Repurposing historical data to investigate aerial insectivore declines

by

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Abstract

Populations of aerial insectivores have decreased since the mid-1980s, possibly due to declines in their prey. However, long-term data on insect abundance in North America are lacking. I evaluated whether brood size manipulation experiments could be repurposed to assess changes in insect availability. A literature review found no evidence that parents' ability to respond to a challenge has changed over time, but study methods varied widely. Therefore, I replicated a brood size manipulation experiment conducted on tree swallows in 1994/1995. Parents did not change how they responded to changes in brood size. However, delivery rates were consistently lower in 2017/2018 because parents delivered smaller boluses and tended to visit the nest less. These results are consistent with the hypothesis that aerial insectivores are declining due to reduced insect availability, but could also arise for other reasons. My thesis highlights the value of historical data for investigating aerial insectivore population declines.

Keywords: feeding behaviour; tree swallow; aerial insectivores; insect availability; brood size manipulation experiment; historical data

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1.1. Introduction

In North America and Europe, birds that feed on flying insects, called aerial insectivores, have been declining at a faster rate than other groups over the last few decades (Sanderson et al. 2006, Nebel et al. 2010, North American Bird Conservation Initiative Canada 2019). There is likely no single explanation for the observed declines in aerial insectivores (Michel et al. 2016). Anthropogenic changes in land use such as agricultural intensification (Stanton et al. 2018), modern forest management practices (Newton 1994) and urbanization (Chace and Walsh 2006) have impacted the availability of nesting sites as well as prey availability on breeding grounds, wintering grounds or migration routes (Newton 2004, Hallmann et al. 2017, Bellavance et al. 2018). The use of pesticides associated with agricultural intensification can also directly affect the behaviour, physiology and survival of aerial insectivores (Stanton et al. 2018). Finally, with climate change, there are more extreme weather events that can cause catastrophic die-offs in bird populations (Hess et al. 2008, Winkler et al. 2013). Population trends vary across species and regions. Within aerial insectivores, swallows, swifts and nightjars appear to be more affected than flycatchers (Smith et al. 2015). Population declines are also stronger in species that migrate long distances (Nebel et al. 2010). Trends follow a geographic gradient, where birds breeding in northeastern North America are experiencing steeper declines (Nebel et al. 2010). While performing small-scale experiments might identify the causes of local population declines, analyzing general and long-term patterns holds more potential to inform global conservation efforts.

Long-term data sets have been used to estimate population trends in aerial insectivores in several studies (Magurran et al. 2010). Continuous nest monitoring efforts allow scientists to measure changes in productivity. Shutler et al. (2012) analyzed long-term nest occupancy records from multiple sites across North America to study population trends in tree swallows. Long-term monitoring data also allowed researchers to determine that some birds breed earlier, likely as a result of warmer spring temperatures (Dunn and Winkler 1999, Townsend et al. 2013). Many non-academic publications that inform conservation efforts such as governmental reports are also based on long-term monitoring efforts (North American Bird Conservation Initiative Canada 2019).

Long-term surveying efforts offer a straightforward method of assessing population trends over time. However, most studies still rarely exceed the scale of a few years, because maintaining such ongoing efforts is expensive and difficult when funding agencies often operate on a 1 to 5 year time scale (Callahan 1984). The short timeframe for most student led projects implies that studies are not necessarily set up with the primary goal of collecting long-term data. Methods can change and short-term experiments can disrupt standardized monitoring efforts. Long-term data may not be properly entered or organized, making the information difficult to find or use. Many researchers conducting long-term studies recommend the use of citizen science and volunteer field work to minimize costs of maintaining systematic monitoring efforts (Katzner et al. 2014, McArthur et al. 2017). Nonetheless, these projects still require significant initial investments to be implemented successfully (Lindenmayer and Likens 2009). Despite the costs and limitations, data from long-term studies may provide valuable insights into ecological trends over time.

1.2. Thesis overview

In this thesis, I explore the use of historical and long-term data to answer modern questions. In this introductory chapter, I compile data on the breeding biology of a wild population of tree swallows at a single site in southeast British Columbia where nestboxes have been monitored with varying degrees of effort since 1986. In Chapter 2, I review the literature on brood size manipulations, focussing on studies about aerial insectivores and feeding behaviour. My main objectives are (1) to compile the existing literature about BSMEs and assess the range of methods used to inform future research; (2) to identify BSMEs on aerial insectivores and feeding behaviour; and (3) to evaluate the potential of these selected publications to be repurposed to assess long-term changes in provisioning performance as an indicator for trends in aerial insect availability. In Chapter 3, I repeat a brood size manipulation experiment conducted in the 1990s and compare measures of feeding visit rate and biomass fed to the chicks. My two main objectives are (1) to test the potential of using brood size manipulation experiments as an alternative to data-collecting for assessing temporal trends in insect availability, and (2) to evaluate long-term changes in reproductive and provisioning performance of tree swallows at a breeding site.

1.3. Methods

1.3.1. Study site

I conducted fieldwork at the Creston Valley Wildlife Management Area (CVWMA), a marshy habitat in southeast British Columbia, Canada (49°07'11.9"N 116°37'52.0"W). The area is in a natural floodplain that was altered in the 1880s to allow for agriculture (Creston Valley Wildlife Management Area n.d.). A multitude of species has been studied there over the last decades, including great blue herons *(Ardea herodias*; Forbes 1987), wood ducks (*Aix sponsa*; Wilson and Verbeek 1995), western grebes (*Aechmophorus occidentalis*; Ydenberg and Forbes 1988), ospreys *(Pandion haliaetus*; Machmer and Ydenberg 1990), tree swallows (*Tachycineta bicolor*; Wiggins 1990), violet-green swallows (*Tachycineta thalassina*; Beasley 1996), northern leopard frogs (*Lithobates pipiens*; Waye 2000, Voordouw et al. 2010) and painted turtles (*Chrysemys picta*;Jensen et al. 2014).

Tree swallow nestboxes at the CVWMA have been maintained and monitored intermittently since 1986. In the late 1980s and early 1990s, a series of students from Simon Fraser University conducted research projects using swallows that occupied about 100 nestboxes. In the late 1990s and early 2000s, monitoring was limited. In 2008, CVWMA staff and volunteers began a more rigorous monitoring program in which all nests were visited between 5 and 13 times every summer. In early April 2017, I restored the 68 pre-existing nestboxes and installed 47 new ones to return nest numbers to 1990s levels. The boxes were constructed in either a square (16.2 x 16.2 x 20.4 cm) or rectangular (13.9 x 13.9 x 25.8 cm) design. The 115 boxes were placed along dykes and paths, at least 6 metres apart.

1.3.2. Study species

Tree swallows (*Tachycineta bicolor*) belong to the guild of aerial insectivores, i.e. birds that forage for flying insects on the wing. These birds often serve as a model species to study ecological trends in this guild (Jones 2003), since they readily select nestboxes during the breeding period (Robertson and Rendell 1990) and tolerate much disturbance without abandoning the nest. Additionally, their populations remain high enough to allow the colonization of enough nest boxes in one area to conduct repeated experiments (Shutler et al. 2012).

Tree swallows naturally nest in tree cavities, but readily select artificial wooden nest boxes (Robertson and Rendell 1990). Breeding pairs lay between 4 and 7 eggs on consecutive days. Incubation lasts 14-15 days and young fledge after 18-22 days (Kaufman n.d.). These birds generally nest only once per breeding season, but sometimes renest after a failed attempt (Ghilain and Bélisle 2008). Renesting after a successful attempt has been observed in rare instances (this study). Tree swallows, especially males, exhibit high fidelity to their nesting site (Fiedler and Grewe 1983, Winkler et al. 2004).

Diptera represents the primary prey for tree swallows (Beck et al. 2013, Michelson 2015, Bellavance et al. 2018). Other prevalent groups of arthropods present in their diet include odonata, ephemeroptera, coleoptera and hemiptera (McCarty and Winkler 1999, Bellavance et al. 2018). During the breeding season, adults are most active in feeding nestlings between 07:00 and 21:00 (Rose 2009). Swallows usually forage less than 500 metres away from the nest (Bryant and Turner 1982). Although cases of polygyny have been observed, tree swallows are considered mostly monogamous (Quinney 1983). Both parents contribute equally to feeding the offspring (Leffelaar and Robertson 1986, Quinney 1986).

1.3.3. Monitoring

I compiled the following data from the historical records made for all nest boxes monitored: nest initiation date (the date the first egg was laid), hatch date, fledging date, clutch size (the maximum number of eggs recorded), number of unhatched eggs, brood size (the maximum number of nestlings recorded), fledging success (the number of fledglings produced per nest initiated), nest fate and nest success. I collected the same basic breeding biology data from nestboxes monitored in 2017 and 2018.

I obtained historical monitoring data from studies conducted at the Creston Valley Wildlife Management Area (CVWMA) from 1986, 1988 to 1990, and 2008 to 2016. I did not have access to any of the field protocols followed. Monitoring data from 1986 and 1988 was provided by David Wiggins. In 1986, 133 boxes were monitored. Monitoring dates ranged from May 9th to June 22nd. Date of fledging was the only missing information for this data set. In 1988, 161 boxes were monitored. Nests were only monitored until the incubation stage, therefore I only had data for the initiation date, clutch completion date and number of eggs. Monitoring data from 1989 and 1990 was provided by Barbara Beasley. In 1989, 42 boxes were monitored and monitoring dates ranged from May 17th to July 26th. In 1990, 20 boxes were monitored and monitoring dates ranged from May 4th to July 17th. Data was available for all breeding parameters of interest. In 2008, volunteers and naturalists began regularly maintaining and monitoring the 68 to 74 nest boxes installed at the CVWMA. Their efforts have been ongoing since then. However, nestbox visits were only conducted irregularly, on average every two weeks, leading to uncertainty about nest initiation, hatch and fledging dates. However, records for the number of eggs and number of nestlings were reliable.

In 2017 and 2018, I visited 115 nests approximately every two days to determine the onset of incubation, hatch and fledge events. Visits were curtailed during the first 10 days of incubation to avoid unnecessary disturbance when risks of abandonment are higher. I assumed fledging success if chicks were still alive 16 days post-hatching (day 1 being the hatch date). In 2017, I monitored nests from April to mid-July, while in 2018, I monitored nests from the beginning of May to the end of June.

1.3.4. Data analysis

I calculated the mean number of eggs, nestlings and fledglings per nest from all nests that laid at least one egg, regardless of the outcome or cause of failure, for each year that data was available (Table 1.1). This included nests that were depredated. The monitoring data encompassed two distinct periods (1986-1990 and 2008-2018) so I compared the nest initiation dates, clutch sizes, brood sizes (the number of chicks that hatched) and fledging success for the two time periods (historical vs recent). I evaluated whether there have been changes in the timing of breeding or breeding performance using two-sample Welch t-test. I used a two-sample Welch t-test to compare the mean number of eggs, nestlings or fledglings between the historical and recent data. I opted not to use the 2008-2016 data when analyzing initiation dates, because nest visits began later in the season which might bias the results.

1.4. Results and Discussion

1.4.1. Timing

At the CVWMA, the first eggs were laid in early May. I observed a bimodal distribution in initiation dates, as there was a second smaller wave of egg laying later in the season. Later nests were initiated until late June. While tree swallows are thought to only lay one clutch per season, I recorded four instances where females initiated a second nest after their first attempt failed and one instance where a female initiated a second nest after their first attempt was successful (Figure 1.1).

Tree swallow nest initiation dates did not differ between the historical (1986-1990) and recent (2017/2018) time period ($t_{381.5}$ = 1.19, p = 0.24; Table 1.1). This finding is counter to previous evidence that indicates that migratory birds have advanced their lay dates in response to warmer spring temperatures (Dunn 2004, Townsend et al. 2013).

