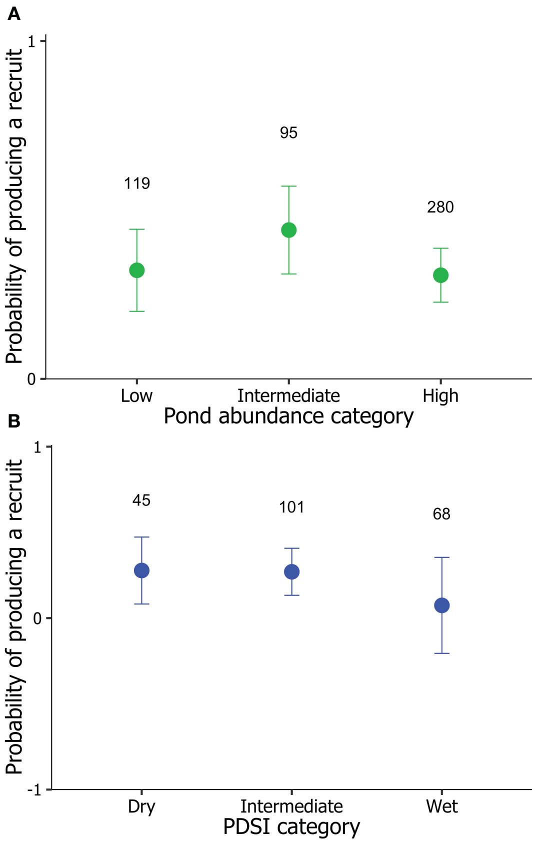

FIGURE 3
Model-predicted mean (± SE) probability that locally recruited tree swallows (*Tachycineta bicolor*) hatched in Saskatchewan (1991–2014, green circles) and British Columbia (2001–2014; blue circles), Canada, would produce a recruit themselves as breeders in relation to **(A)** pond abundance and **(B)** Palmer drought severity index (PDSI) conditions they experienced as nestlings during development. Model-predicted mean ± SE are based on the top-supported model in Tables 2, 3. Sample sizes for the number of local recruits are given above error bars.

While a positive association between maternal body condition and nestling body mass at the SK site (Harriman et al., 2017) persisted in adulthood (Supplementary Table S8; Supplementary Figure S6), models including these variables were not supported. Such a finding, however, does align with previous work in female tree swallows (Berzins et al., 2020), great tits (*Parus major*, Verhulst et al., 1995), and northern wheatears (*Oenanthe Oenanthe*, Pärt et al., 2017) showing that individual traits are less influential for achieving high LRS_a than environmental factors.

Effects of the natal environment on LRS_a were context-specific, depending largely on the locally varying temperature and moisture conditions. At the SK site, local recruits that developed in warmer temperatures were heavier prior to fledging (Berzins et al., 2021) and achieved higher LRS_a as adults, consistent with positive silver-spoon effects. Contrary to our hypothesis, however, we found a negative trend of warmer temperature on LRS_a at the BC site. Dawson et al. (2005) demonstrated that nestlings may have benefited from being reared in experimentally heated nests at the BC site as they were heavier prior to fledging. The contrasting results between studies in the same study population may be explained by the magnitude in temperature increase that nestlings were exposed to during development. For instance, Dawson et al. (2005) experimental study elevated the temperature of nests within the range of normal variation, whereas in our study, the highest temperatures experienced by local recruits during development overlapped with record-breaking heat waves (The Canadian Press, 2013). The temperatures local recruits experienced while growing during the heat waves in June of 2004 and 2013, were ~1.5 to 3.5°C greater than the mean T_{max} for the month of June and during the period of nestling growth for all nests in those years (Supplementary Figure S8). It is therefore possible that at the BC site, where temperature is generally cooler during the breeding season than the more arid SK site in the prairies (Table 1), high temperature extremes may instead reflect unfavorable environmental conditions. A positive relationship between the pre-fledging body mass of local recruits and temperature during development (Supplementary Table S8; Supplementary Figure S7) may suggest that only local recruits that were relatively high-quality (i.e., heavier as nestlings) were able to buffer the effects of developing in such high temperatures in the short-term but still incurred fitness costs as adults, consistent with the silver-spoon hypothesis. Although

TABLE 3 Summary of model selection results of generalized linear models examining the effect of natal conditions on apparent lifetime reproductive success (LRS_a; binomial = produced at least one recruit, produced no recruits) of locally recruited tree swallows (*Tachycineta bicolor*) hatched in British Columbia (2001–2014; n = 214), Canada.