1.4.2. Breeding success

Tree swallow laid clutches that contained between 1 and 8 eggs. Clutches laid in 1986-1990 did not differ in size from those laid between 2008-2018 ($t_{377.9}$ = - 1.61, p = 0.11). Broods contained between 0 and 8 nestlings. Broods in 1986-1990 contained on average 0.82 less chicks than broods in 2008-2018 (mean ± SE; mean historical = 4.59 ± 0.15 nestlings, mean recent = 3.78 ± 0.082 nestlings; $t_{212.8}$ = -4.73, p < 0.001). Similarly, between 0 and 8 nestlings successfully fledged per nest. The number of fledglings has decreased on average by 0.87 chicks (mean historical = 3.58 ± 0.15 fledglings, mean recent = 2.70 ± 0.085 fledglings; $t_{168.9}$ = -3.94, p < 0.001) between the two time periods. These results suggest that productivity at this breeding site has decreased since the late 1980s. This difference appears to arise primarily because of differences in hatching success, since differences in productivity between the two time periods are only observed in post-hatching nesting stages.

Conclusions about changes in productivity should be treated with some caution for two reasons. First the data compiled comes from four different sources and it is possible that there were slight differences in field methods in the two time periods.

Second, the late period encompassed far more years making it more likely that “bad” years, in this case 2010, 2014 and 2016 (Figure 1.2), were experienced and included in the analysis. The apparently greater variation in breeding performance over the last decade warrant further examination of the causes for the variation in brood size and fledging success across years.

1.4.3. Female return rates

I captured 72 females in 2017 and 63 in 2018. Of the 63 birds captured in 2018, 21 had been banded in 2017. This implies a return rate of at least 29% (21/72). This estimate was slightly lower than adult return rates reported in other tree swallow studies (53% De Steven 1980, 44-59% Ardia 2005, 36-49% Bulit et al. 2014). However, I did not capture all the breeding females nesting at this site, so return rates are likely to have been underestimated. At least 11 of the 72 (15%) total captures in 2017 and 15 of the 63 (24%) in 2018 were younger second-year females.

Table 1.1. **Annual variation in clutch size, brood size and fledging success of tree swallows in Creston, BC. Mean ± standard deviation, with sample size in parentheses.**

	Initiation date	Clutch	Brood	Fledging success
1986	139.4 ± 7.1 (84)	5.60 ± 1.32 (85)	5.04 ± 1.72 (70)	3.57 ± 2.47 (60)
1987	NA	NA	NA	NA
1988	141.0 ± 11.7 (96)	5.15 ± 1.15 (96)	NA	NA
1989	148.9 ± 10.6 (37)	4.86 ± 0.98 (37)	4.24 ± 1.34 (37)	3.83 ± 1.59 (36)
1990	146.2 ± 13.9 (23)	4.76 ± 1.48 (25)	3.78 ± 1.95 (23)	3.18 ± 2.26 (22)
1991-2007	NA	NA	NA	NA
2008	NA	4.58 ± 1.15 (62)	3.44 ± 1.91 (62)	2.27 ± 2.17 (62)
2009	NA	5.61 ± 0.95 (67)	4.37 ± 1.91 (67)	3.01 ± 2.51 (67)
2010	NA	4.91 ± 1.06 (32)	3.16 ± 2.27 (32)	1.75 ± 2.05 (32)
2011	NA	5.48 ± 1.08 (58)	3.93 ± 1.81 (57)	3.21 ± 2.21 (56)
2012	NA	5.39 ± 1.10 (76)	3.85 ± 1.96 (75)	2.96 ± 2.08 (75)
2013	NA	5.61 ± 0.99 (72)	4.26 ± 2.12 (72)	3.83 ± 2.20 (72)
2014	NA	5.07 ± 1.24 (69)	1.42 ± 2.39 (69)	1.30 ± 2.31 (69)
2015	NA	5.34 ± 1.24 (61)	3.96 ± 2.10 (57)	3.74 ± 2.25 (57)
2016	NA	5.34 ± 1.33 (58)	3.45 ± 2.54 (55)	1.75 ± 2.34 (44)
2017	143.2 ± 14.9 (97)	5.57 ± 1.11 (130)	4.49 ± 2.14 (130)	2.74 ± 2.80 (114)
2018	140.8 ± 11.8 (105)	5.54 ± 1.14 (105)	4.05 ± 2.38 (99)	2.51 ± 2.66 (90)

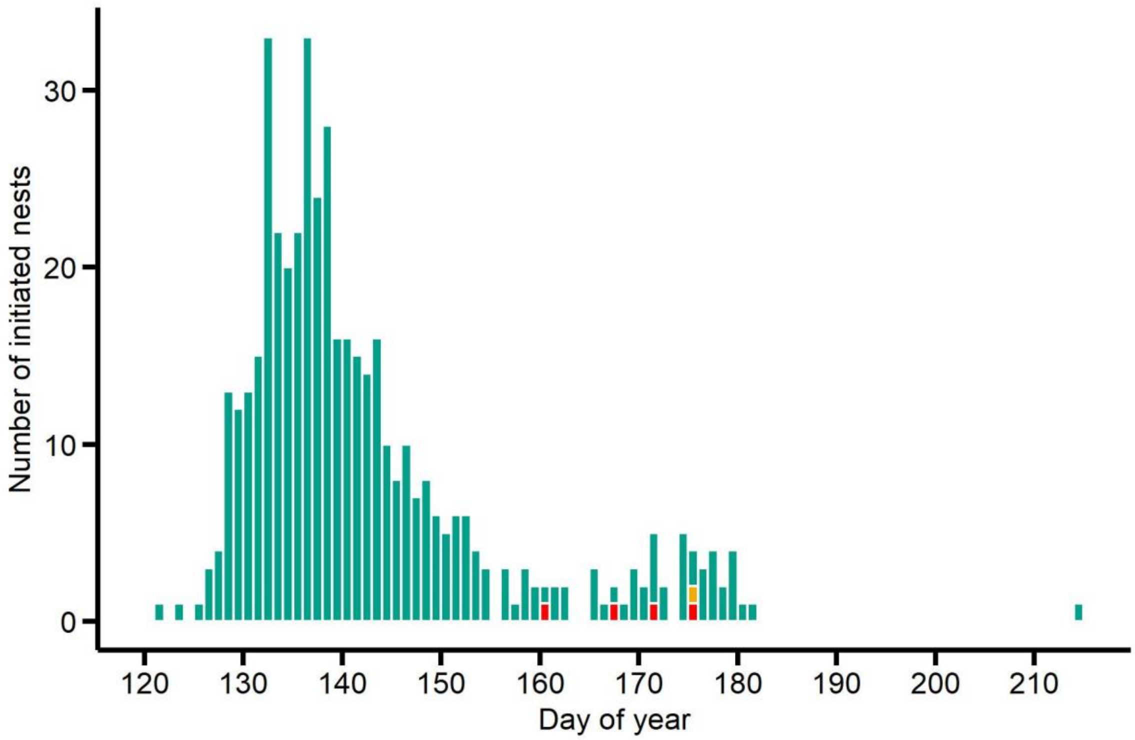

Figure 1.1. Frequency distribution showing the number of nests initiated on each day of the year (January 1 = 1). Data from 1986 (n = 84), 1988 (n = 97), 1989 (n = 37), 1990 (n = 23), 2017 (n = 98) and 2018 (n = 115) is combined. The red bars represent renesting attempts following a failure (3 attempts in 2017 and 1 in 2018). The yellow bar represents a renesting attempt after a success (in 2017).

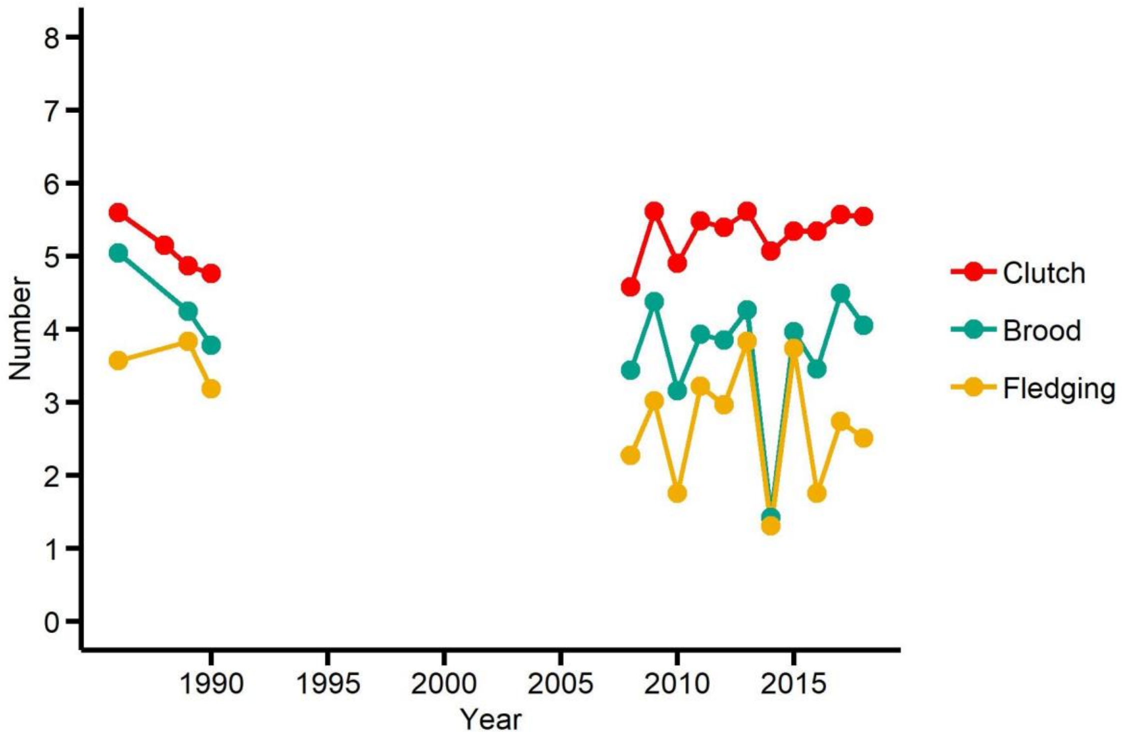

Figure 1.2. Annual variation in clutch size, brood size and fledging success of tree swallows in Creston, BC. Points display the means for each year where data is available.

Chapter 2. A Scoping Review of Brood Size Manipulation Experiments on Aerial Insectivores

2.1. Introduction

Populations of aerial insectivores, namely swallows, swifts, nightjars and some flycatcher species, have been decreasing both in Europe and North America (Sanderson et al. 2006, Nebel et al. 2010, Thaxter et al. 2010). In North America especially, aerial insectivores are amongst the guilds experiencing the steepest declines (North American Bird Conservation Initiative Canada 2019). Declines in these birds may be caused by changes in prey abundance resulting from agriculture intensification (Paquette et al. 2013, Conover et al. 2014, Stanton et al. 2018). In Europe, some studies have reported concurrent declines in bird populations and their insect prey (Shortall et al. 2009, Hallmann et al. 2017). However, there is a lack of long-term data on insect abundance that could allow us to directly test the hypothesis that aerial insectivore declines in North America are due to declines in flying insects. In contrast, the literature contains an abundance of studies examining the breeding and feeding behaviour of aerial insectivores. There are likely even more data available in theses and in the grey literature. Here I argue that these data can be repurposed to test the idea that aerial insects have declined in abundance, and that the reduced prey availability underlies the steep decline in aerial insectivores.

Brood size manipulation experiments (BSMEs) represent an ideal opportunity to repurpose historic data, because they are accessible and have been performed since the 1960s (Rice and Kenyon 1962, Vermeer 1963, Nelson 1964). After Lack introduced the optimal clutch size hypothesis (Lack 1954, 1966), many studies performed BSMEs to investigate the relationship between clutch size and parental feeding ability (Askenmo 1977, Finke et al. 1987, Briskie and Sealy 1989). Many studies demonstrated that parents could successfully rear additional chicks (Ydenberg and Bertram 1989, Vanderwerf 1992). More recent research has shifted to use BSMEs to investigate the broader costs and trade-offs of reproduction (Murphy et al. 2000). Other studies have used BSMEs to simulate food deprivation, increase sibling competition or mimic variation in yearly conditions by controlling parental effort (Saino et al. 2000, de Ayala et al. 2006). Since brood size manipulation experiments typically impose additional breeding cost and energetic challenge to parents, changes in environmental conditions that reduce prey availability could alter the willingness or ability of parents to respond to experimental increases in brood size. If insect populations have declined, I would therefore expect that parental responses to brood enlargements would be reduced if experiments were replicated several years later.

Despite having been widely used for more than 60 years, there has been no recent review that provides a synthesis of the body of literature on BSMEs. In this chapter, I conduct a scoping review of the literature on BSMEs. Scoping reviews (sensu Pham et al. 2014) are a relatively new type of literature review that aims to outline the available literature on a broad topic to guide future research, systematic reviews or meta-analyses. This type of review has rarely been used in the field of ecology (Gabriele-Rivet et al. 2019). With this scoping review, I aim (1) to compile the existing literature about BSMEs and assess the range of methods used to inform future research; (2) to identify BSMEs on aerial insectivores and feeding behaviour; and (3) to evaluate the potential of these selected publications to be repurposed to assess long-term changes in provisioning performance as an indicator for trends in aerial insect availability.

2.2. Methods

2.2.1. Research question

I developed the methodology for this scoping review based on the guidelines outlined by Arksey and O’Malley (2005). This review was guided by the questions: What are the characteristics and range of methodologies used in brood size manipulation experiments in the literature? How many of the BSMEs focussing on aerial insectivores and feeding behaviour hold the potential to be repurposed to test the idea that there has been a reduction in prey availability over the last two to three decades?

2.2.2. Literature search

I performed a search on the online Web of Science Core Collection and the Zoological Record databases using the keywords ([brood*] NEAR/2 [manip*]) OR ([brood*] NEAR/2 [enlarg*]) in topics, which resulted in a total of 535 and 481 publications respectively. This list was complemented with articles found through Google Scholars and references from the initial articles. Literature was last searched and updated in May 2019.

2.2.3. Data management and screening

All references were imported and managed using Mendeley version 1.19.4 (MendeleyLtd., 2019). All publication data was exported to Microsoft Excel (Microsoft Corporation, 2016) to be categorized. The preliminary exploration, reading and annotation of articles were facilitated through NVivo version 12.4.0.0741 (QSR International, 2019). Data was subsequently imported into R version 3.5.3 (R Core Team, 2019) to perform data manipulations and generate figures.

I first removed duplicates manually and as I identified them throughout later analysis. I then screened articles for relevance to our research question, extracting different types of information at each level of screening (Figure 2.1).

For the first level of screening, I reviewed only titles and abstracts to include brood size manipulation experiments conducted on birds. I excluded articles featuring research conducted on other animals such as insects and fish, or experiments manipulating brood sex ratio or synchrony. From the resulting studies, I used titles and abstracts to categorize publications by study species. Species were grouped based on similarities in diets, habitat and taxonomy. The groups were defined as: corvids, passerine: aerial insectivores, passerine: granivores, passerine: insectivores, passerine: omnivores, raptors, seabirds, shorebirds, waterfowl, woodpeckers and others (doves, herons, parrots and grouse). I then illustrated the number of studies conducted on each species in relation to year of publication to generate a historical profile of BSMEs.

For the second level of screening, I selected studies conducted on aerial insectivores only. I used abstracts, or full-text articles if details were absent from abstracts, to identify the main responses measured following brood size manipulations. These effects of brood size manipulations were classified into broader topics: costs to chicks, costs to adults, changes in feeding behaviour or other.

For the third and last level of screening, I examined the full-text articles of each brood size manipulation study measuring a response in provisioning performance, i.e.

feeding visit rate and/or load mass. I extracted the main parameters in the methodology. These parameters included: species, region, year of experiment, day of manipulation, brood size change, day of observation, observation method and sample size. This was done to identify potential challenges of replicating these experiments. I then ranked the studies on a scale of 0 to 4 based on their potential to be repurposed to investigate another research question, or “repurposability” (Table 2.1). Ideal studies would present raw data or summary statistics that allow calculating a standardized effect size between enlarged and control broods for a measure of provisioning performance. Rating was determined as follows: 4: raw data is accessible and suitable, 3: data presented in paper is readily usable, i.e. measures of mean/least square mean, standard deviation/standard error and sample size classified into treatments for reduced, control and/or enlarged broods are easily found, 2: data is available from paper, but has to be transformed or extracted from figures, 1: data is potentially suitable but the author would need to be contacted to obtain the information needed to calculate an effect size, 0: data is not suitable, methods are too vague or inconsistent, there is no control group or sample sizes are too small.

2.2.4. Data analysis

I extracted data from 13 articles that were rated with a repurposability score of 2 or higher, i.e. articles that included the information needed to calculate a standardized effect size. I calculated effect sizes associated with enlarging a brood by any number of chicks, typically two. I used the mean or least squared mean, the standard deviation or standard error and the sample size of control and enlarged broods to calculate Cohen’s d effect size using the esc package (Lüdecke 2019). I then used a linear model to examine whether effect sizes decreased over time.

2.3. Results

In total, I identified 408 papers related to brood size manipulation experiments in birds that were published between 1962 and 2019. Our oldest record of published BSME dates to 1962 (Figure 2.2). Since then, the number of BSME articles published has increased every decade. The term “brood size manipulation” became widespread in the 1980s. The first recorded mention was in 1980 (Loman 1980). Before 1980, 71% (n =

12) of the studies were conducted on seabirds. Since 2010, 81% (n = 100) of the published studies targeted passerine species.

In the 408 studies about brood size manipulations, 108 different species of birds were studied (Figure 2.2). The most common species included: great tits (n = 61), zebra finches (n = 40), blue tits (n = 36), collared flycatchers (n = 23), tree swallows (n = 22), barn swallows (n = 21) and pied flycatchers (n = 18). I noted that most studies on zebra finches were conducted on captive birds.

2.3.1. Measured responses

Twenty-six percent (n = 107) of all 408 BSME publications studied aerial insectivores. I categorized responses into 4 groups (Figure 2.3). Feeding responses included: feeding visit rates (n = 36) and load size or content (n = 7). The recorded effects on chicks included: development (e.g. mass, size or wing length; n = 67), fledging success (n = 33), physiological measurements (e.g. immune response, stress, oxidative damage; n = 21), recruitment (n = 15), future reproductive success of fledged chicks (n = 3). Effects on adults included: body condition (e.g. mass and plumage, n = 25), survival in subsequent years (n = 19), physiological measurements (n = 13), energy expenditure of adults (n = 4) and future reproductive success (n = 6). Other measured responses involved: begging intensity (n = 6), intensity of parasite infestation (n = 5), timing of life history events (n = 3) or other miscellaneous behavioural observations (n = 9).

2.3.2. Methodologies

Thirty-four percent (n = 36) of the BSME publications on aerial insectivores measured a response in feeding behaviour (Figure 2.3). Three pairs of these publications reported on the same experiments, thus were grouped together to yield a total of 33 studies with unique BSMEs (Table 2.1). Sixteen studied swallows, swifts or matins, while the other 17 focussed on flycatcher species. The selected experiments were all performed between 1982 and 2016. Nineteen took place prior to 2000. Thirty-six percent (n = 12) of these experiments took place in North America. I noted one case where an experiment using similar methodologies was conducted at the same location with a time interval of 28 years (Leffelaar and Robertson 1986, Bonier et al. 2011), although standardized effect sizes could not be calculated for Leffelaar and Robertson

(1986) study. I noted an additional five cases where experiments were repeated at the same location, but in these cases the time interval between the two experiments never exceeded 5 years.

The methods used to perform BSME on aerial insectivores varied widely between studies (Table 2.1). The magnitude of the brood size manipulation ranged from enlarging or reducing the broods by one to four chicks. However, in a majority of studies (18), brood size was modified by two chicks or about 50% of the original brood size. The timing and duration of the brood size manipulation also varied. Manipulations were conducted during and just after egg-laying through to the late nestling stage and could be temporary (lasting from hours to days) or permanent. There was greater consistency in how parental responses to the BSMEs were measured. All 33 studies but one measured the rate of feeding visits to the nest. However, the timing of when parental provisioning was monitored, the duration of observations, and whether parents were observed on multiple occasions varied. Most (26) recorded parental provisioning rates around 10-13 days post-hatching. Only 7 studies recorded prey types or the biomass of prey fed to chicks. Three measured the mass of the load delivered using scales placed in the nestbox, one collected bolus samples retrieved by parents, two estimated prey size, one counted the number of items and one identified the type of prey.

Of the 33 studies that measured the response of parents to the BSMEs, 14 provided sufficient information to allow an effect size to be calculated (repurposability score >1, Table 2.1). I also identified 12 studies that measured the responses of interest, but that did not report the values necessary to calculate standardized effect sizes. Finally, I completely rejected 7 studies due to inconsistent or vague methods.

2.3.3. Preliminary meta-analysis

Most studies reported that the average parental nest visit rate increased when provisioning an enlarged brood compared to a control. However, in only five cases were the effect sizes significantly different from 0 (Figure 2.4). There was no evidence to suggest that experimental responses have changed over time ($F_{1,14} = 0.54$, $p = 0.48$). All older studies that were conducted prior to 2000 with readily available data were on flycatchers.

2.4. Discussion

In this chapter, I provided an overview of brood size manipulation experiments published in the literature. I specifically identified potential studies that could be repurposed to assess insect availability by measuring the provisioning performance of aerial insectivores. An extensive search of the literature on brood size manipulation experiments in birds identified 408 studies spanning from 1962 to 2019. A substantial proportion of these studies were conducted on aerial insectivores, with 33 studies describing how parental provisioning behaviour responded to the challenge of feeding an enlarged brood. Unfortunately, there was considerable variation in how results were presented that limited the number of studies where standardized effect sizes could be calculated. For the 14 studies where effect sizes could be calculated, there was no evidence that feeding visit rates have changed over the last three decades. Based on the range of methodologies and quality of results presented in those publications, I propose some recommendations for future BSMEs to be replicated. We discuss some of the limitations and advantages of repurposing historical BSMEs as a way of evaluating whether insect populations have declined across North America.

Brood size manipulation experiments challenge parents to increase their provisioning rate in response to a short- or long-term increase in brood size. My literature review identified 33 studies on 11 species of aerial insectivores that manipulated brood size and measured changes in the provisioning behaviour of the parents. I had suggested that if insect abundance has declined, we would expect that the response in provisioning performance of parents challenged to feed additional nestlings would decrease over time. I did not detect a change in how parental responded to enlarged broods, as the standardized effect sizes between enlarged and control treatments did not vary over the years. However, there were four major limitations in the usefulness of these studies as a tool to evaluate changes in responses to BSMEs over time. Firstly, many publications did not report sufficient data to calculate a standardized effect size. This absence of information highlights the benefits of publishing raw data along with the articles so they could be used in future meta-analysis. Secondly, most experiments measured nest visit rates but did not attempt to measure load sizes or estimate energetic delivery rates. Only 4 studies examined load mass delivered to the chicks, and these sampling methods were inconsistent between studies. Furthermore, the methods used to perform BSMEs varied considerably between studies, making the comparison between these studies more challenging. Namely, studies varied in when the data were recorded. The date of feeding observations may affect the measured visit rate, since feeding demand increases with chick age, peaking around day 13 (Morehouse and Brewer 1968, Leonard and Horn 2006, Lundberg and Alatalo 2010). If data was not collected during peak feeding demand, parents may not have been experiencing a challenge despite the additional chicks to feed. Finally, the date of manipulation in relation to the date of observation differed between studies. This may affect the parental response to brood size manipulations if parents cannot maintain increased efforts for long periods. The failure to detect a change in the response to brood size enlargement in experiments conducted between 1988 and 2011 could therefore be due to the lack of measurements of prey type or biomass to estimate actual delivery rates, and differences in the methodologies of BSMEs that were not controlled in this chapter.