Model structure	K[a]	ΔAIC_c[b]	AIC_c weight[c]	Log- likelihood[d]
PDSI + T_{max}	4	0.00	0.61	-110.36
Null	1	3.38	0.11	-115.14
PDSI + T_{max} + maternal body condition + hatching date + pre-fledging body mass + pre-fledging structural size	8	4.92	0.05	-108.57
Pre-fledging body mass + pre-fledging structural size	3	5.02	0.05	-113.91
PDSI * maternal body condition	6	5.68	0.04	-111.10
Maternal body condition + hatching date	3	5.76	0.03	-114.28
T_{max} * hatching date	4	6.02	0.03	-113.38
PDSI * hatching date	6	6.05	0.03	-111.28
Pre-fledging body mass * maternal body condition + pre-fledging structural size	5	6.59	0.02	-112.61
T_{max} * maternal body condition	4	7.13	0.02	-113.93
Pre-fledging body mass * hatching date + pre-fledging structural size	5	8.16	0.01	-113.39

Maximum temperature (°C) is denoted as T_{max}, while Palmer drought severity index is PDSI. Where interaction terms are shown, main effects were included in models. Refer to Supplementary Table S1 for description of variables characterizing natal conditions.

[a] Number of parameters estimated in the model.

[b] Difference between AIC_c of each model and minimum AICc.

[c] Weight of evidence for a model being the best-supported.

[d] Log-likelihood of each model.

suggestive, our results add to the increasing number of studies reporting negative effects of extreme heat-related events on fitness prospects of offspring (Eastwood et al., 2022; Lv et al., 2023).

Moisture conditions, such as pond abundance and PDSI, are driven largely by precipitation and have contrasting effects on the local population dynamics of tree swallows across their range (Weegman et al., 2017). At the more arid SK site, wetter conditions are generally favorable, reflecting abundant ponds (Weegman et al., 2017; Berzins et al., 2020), and by association increased abundance of aerial insects with aquatic larval stages (Berzins et al., 2022). Since ponds in the prairies of North America unequivocally benefit breeding birds (Bartzen et al., 2010; Zhao et al., 2019; Devries et al., 2023), including tree swallows (Michelson et al., 2018; Berzins et al., 2021), it is unclear why local recruits reared when pond abundance was high did not achieve the highest LRS_a as adults. One possibility is that the nutritional environment under higher pond abundance may actually be inferior to intermediate pond conditions due to extensive flooding and lower productivity of ponds. For instance, larger ponds can become deeper, permanent, lake-like systems during extensive flooding events (Cressey et al., 2016; Hayashi et al., 2016), which have less diverse invertebrate communities and lower nutrient turnover than smaller seasonal and temporary ponds (McLean et al., 2020; Fritz and Whiles, 2021). A study in tree swallows recently invoked this reasoning, i.e., sites with more pond area, but containing a few large lake-like ponds, may provide less aquatic insect food during growth, to explain why the observed increase in nestling quality and predicted survival leveled off when the surface area of ponds in a region was at intermediate levels (Berzins et al., 2022). While the SK site experienced an extended wet period from 2011 to 2017, with expansion of several larger ponds, ponds of varying sizes, depths, and permanence still existed within this wetland complex. We do not, however, have additional data on pond area and aquatic insect availability to further explore these relationships over the SK time series. Nevertheless, how the type and surface area of ponds in the landscape influence the nutritional environment experienced by aerial insectivores on the breeding grounds warrants further investigation.