To detect temporal trends in the responses to manipulations despite the incompatibility of the methodologies, experiments may need to be replicated to remove the range of confounding effects on parental responses. Differences in parental response between the manipulations may be measured by calculating effect sizes of manipulated broods in relation to controls. I identified only 1 case where a study was replicated with similar but not identical methods at a single study site with a time interval of over a decade. However, one of these studies did not provide the appropriate information to calculate the standardized effect sizes (Leffelaar and Robertson 1986). Not only can replication of scientific experiments allow us to test the validity or variability of prior research (Fidler et al. 2017), it can also be used as a way to assess changes in the level of response over time. Unfortunately, the field of ecology is particularly prone to a lack of replication due to the variable nature of ecological study systems (Schnitzer and Carson 2016). Based on my preliminary analysis of the available literature, studies that measure both nest visit rate and prey type or mass of food delivered, if replicated, would have the greatest potential to evaluate whether parental responses have changed over time as a result of changes in insect abundance. Further work could also explore the utility of studies that assess costs of brood size enlargements to the chicks, since these measures may better reflect overall delivery rates. However, this response is less directly linked to insect availability. Ultimately, by replicating multiple studies in North

America and analyzing the differences in response over time, we could generate temporal gradients of trends in provisioning performance and circumvent the lack of data on insect abundance.

In conclusion, there is enough historical data available to be repurposed, though some additional efforts might be required to find the relevant information. When selecting the studies to replicate with intention of repurposing them, I suggest prioritizing studies from the selected list (Table 2.1) that were conducted (1) on swallows, swifts or nightjars, because this group of species experiences distinctive population trends compared to flycatchers (Smith et al. 2015), (2) in North America, because long-term data is especially lacking in that part of the world compared to Europe and (3) more than 20 years ago, because we are interested in long-term trends since aerial insectivore populations have started declining. I also suggest replicating studies in order of “repurposability” to maximize the efficiency of research efforts. Publications with higher scores of “repurposability” would involve less work to find or extract the data. While the scope of this review was mostly limited to aerial insectivores, the selection of potential studies could be extended to include other insectivorous birds to examine trends in all insect groups. Moreover, this review only focussed on published research. However, I suspect that there are several unpublished data sets that would be ideal to repurpose, especially in field locations with ongoing monitoring of bird populations. I recommend researchers who have access to these data to take advantage of this valuable historic information. In the next chapter, I put this concept to the test by repurposing unpublished data and replicating a BSME conducted in the 1990s.

Table 2.1. **Comparison of methodologies used in brood size manipulation experiments conducted on aerial insectivores that measure provisioning performance. Studies for which Cohen's d standardized effect sizes were calculated in the preliminary analysis are indicated by asterisks.**

Reference	Species	Location	Year of exp.	Manip. day[a]	Brood size change	Obs. day[a]	Obs. duration	Obs. method	Feeding Response measured	Sample size	Repur.[b]
(Saino et al. 1997)	barn swallow	northern Italy	1996	NA	3-6±1	every day	1-1.25h daily	observer	visits/h	34	1
(Saino et al. 2000)	barn swallow	northern Italy	1997-1999	≤d1 nest.	n±1	d12	~3.78h	observer	visits/h of individual nestlings	36	0
(Pap and Márkus 2003)*	barn swallow	east Hungary	2000-2001	d2 nest.	n±1	d10-12	1h	observer	visits/h	78	3
(Vitousek et al. 2017)*	barn swallow	Colorado, USA	2010	d2 nest.	n±2	d6	30 min	observer	visits/h	60	2
(Magrath et al. 2007)*	fairy martin	south-western New South Wales, Australia.	2001	d11-18 nest.	2-4±1-2	2 days after manipulation	2 days (temporary)	transponder	visits/h	43	2
(Martins and Wright 1993a), (Martins and Wright 1993b)	common swift	Oxford, United Kingdom	1988	d6 nest.	2-3:1-4	every 5 days nest.	1 day	observer, scale	visits/day, load mass	20	1
(Cucco and Malacarne 1995)	pallid swift	northwestern Italy	1990-1992	d3-5 nest.	3±1	every 5 days nest.	~8 x 8h	video, scale	visits/h, load mass	36	1

Reference	Species	Location	Year of exp.	Manip. day[a]	Brood size ± change	Obs. day[a]	Obs. duration	Obs. method	Feeding Response measured	Sample size	Repur.[b]
(Leffelaar and Robertson 1986)	tree swallow	Ontario, Canada	1982	d4-6 or d15-17 nest.	5-6±2	every 4 days nest.	4 days x 4 x 30 min	observer	visits/h	28	1
(Bonier et al. 2011)*	tree swallow	Ontario, Canada	2010	d4 nest.	n±2	d10 nest.	> 3.9 h	video	maternal visits/h	16	2
(Jones 1987)	tree swallow	Scotland, UK	1985	d2-17 nest.	-2-3, +3-4	NA	NA	observer, scale	visits/h, load mass	8	0
(Shutler et al. 2006)	tree swallow	Saskatchewan, Canada	1992	<d4 incu.	n±1	d8, 12 & 16, morning and afternoon	6 x 20 min	observer	visits/h	45	1
(Bortolotti et al. 2011)*	tree swallow	Saskatchewan and BC, Canada	2008	d3 nest.	n±2	d9, 11 or 13 nest.	>1h	microphone	visits/h	79	2
(Murphy et al. 2000)	tree swallow	New York, USA	1997	d2-3 nest.	6±1-4	d10-14	3x1h	observer	visits/h	21	1
(Ardia 2005)*	tree swallow	Tennessee and Alaska, USA	2001-2003	d4 nest.	n±50%	d9-12 nest.	3 x 60 min	video	visits/h	54 TN, 49 AK	3
(Ardia 2007)*	tree swallow	New York and Alaska, USA	2000, 2002	d4 nest.	n±50%	d9-12 nest.	3 x 60 min	video	visits/h	49 NY, 49 AK	2
(Hainstock et al. 2010)	tree swallow	Nova Scotia, Canada	2001, 2003, 2004	d1 incu.	n±2	d8, 12 & 16, morning and afternoon	6 x 20 min or 45 min	observer or video	visits/h	82	1

Reference	Species	Location	Year of exp.	Manip. day[a]	Brood size change	Obs. day[a]	Obs. duration	Obs. method	Feeding Response measured	Sample size	Repur.[b]
(Berzins and Dawson 2016)*	tree swallow	British Columbia, Canada	2010-2011	d3 nest.	n±2	d6,8 & 10 nest.	40 min	observer	male visits/h	42	2
(Bulit et al. 2014)	white-rumped swallow	Buenos Aires Province, Argentina	2006-2009	d1 nest.	n±2-3 (±50%)	d5 & 13 nest.	2h	video	visits/h	76	1
(Pärt and Doligez 2003)*	collared flycatcher	Baltic Sea	1988	d8-9 nest.	n±2	d11	3h	observers (2)	visits/h	36?	2
(Laczi et al. 2017)	collared flycatcher	Hungary	2015-2016	d3 nest.	n±2	d11 nest.	1h	video	visits/h	39	1
(Maigret and Murphy 1997)	eastern kingbird	New York, USA	1992-1993	d3-4 nest.	n±1-2	d7-14 nest.	≥1h	observer	visits/h	46	1
(Conrad and Robertson 1992), (Conrad and Robertson 1993)*	eastern phoebe	Ontario, Canada	1989-1990	≤d2 incu.	n±2	d4 & 10 nest.	2 x 30 min	observer	visits/h	48	2
(Moreno 1989)	northern wheatear	Baltic Sea	1985-1987	NA	NA	NA	>3h	EPSON portable computer	visits/h	18	0
(Moreno 1987a), (Moreno 1987b)	northern wheatear	eastern Sweden	1982-1985	soon after hatching	6-7±1-2	nearly all nest. ages	1-18h	observer	visits/h, approx. prey size	21 (6 manip.)	0

Reference	Species	Location	Year of exp.	Manip. day[a]	Brood size change	Obs. day[a]	Obs. duration	Obs. method	Feeding Response measured	Sample size	Repur.[b]
(Siikamäki et al. 1998)	pied flycatcher	central Finland	1991-1993	incu.	n±1-2	d5 or >d8	NA	sampling	beakload mass, prey type & length	94F/83M	0/2 (bolus only)
(Moreno et al. 1995)*	pied flycatcher	central Spain	1992	≤d1 nest.	6±2	d7 nest.	1h	observer	visits/h, # of prey	14M, 11F	3-4
(Moreno et al. 1999)*	pied flycatcher	central Spain	1998	d2 incu.	n±2	d3 and 13	2 x 1h	video	visits/h	26	2-3
(Sanz 1997)*	pied flycatcher	central Spain	1994	d2 incu.	5-6±2	d13	1h	observer	visits/h	57	3
(Sanz 2001)*	pied flycatcher	central Spain	1997	d2 incu.	6-7±2	d13	1h	video	visits/h	41	3
(Schuett et al. 2017)	pied flycatcher	Finland	2012	d4 nest.	n±1	d10	24h	receiver reading systems	visits/day	66	1
(Westneat et al. 2017)	pied flycatcher	North Wales, UK	1998-1999	d2-3 nest.	n±2-3	d7-12	6 x 1.5h	video, scale	inter-visit intervals, load mass	30	0
(Lifjeld and Slagsvold 1991)	pied flycatcher	southern Norway	1987-1988	d3	n±2	d6, 10, 14	30 or 60 min	observer	visits/h	11	0
(Källander and Smith 1990)	pied flycatcher	southern Sweden	1987-1988	d6 nest.	n±2 or 50%	d11-12	1 or 2 days	automatic recorder	visits/day	70	1

Abbreviation meanings: nest.: of nestling phase, incu.: of incubation, exp.: experiment, manip.: manipulation, d: day, obs.: observation, n: initial brood size, repur.: “repurposability,” -: to a: Assume a ± day difference, considering the wording used in papers may not be consistent depending on whether day of incubation/hatching is considered day 0 or day 1. If unspecified, I assumed that day 1 corresponded to the day of hatching, and that n day-old chicks were at n+1 days post-hatching.

b: The articles were rated from 0 to 4 based on their potential to be repurposed. Rating was determined as follows: 4: raw data is accessible and suitable, 3: data presented in paper is readily usable, i.e. measures of mean/least square mean, standard deviation/standard error and sample size classified into treatments for reduced, control and/or enlarged broods are easily found, 2: data is available from paper, but might require to be transformed or extracted from figures, 1: data is potentially suitable but the author would need to be contacted to obtain the information needed to calculate an effect size, 0: data is not suitable, methods are too vague or inconsistent, there is no control group or samples sizes are too small.

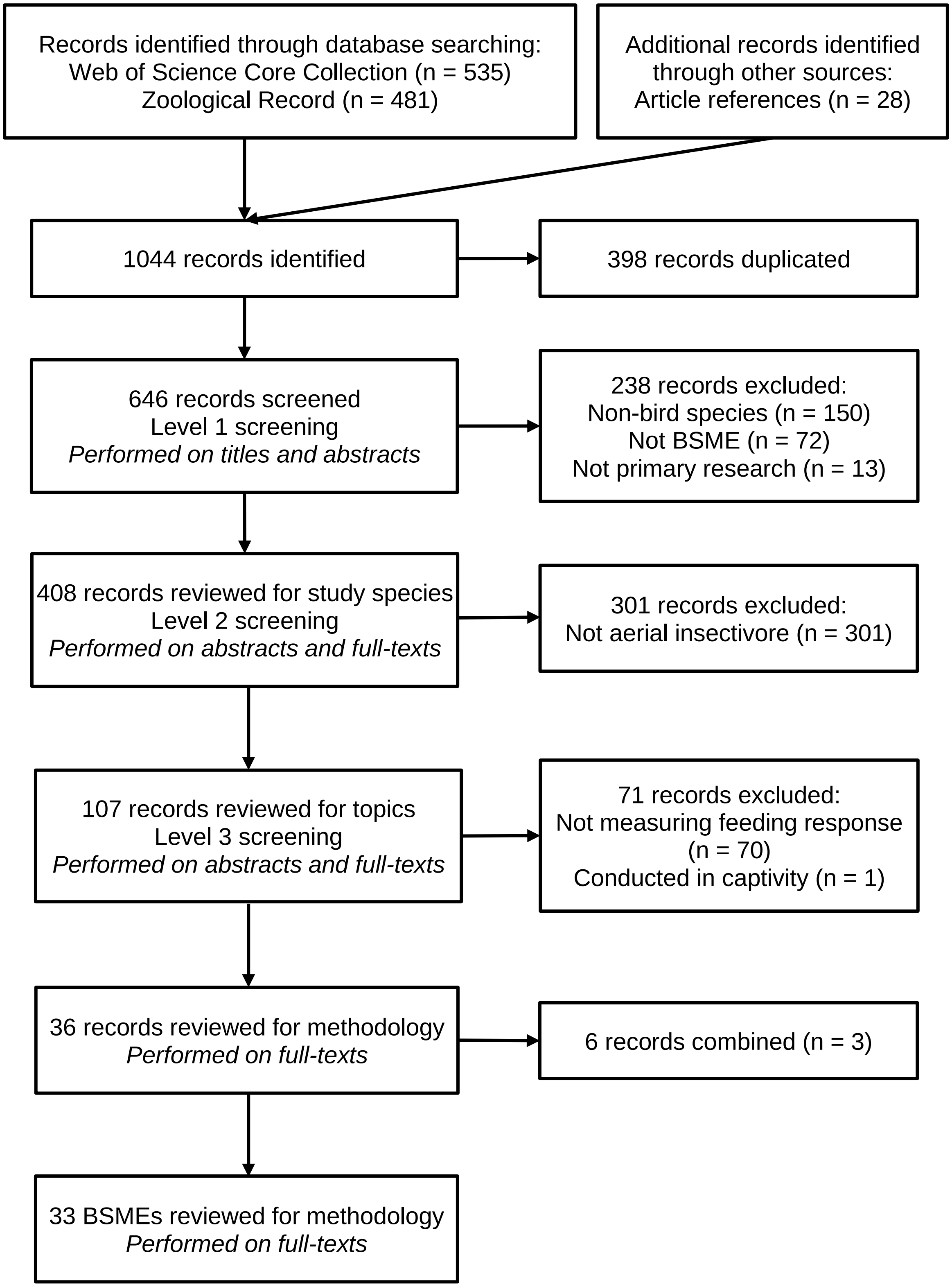

Figure 2.1. Flowchart showing the screening process used in the literature review modified from a Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) flowchart.

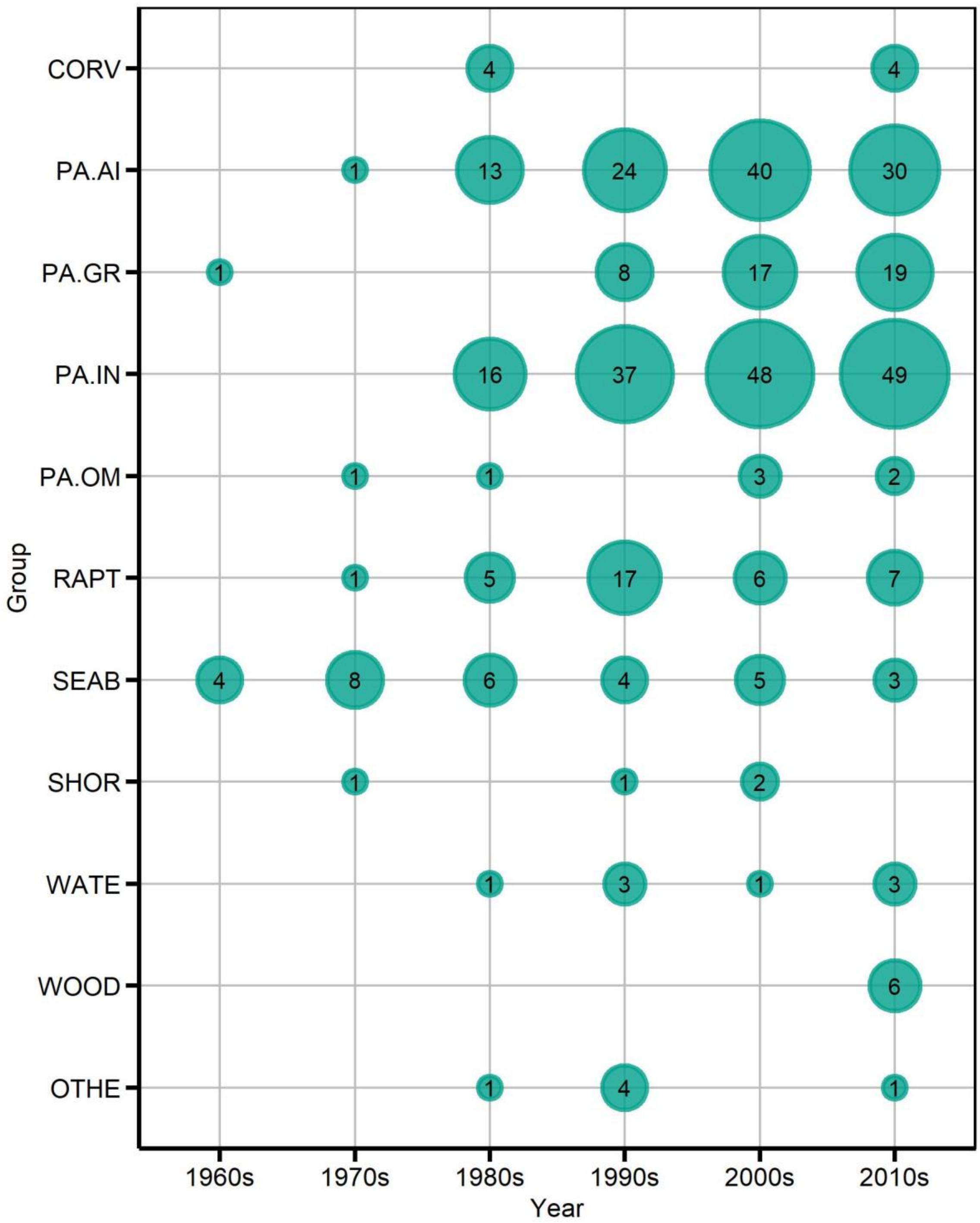

Figure 2.2. **Summary of number of papers describing brood size manipulation experiments in each decade since there first identified publications in the 1960s. Papers are separated into species groups: corvids (CORV), passerine: aerial insectivores (PA.AI), passerine: granivores (PA.GR), passerine: insectivores (PA.IN), passerine: omnivores (PA.OM), raptors (RAPT), seabirds (SEAB), shorebirds (SHOR), waterfowl (WATE), woodpeckers (WOOD) and others (OTHE). "Others" include doves, herons, parrots and grouse.**

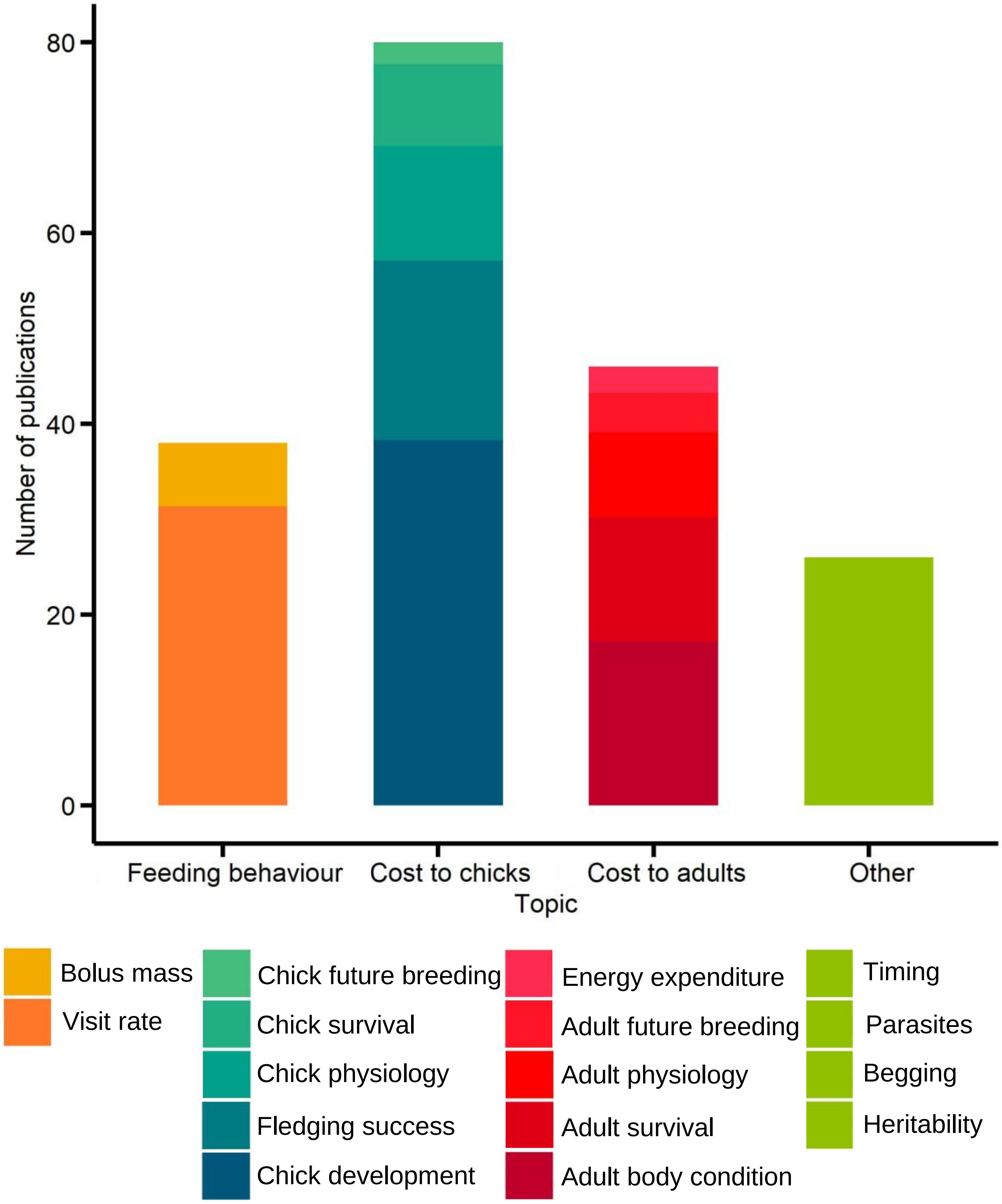

Figure 2.3. **Summary of the responses measured in the 108 papers documenting brood size manipulation experiments on aerial insectivores. Papers may measure multiple responses.**