Our study focused on testing for silver-spoon effects of natal conditions on LRS_a, which predict fitness benefits to individuals developing in a good environment, independent of the adult environment (Monaghan, 2008). However, we recognize that LRS_a may also be influenced by current environmental conditions experienced by local recruits during breeding. Previous studies at the SK site have shown that LRS_a and apparent survival of tree swallows were higher when breeders experienced relatively high pond abundance (Clark et al., 2018; Berzins et al., 2020). Therefore, our results may also be explained by local recruits reared when pond abundance was highest being more likely to encounter poorer pond conditions as breeders due to cycling in pond abundance during wet-dry periods (Supplementary Figure S9). This reasoning would also explain the fewer breeding attempts made by local recruits reared in high versus intermediate pond abundance (Supplementary Table S10; Supplementary Figure S10). In other species, such as tawny owls (*Strix aluco*), the phase of the vole cycle (i.e., increasing or decreasing) that local recruits experience as first-time breeders was more influential for LRS than natal conditions (Millon et al., 2010). For tree swallows at the SK site, females generally begin breeding at 2 years old or older (Berzins et al., 2020), in contrast to males (Supplementary Figure S1). Age of first breeding does not appear to vary with natal pond abundance for females, but it does for males (Supplementary Figure S10). This points to the possibility that males hatched in years of differing natal pond abundance may encounter different competitive environments at recruitment that affects their opportunity for breeding (i.e., mismatched natal and adult environments; Monaghan, 2008). When natal pond numbers are relatively low and few males recruit to the breeding population, competition for nest boxes may be reduced which allows males to breed at younger ages and have more lifetime breeding attempts (Supplementary Figure S10). In contrast, when natal ponds are abundant and more males recruit, competition for breeding sites, particularly in SK where occupancy of nest boxes is high, becomes more intense, resulting in a concomitant delay in age at first breeding and a decrease in the number of lifetime breeding attempts (Supplementary Figure S10). While outside the scope of our present study, that LRS_a of local recruits could potentially be influenced by complex interactions with pond conditions across life stages, depending on whether ponds are increasing or decreasing during wet-dry periods, is an idea that warrants further investigation.

In contrast to the more arid SK site, wetter conditions in BC are generally unfavorable (Berzins et al., 2020), as is also evident in other parts of the range of tree swallows (Weegman et al., 2017). For instance, in Ontario and Quebec, Canada, prolonged precipitation reduces the availability of insects, and so negatively affects the quality and fledging success of nestlings (Cox et al., 2019; Garrett et al., 2022). Our results at the BC site indicate that the negative effects for nestlings reared in wetter natal conditions may also carry-over to affect their fitness as adults, in accordance with the silver-spoon hypothesis. Breeding at earlier ages may enhance fitness by increasing the number of lifetime breeding attempts (Blums and Clark, 2004), especially in short-lived species (Gustafsson and Pärt, 1990). We suspect that local recruits experiencing wetter PDSI conditions had lower LRS_a because they delayed breeding to 2 years old or older, and tended to breed fewer times than recruits hatched when PDSI conditions were intermediate (Supplementary Table S10; Supplementary Figure S11).

Our results have important conservation implications as climate change is predicted to increase local weather variability, and the frequency and severity of temperature extremes and drought. In the interior of BC, wetter and warmer natal conditions that resulted in reduced LRS_a suggest that potential increases in precipitation and heat waves with climate change (IPCC, 2021) could have adverse demographic consequences in the future. Indeed, the number of extreme heat-related events is already increasing (Parisien et al., 2023), with the highest ever recorded temperatures in 2021 exceeding >35°C during nestling development. While warmer temperatures at the SK site had positive carry-over effects on LRS_a, suggesting tree swallows may benefit from increasingly warm temperatures associated with climate change (Mantyka-Pringle et al., 2019), results from the BC population caution that higher than average temperatures as predicted for the prairies (IPCC, 2021) could led to reductions in fitness of tree swallows in the future. For instance, higher temperatures may not only increase the evaporation of ponded water, but also the susceptibility to drought (Douville et al., 2021). Recent evidence at the SK site highlights the importance of abundant ponds for promoting the population stability of tree swallows (Clark et al., 2018; Berzins et al., 2020, 2021). However, ongoing losses of ponds to agricultural drainage and infilling (Bartzen et al., 2010), combined with the predicted drying of ponds in parts of the prairies (Johnson et al., 2010; Londe et al., 2023) may lead to population declines via lower recruitment and $LRS_{a.}$ Conserving and restoring prairie ponds may therefore be critical for sustaining tree swallow populations in a changing climate.

Aerial insectivores have experienced steep population declines in North America (Rosenberg et al., 2019), but within species there is high spatiotemporal variability in population trends across their ranges (Michel et al., 2016). By evaluating two distinct populations of tree swallows, we show locally varying natal environments had carry-over effects on adult LRS_a. Consequently, natal environmental conditions that generate differences in fitness may explain trends in population-level demographics. Unveiling population responses to environmental variability on the breeding grounds is important as offspring will be increasingly exposed to modified natal environments as climate and land use changes intensify across the globe.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was approved by University Animal Care Committee, University of Saskatchewan; Animal Care and Use Committee, University of Northern British Columbia. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

LB: Conceptualization, Formal analysis, Investigation, Visualization, Writing – original draft, Writing – review & editing. RD: Conceptualization, Funding acquisition, Investigation, Writing – review & editing, Resources. RC: Conceptualization, Funding acquisition, Investigation, Writing – review & editing, Resources.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fbirs.2024.1348114/full#supplementary-material

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