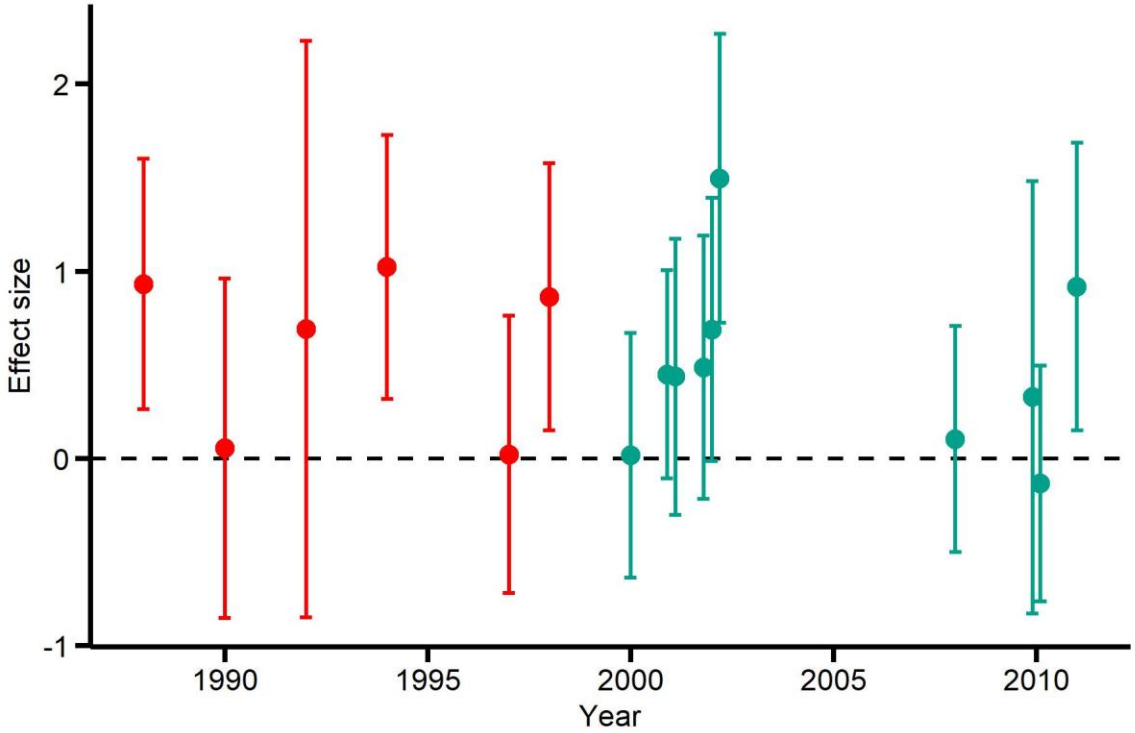

Figure 2.4. **Historical variation in the effect of brood size enlargement on parental nest visitation rate, based on 14 studies of aerial insectivores (red = flycatchers, blue = swallows and swifts). Shown is Cohen's d ± 95% confidence interval. Two studies involved two BSMEs in different locations.**

Chapter 3. Repurposing brood size manipulation experiments to assess declines in insect availability

3.1. Introduction

Aerial insectivore populations have been declining since the mid-1980s (Nebel et al. 2010, Smith et al. 2015). These trends have been observed in bird species that breed in both North America and Europe (Sanderson et al. 2006, Nebel et al. 2010, Thaxter et al. 2010). The causes of these declines in aerial insectivores remain unclear, but likely involve a combination of factors (Michel et al. 2016). Prey availability on breeding grounds, wintering grounds or migration route may have declined as a consequence of human activities (Newton 2004, Bellavance et al. 2018). Nesting sites have also been lost due to agricultural intensification (Stanton et al. 2018) and modern forest management practices (Newton 1994). Agricultural intensification is also associated with an increased usage of pesticides, which can directly affect the behaviour, physiology and survival of aerial insectivores (Stanton et al. 2018). Extreme weather events stemming from climate change can increase instances of catastrophic die-offs in bird populations (Hess et al. 2008, Winkler et al. 2013).

Declines of species abundance in the aerial insectivore guild are likely linked with their diet, as this is the predominant shared trait. Several recent studies suggest that there has been a worldwide decline in the abundance of aerial insects. In Europe, populations of flying insects such as flies, moths and butterflies are dropping (Conrad et al. 2006, Shortall et al. 2009, Van Dyck et al. 2009, Groenendijk and Ellis 2011). Hallman et al. (2017) reported 76% declines of aerial insect biomass over the past 27 years in Germany. Globally, these population declines may be sufficient to cause the extinction of 40% of insect species over the next few decades (Sánchez-Bayo and Wyckhuys 2019). Across the Northern hemisphere, these dramatic declines in arthropod abundance have been associated with several factors: widespread changes in climate (Shutler et al. 2012, Winkler et al. 2013), the use of pesticides such as neonicotinoids (Nocera et al. 2012, Hallmann et al. 2014) and changes in land use towards intensive agriculture (Stanton et al. 2016). The impact of reduced prey availability on aerial insectivore populations may be exacerbated by a predominant depletion of high quality, high trophic level prey (English et al. 2018), but little is known about which types of food are truly more energetically profitable for aerial insectivores (Turner 1982, Mcclenaghan et al. 2019). Changes in prey abundance and composition could influence both the breeding performance and survival of aerial insectivores, explaining why their populations are diminishing. Low food availability may reduce the young's chances of survival before and after fledging (Naef-Daenzer and Grüebler 2016) by hindering chick growth (McCarty and Winkler 1999, Brzek and Konarzewski 2004) or impact the survival of adults (Clark et al. 2018). Nonetheless, there is a scarcity of long-term studies that could allow us to assess the availability of flying insects in North America.

Here, I argue that the deficit of long-term studies on insect abundance can be mitigated by repurposing brood size manipulation experiments to re-examine the provisioning performance of birds. Brood size manipulation experiments involve permanently or temporarily changing the number of chicks in a nest and measuring the response of the parents or the chicks. These types of studies have been widely used in the past to investigate the costs of breeding (De Steven 1980, Murphy et al. 2000). Brood manipulation experiments therefore challenge birds to meet the increased energetic demands of their brood, allowing us to assess the ability or willingness of parents to increase their provisioning rate. Declines in insect availability may have been offset by declines in avian population size, reducing competition for food resources such that natural provisioning rates are maintained. However, when exposed to the challenge of feeding a larger brood, I would expect that the feeding abilities of the parents would be reduced if prey availability has declined. Repeating brood experiments conducted in past decades could therefore provide an indirect method to assess long-term changes in insect abundance on breeding grounds.

To test the hypothesis that insect availability for breeding tree swallows has declined, I repeated a brood size manipulation experiment that was performed in 1994/1995 in southeast British Columbia (Dyck 1995). I used the provisioning performance of adults as an indicator of insect availability. In the past experiment, parents increased their delivery rates when challenged to feed an enlarged brood, but did not completely meet the increased energetic demands of their brood (Dyck 1995). Other passerines have also shown immediate responses to short-term brood size manipulations (García-Navas and Sanz 2010). Therefore, I predicted that if insect availability has decreased over the past decades, then a) birds today would show lower provisioning performance in response to an increased challenge compared to two decades ago. More specifically, b) birds exposed to an enlarged brood would be less able to cope with the challenge of feeding extra chicks today than in 1994/1995. Our main objectives in this chapter were therefore (1) to test the potential of using brood size manipulation experiments as an indirect method of assessing temporal trends in insect availability, and (2) to evaluate long-term changes in provisioning performance of Tree Swallows at a breeding site.

3.2. Methods

3.2.1. Breeding phenology and monitoring

In all four years of study reported here (1994, 1995, 2017, 2018), nests were visited approximately every two days to determine when females initiated breeding, clutch size, onset of incubation, hatch date, and fledging success. However, visits were curtailed during the first 10 days of incubation to avoid unnecessary disturbance when risks of abandonment are higher.

In 1995 and 2017/2018, chicks were measured on day 12 post-hatching (day 1 being the day of hatching), when visiting the nestbox does not risk premature fledging. Tree swallows typically fledge starting on day 16 (Winkler et al. 2011). Chicks were weighed to the nearest 0.01 g using a small portable electronic scale (OHAUS, YA102) and the wing length was measured to the nearest 0.5 mm using a wing ruler. In 2017 and 2018, I weighed chicks from both experimental and non-experimental nests, while the data from 1995 only included experimental nests.

In 2017 and 2018, I captured females from nestboxes at day 10 of incubation (day one being the first day after clutch completion). I assigned gender based on plumage colour, if possible, or the presence of a brood patch (Hussell 1983, Stutchbury and Robertson 1987). All birds captured were females. I banded birds with a single aluminum band provided by the Canadian Bird Banding Office (Environment Canada Banding permit 10759). I weighed birds to the nearest 0.5 g using a Pesola scale and measured length of tarsus and head-bill to the nearest 0.01 mm using digital calipers, and wing and tail to the nearest 0.5 mm using a ruler.

3.2.2. Brood size manipulation experiment

A brood size manipulation experiment was conducted in June 1994 and 1995 and replicated using the identical protocol in 2017 and 2018. All experiments in the two time periods took place in June (1994/95: June 1-25; 2017/18: June 2-20). Brood manipulations were conducted on broods containing five, six or seven nestlings with each trial involving two treatments and a control (Table 3.1). Natural brood size was determined based on the number of hatched nestlings, regardless of the number of eggs laid. Brood enlargements involved adding 1 or 2 nestlings of the same age (±1 day) as the experimental brood. Brood reductions involved removing 1 or 2 random nestlings. These nestlings were placed in non-experimental nests for the duration of the trial. Control trials involved handling a random nestling to simulate a manipulation. Nestlings that were added, removed or manipulated (control) were identified using a non-permanent, nontoxic marker. The sets of trials were performed over three consecutive days, when nestlings were aged between 6 and 9 days old. The order of the treatments was randomized. The experiments were conducted between 9:00 and 17:00 to allow nestlings to receive food before the beginning of the experiment, and several hours before nightfall. Chicks that died between trials (n = 5) were replaced by chicks of similar age and size. Trials were conducted during all types of weather, except during extreme rain or wind.

After moving and handling chicks, brood hunger was standardized by plugging the nestbox for 45 minutes. The experimenters then removed the plug and waited 15 to 30 minutes to allow parents to resume regular provisioning, i.e. returned at least once to the nest. Observers recorded times at which parents entered or exited the box for 30 minutes. Nests were observed from at least 10 metres away. After completing the 30-minute feeding observation, all chicks were collared using green pipe-cleaners. Parental visits were recorded once more, for 40 minutes or a maximum of 8 visits to prevent chicks from regurgitating the surplus food.

Food pellets were then collected from the chicks' throats or the nestbox floor. Pellets were typically collected as a discrete bolus, but were occasionally in pieces. Food pellets or pieces collected from each nestling were preserved in a glass vial containing 95% ethanol prior to being processed in the laboratory. To offset the withdrawal of food, the nestlings from which a bolus was collected were fed 5-10mg of moistened cat food. Finally, the manipulated chicks were returned to their original nestbox.

3.2.3. Bolus sample

In both time periods, bolus samples were separated into discrete prey items in the lab. In 2017 and 2018, each individual arthropod was identified to order and measured in length to the closest 1 mm. In 1995, prey items were only measured. The arthropod samples were then grouped by order and bolus and filtered using filter papers. The samples were dried to constant mass in a general-purpose heating and drying oven. In 1994 and 1995, the samples were dried at 37°C while in 2017 and 2018, they were dried at 60°C for at least 24 hours. After performing preliminary drying tests at both 37 and 60°C, I established that constant weight was achieved within 1 hour at both temperatures.

3.2.4. Statistical analyses

I conducted a series of preliminary analyses to examine the effects of six potentially confounding variables on visit rate and bolus size: temperature, wind speed, chick age, time of day and day of year. I explored the relationship of each of these variables with the provisioning responses (visit rate, bolus mass, delivery rate) of control nests. Historical weather data from Environment and Climate Change Canada was obtained from a Creston weather station (Creston Campbell Scientific, 49°4'59.88''N 116°30'0''W) and downloaded using the weathercan package (LaZerte and Albers 2018). I extracted the temperature and wind speed corresponding to the hour of the first feeding observation. These preliminary analyses indicated a correlation between bolus size and date. Therefore, I included day of year as an additional numeric fixed effect in further models to examine its potential effect on feeding responses. All data manipulation, modelling and statistical analysis was done using R version 3.5.3 (R Core Team 2019).

I examined the bolus mass distribution because of concerns that samples could include pieces of a bolus or multiple boluses delivered by a parent. Samples collected from a single chick in the field occasionally appeared to contain two boluses. The frequency distributions for 1994 and 2017/2018 appeared bimodal with a long-tail. I therefore excluded samples where the bolus mass was outside 1 interquartile range

(IQR) of the bolus distribution for that time period (Figure 3.1). I also compared the proportion of bolus samples retrieved to the number of feeding visits made to the nest while the chicks were collared in 1994, 2017 and 2018. Historical data was not available for 1995. The ratio of bolus samples to deliveries was approximately 0.5 in both time periods ($W_{ilcoxon}$ = 1544, p = 0.90, Figure 3.2), suggesting that boluses were collected consistently between years despite having different experimenters performing the neck ligatures. The ratio is likely below 1, even though parents are assumed to deliver a bolus on each nest visit (see below), because neck ligatures are difficult to apply and some collars may not have prevented nestlings from swallowing the prey item delivered.

I was primarily interested in whether changes in responses to parental provisioning rate or average chick weights varied in the two time periods that brood size manipulation experiments. After using a linear mixed model and a pairwise comparison to evaluate the variation in responses between years, I pooled data where I found no evidence for year-to-year differences in visit rate, bolus mass, or chick weight.

I used linear mixed models to examine how three measures of provisioning performance (visit rate (mg/30 minutes), bolus mass (mg) and delivery rate (mg/minute)) were influenced by the brood size manipulations conducted during the two different time periods. Visit rate is a measure of the number of visits per time. Bolus mass is the average dry weight of boluses recovered at the end of a trial. Bolus mass was log-transformed so that models conformed to the assumptions of homoscedasticity and normality. Delivery rate represents the amount of biomass brought back per time. I assumed that every nest visit corresponded to a food delivery (McCarty 2002; but see above). Delivery rate was therefore calculated by multiplying the visit rate with the average bolus mass. Linear mixed models can account for the high individual variation in feeding behaviour between parental pairs, and the missing treatments in some sets of trials. I excluded sets of trials that were missing more than one treatment or that were spread over more than four days. All models included natural brood size, brood size change, period and day of year as fixed effects and nest as random variable. All effects except day of year were input as factors, since birds do not necessarily respond linearly to changes in brood size (Murphy et al. 2000). All models also included two interaction terms (period *brood size change and period*natural brood size). Mixed models were implemented in lmerTest (Kuznetsova et al. 2019) with the significance of main effects and interaction terms estimated using the ANOVA command. I calculated estimated marginal means, estimated the significance of the main effects, and conducted pairwise multiple comparisons with Tukey-adjusted p-values using the emmeans package (Lenth et al. 2019).

Since delivery rates varied with time period (see Results), I subsequently used a linear model to examine whether chick weights at day 12 (averages for each brood) varied across the three years where this data was collected (1995, 2017 and 2018). Chick mass data collected in 2017 and 2018 was not pooled because preliminary analyses found evidence for differences in chick mass at day 12 in these years. This model included year and natural brood size as fixed factors. I calculated estimated marginal means, estimated the significance of the main effects, and conducted pairwise multiple comparisons with Tukey-adjusted p-values using the emmeans package (Lenth et al. 2019). Additionally, I used a two-sample Welch t-test to compare the mean weight of females in 2017 and 2018.

Finally, I compared environmental conditions between years, as these variations might provide insight into any yearly differences observed. I used a chi-squared test to compare the distribution of insect sizes in the chicks' diets. I divided insects into two size categories (≥10 mm and >10 mm) and compared them between time periods. Historical data for insect size was only available for 1995. I also extracted the maximum daily temperatures for the month of June in each experimental year. Note that temperature data were occasionally missing for an hour or two per day in 1994, but I determined that these missing data points were not important enough to bias the computation of maximum daily temperature. I statistically compared maximum daily temperatures by performing a linear model with year as fixed effect. I used ANOVA to compare the mean maximum daily temperatures between the four years. I then used a multiple comparison procedure to examine the pairwise differences between years using the emmeans package (Lenth et al. 2019).

3.3. Results

I used data from experiments on 21 historical nests (1994 = 5, 1995 = 16) and 37 contemporary nests (2017 = 18, 2018 = 19). Raw data are summarized in Figure 3.3.

3.3.1. Feeding visit rate

Visit rate was strongly affected by the change in brood size in both time periods (Table 3.2; Figure 3.4). After controlling for the effects of initial brood size, period and day of year and contrasting visit rates for each brood size change, adults tended to decrease their visit rate in experimentally reduced broods compared to slightly increased broods (Figure 3.4; -2 vs +1: $t_{101} = -2.9$, $p = 0.035$; -1 vs +1: $t_{102} = -2.8$, $p = 0.052$), but did not significantly increase their efforts in response to a large brood enlargements (control vs +2: $t_{100} = 0.27$, $p = 0.99$). I found no interaction between the effects of period and brood size change ($F_{4,72.4} = 1.16$, $p = 0.32$).

Nest visit rates also tended to be lower in 2017/2018 than in 1994/1995 (Table 3.2). After controlling for the other factors in the model, I estimated that parents in recent trials made on average 1.7 fewer visits over the course of the 30-minute observation period (mean ± SE; 11.4 ± 0.7 visits in 1994/1995 and 9.7 ± 0.5 visits in 2017/2018).

Nest visit rates also tended to vary with the natural brood size (Table 3.2). After controlling for the brood size change and for other factors in the model, the estimated marginal means suggests that parents with natural broods of five visited their nest on average 9.8 ± 0.7 times, parents with natural broods of six visited their nest on average 9. ± 0.7 times and parents with natural brood sizes of seven visited their nest on average 12.0 ± 0.8 times. Nest visit rates were independent of date (Table 3.2).

3.3.2. Bolus samples

Boluses weighed between 0.7 to 143.8 mg. I excluded boluses within 1 inter-quartile range for each time period, i.e. boluses over 76.7 mg from 1994/1995 and over 60.0 mg from 2017/2018 (Figure 3.1). In total, 158 boluses were collected in 1994, 184 in 1995, 160 in 2017 and 170 in 2018. After excluding outliers and samples from unsuitable trials, the analysis included 62 boluses from 1994, 175 from 1995, 148 from 2017 and 150 from 2018.

Prey sizes differed significantly between time periods ($X^2_1 = 57.2$, $p < 0.0001$, Table 3.3). There was a bigger proportion of larger insects (>10 mm) in recent boluses (1995 = 2.4%, 2017 = 5.6%, 2018 = 3.8%). In 2017 and 2018, when prey was classified by size and order, the most abundant group of insects identified from all bolus samples were flies. Out of a total of 6969 arthropods identified, 5816 were flies. All flies accounted for 61.4% of the total biomass collected (Figure 3.5). The second biggest contributors in dry mass were damselflies and dragonflies. The 230 identified individuals from this group accounted for 18.0% of the total dry mass. Dragonflies and damselflies also represented the most efficient source of energy. The average dry mass of one dragonfly was 20.4 (SD = 16.6) mg. Other orders that I found in our samples included, in order of abundance: ephemeroptera (296), trichoptera (114), hymenoptera (58), aranea (44), coleoptera (44), and plecoptera (6).

The average mass of each bolus parents delivered to the nest in 2017/2018 was significantly lower than those delivered in 1994/1995 (Figure 3.6; Table 3.2). After controlling for the effects of natural brood size, brood size change and day of year, boluses were on average 8.3 mg smaller in recent years compared to the historical data (32.8 ± 2.5 mg in 1994/1995 and 24.5 ± 1.5 mg in 2017/2018). Bolus mass was independent of natural brood size, the brood size change and the date at which the trial was conducted (Table 3.2). We found no evidence of interactions between the effects of period and brood change or period and natural brood size.

3.3.3. Delivery rate

As a combination of responses, delivery rate was expectedly affected by variables that had significant effects on visit rate and bolus mass. Delivery rate consequently varied with changes in brood size and was lower in 2017/2018 than in 1994/1995, but there was no evidence of a change in brood size*period interaction (Table 3.2). Delivery rates were reduced when brood sizes were reduced and increased when brood sizes were enlarged by one but not two chicks (Figure 3.7). Delivery rates were almost a third lower in recent years compared to the 1990s (6.5 ± 0.5 mg/min in 1994/1995 and 4.4 ± 0.5 mg/min in 2017/2018). Delivery rates in the experiment were independent of the natural brood size being raised by the parents.

3.3.4. Body weights

I obtained measurements for mean chick weight at day 12 for 14 nests in 1995 and 122 nests in 2017/2018. I found strong evidence that chick weights on day 12 differed between years ($F_2 = 11.67$, $p < 0.0001$). A pairwise comparison indicated evidence of a difference in mean chick weight between 2018 and the other years (t_{102} = 3.65, p = 0.0012 and t_{102} = 4.11, p = 0.0002). Natural brood size strongly affected chick weight ($F_{2,102}$ = 4.35, p = 0.015). After accounting for those factors, 12-day-old chicks from 2018 weighed, on average, 2.0 g less than in 1995 and 1.4 g less than in 2017 (Figure 3.9).

I also measured the weights of females at day 10 of incubation in 2017 and 2018. I found evidence that female weights were lower in 2018 compared to 2017 ($t_{121.95}$ = 2.32, p = 0.022). The estimated difference in the mean weight was 0.47 ± 0.20 g. The other body measurements (lengths of tarsus, head-bill, wing and tail) did not vary between the two years.

3.3.5. Annual variation

I found strong evidence of a difference in the mean maximum daily temperature between years ($F_{3,224}$ = 6.69, p = 0.0002). Further investigation showed that mean maximum temperature was significantly higher in 2017 compared to the other years. I found no evidence of a difference in mean maximum temperatures between 1994, 1995 and 2018.

In their studies of tree swallows, Winkler et al. (2013) show that insect flight activity is reduced below a temperature threshold of 18.5°C, leading to higher nestling mortality due to poor feeding. At Creston in 1994, there were 12 days on which the maximum temperature remained below 18.5°C, including two sets of 4 consecutive cold days (Figure 3.10). In 1995, there were 7 days below the threshold temperature, including two sets of 2 consecutive days. June was warmer in 2017, with only 2 cold days, and there were 5 cold days in 2018.

3.4. Discussion

Over a hundred brood size manipulation experiments on aerial insectivore species have been carried out since the 1980s (this study). I suggested that these experiments could be repeated and repurposed to test the hypothesis that prey (aerial insect) availability has declined over recent decades. I predicted that if insect abundance has declined, parents challenged by the demands of an enlarged brood would be less capable of increasing their delivery rate now than in the past. In contrast, I expected that parents with reduced broods would be able to modify their delivery rate downwards now and in the past. I therefore expected a brood size change*period interaction. Contrary to expectations, parents responded identically to changes in brood size in both time periods. Delivery rates were sensitive to the brood size change and consistently lower in 2017/2018 than in 1994/1995. This decline was driven by a shift in the mass of the boluses delivered to the nest and a somewhat lower feeding visit rate (Figure 3.8). On average, bolus masses decreased by 25% since the past experiments while visit rates were reduced by 10%. These observed declines in provisioning performance could be a consequence of changes in the composition or abundance of their insect prey.

Parental feeding rates are a combination of the rate at which parents visit the nest and the amount of food delivered during each visit. I found that visit rate was mostly affected by brood size manipulations, while bolus size varied mostly between time periods. Nest visit rates of tree swallows are fairly consistent across time and space (Murphy et al. 2000 Figure 2, Shutler et al. 2006 Figure 4, this study). Experiments frequently show that parents increase their nest visit rate in response to experimental increases in brood size (Murphy et al. 2000) or nestling begging intensity (Leonard and Horn 1996, 1998; Whittingham et al. 2003). Passerines exhibit a flexible foraging strategy as they are able to quickly adjust their feeding efforts to short-term changes in the brood (García-Navas and Sanz 2010). Visit rate represents a good measure of food delivery (McCarty 2002, Rose 2009), but does not necessarily vary with insect abundance (Bortolotti et al. 2011). It therefore appears that visit rate is more limited by parental abilities than by insect availability. In contrast, bolus sizes vary considerably across studies. In Creston, British Columbia, I measured that the average bolus mass in unmanipulated broods was 39 mg in 1994/1995 and 27 mg in 2017/2018, which falls within the range of reported values from other North American studies. Mean bolus mass for tree swallows was measured to be 24 mg in Ithaca, New York (McCarty 2002), 28 mg in Port Rowan, Ontario (Quinney 1986), 30 mg in Ottawa County, Michigan (Johnson and Lombardo 2000), 34 mg in southern Québec (Bellavance et al. 2018), between 40 mg and 50 mg in Tofield, Alberta (Dunn and Hannon 1992) and 73 mg in central Scotland (Bryant and Turner 1982). This wide range of measurements across sites and years indicates that bolus size may be more strictly constrained by local conditions, such as insect availability. Parents exposed to experimental manipulations do not appear to modify the biomass or energetic content of the food delivered each time they visit the nest (Dunn and Hannon 1992, this study). Average bolus size may therefore better reflect differences in prey abundance and/or availability than visit rate, which varies considerably due to the flexibility in the feeding strategy of tree swallows.

The 25% decline in the average size of boluses delivered to chicks suggests that there have been changes in the abundance and/or composition of the prey that tree swallows feed to their nestlings. The distribution of insects may have shifted towards bigger prey items that include less flies. Tree swallows are considered Diptera specialists, as they preferentially select flies when foraging (Beck et al. 2013, Michelson 2015, Bellavance et al. 2018). Parents catch many small flies that are combined in a single bolus to feed a single chick. They also hunt larger flies, dragonflies or damselflies that are more likely to be delivered as single prey items. Boluses containing bigger food items can also contain less biomass since birds cannot handle many large preys at once (Bryant and Turner 1982). In the experiments from the 1990s, insects were only sorted into size categories, rather than size and taxonomic groups. I observed that boluses in 2017 and 2018 contained more large-sized prey items (> 10 mm) compared to 1995, which indicates a shift in prey composition. Smaller boluses may also be caused by declines in insect abundance since parents might struggle to find sufficient amounts of food. This possibility is consistent with reports of global insect declines (Hallmann et al. 2017, Sánchez-Bayo and Wyckhuys 2019). Alternatively, the reduced provisioning performance could indicate changes in the physiological health of parents that affect their ability to retrieve food. Regardless of whether overall insect abundance has collapsed, preys have become larger resulting in smaller boluses being delivered or parents' foraging ability has deteriorated, chicks receive less food than in the past and would be expected to suffer from this impoverished diet.

The reduced delivery rate resulting from changes in the bolus size would be expected to have negative consequences on chick quality. Chick weights were not impacted in 2017, but were lower in 2018. After controlling for brood size effects, twelve-day-old chicks in 2018 were on average 2 grams smaller than in 1995. However, chick mass was not different between 2017 and 1995, despite the significant differences in provisioning performance between those two years. I offer three explanations for the surprisingly high chick weights in 2017. Firstly, maximum daily temperatures during peak breeding period (June) were higher in 2017 compared to the other years. Though the mechanisms are not fully understood, colder temperatures can be detrimental to chick growth and survival (Ardia et al. 2006, Winkler et al. 2013). Secondly, a higher-quality diet may have offset the consequences of a lower delivery rate. In 2017, Diptera composed 69% of the chick diet in biomass, compared to only 53% in 2018. Unfortunately, I did not have data about insect orders from 1995 to compare with the modern insect data. Similarly, a larger proportion of the chicks' diet was composed of bigger prey items in 2017 compared to 1995 and 2018. While it is energetically more profitable for birds to forage for a mixture of sizes in food items, larger food items provide a higher caloric intake (Turner 1982, Mcclenaghan et al. 2019). Perhaps the distribution of sizes in available prey in 2017 was closer to the ideal mixture of sizes for optimizing energy expenditure during foraging. A higher quality diet would also explain why females weighed more in 2017 than in 2018. Lastly, parents may have compensated for a lower delivery rate by extending their daily foraging hours, especially if higher temperatures throughout the day have prolonged the hours of optimal insect activity (Winkler et al. 2013). However, I did not monitor parental foraging throughout the entire day, therefore this possibility remains speculative. Further research about daily foraging hours of tree swallows in relation to temperature and feeding behaviour could allow to answer this question. All in all, the mismatch between delivery rate and chick sizes in 2017 could be due to higher temperatures enhancing chick health and/or extending daily foraging hours, as well as higher-quality diet composed of more flies and bigger prey items.

Ultimately, our key findings highlight how replicating past experiments to assess changes in animal behaviour such as provisioning performance can contribute to identifying long-term ecological trends. Experimental and observational studies conducted in the 1980s and 1990s provide a wealth of information that could be exploited (De Steven 1980, Quinney and Ankney 1985, Quinney 1986, Dunn and Hannon 1992). I urge scientists to exploit these accessible data to readily evaluate long-term changes in aerial insectivore diet. To the best of our knowledge, our study was the first to compare how the feeding behavior of an aerial insectivore has changed over the last 24 years. Given the results of this first study, replicating experimental and observational studies that measure the prey composition, biomass and energetic content of the food delivered may be the most informative to detect differences in insect supply. I also recommend measuring daily feeding visits, which was not implemented in this study, as it could provide additional insight about the costs defrayed by the parents

(Turner 1980, Rose 2009). The application of RFID technology could facilitate the recording of these measurements (Stanton et al. 2016). This method would also allow distinguishing males from females, which do not adopt the same feeding strategies (Ardia 2007). Our study also indicates that collecting data over multiple years in the past may be better able to conclude that differences are due to long-term differences rather than simple annual variation in prey availability (Vaughn and Young 2010). Ultimately, replicating studies of feeding behaviour across several sites in North America would allow us to generate a broad-scale assessment of changes in insect availability over time. A decrease in provisioning performance at other breeding sites would provide compelling evidence that aerial insectivore populations are declining because of reduced insect availability. Our research provides an efficient solution to fill the knowledge gap about the status of insect abundance in North America.

Table 3.1. Brood size manipulation treatments

		Modified brood size		
		5	6	7
Natural brood size	5	control	+1	+2
	6	-1	control	+1
	7	-2	-1	control

Table 3.2. **Output of linear mixed effect models modelling for visit rate (A), log bolus mass (B) and delivery rate (C).**

	Effect	Numerator df	Denominator df	F value	Pr(>F)
A	Natural brood size	2	71.6	2.6	0.083
	Period	1	57.2	3.9	0.053
	Brood change	4	101.1	3.2	0.017
	Date of trial	1	55.1	0.002	0.96
	Natural brood size*Period	2	72.4	1.1	0.32
	Brood size change*Period	4	101.1	0.09	0.98
B	Natural brood size	2	66.7	0.7	0.48
	Period	1	56.8	8.1	0.0063
	Brood change	4	96.4	1.5	0.20
	Date of trial	1	61.8	1.8	0.19
	Natural brood size*Period	2	67.1	0.4	0.66
	Brood size change*Period	4	96.4	0.9	0.46
C	Natural brood size	2	72.9	0.8	0.43
	Period	1	56.0	11.3	0.0014
	Brood change	4	95.1	3.0	0.023
	Date of trial	1	53.0	3.8	0.056
	Natural brood size*Period	2	73.9	1.1	0.33
	Brood size change*Period	4	95.1	0.2	0.96

Table 3.3. Distribution of prey sizes in 1995 and 2017/2018.

		Size category		Totals
		Small (≤10 mm)	**Large (>10 mm)**	
Period	**1995**	97.6%	2.4%	7 229
	2017	94.4%	5.6%	3 688
	2018	96.2%	3.8%	3 049
	Totals	13 469	497	13 966

Table 3.4. **Visit rate, bolus mass and delivery rate for the four years brood size manipulation experiments were conducted. Mean ± standard deviation, with sample size of trials in parentheses. All brood size manipulation treatments were included in calculations.**

Year	Visit rate (visits/30 mins)	Bolus mass (mg)	Delivery rate (mg/min)
1994	11.33 ± 2.74 (15)	39.12 ± 11.48 (15)	7.05 ± 2.77 (15)
1995	11.89 ± 3.47 (46)	34.94 ± 10.56 (46)	6.54 ± 2.95 (46)
2017	9.69 ± 4.28 (52)	26.38 ± 8.93 (45)	4.20 ± 2.28 (45)
2018	10.17 ± 3.61 (54)	27.06 ± 10.03 (51)	4.36 ± 2.46 (51)

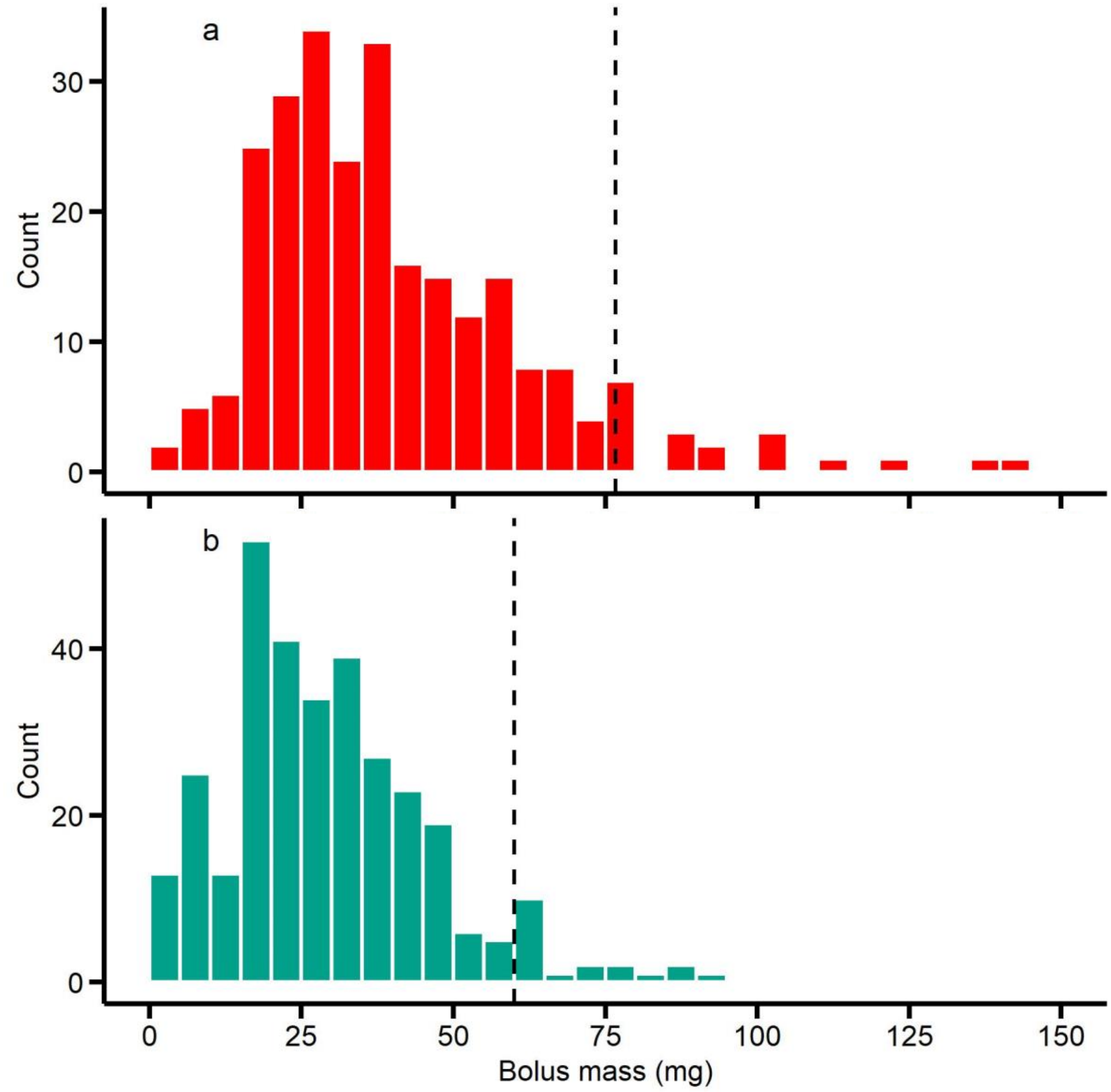

Figure 3.1. Distribution of bolus sizes in 1994/1995 (a, red) and in 2017/2018 (b, blue) illustrating the cutoff for outliers (dashed line).

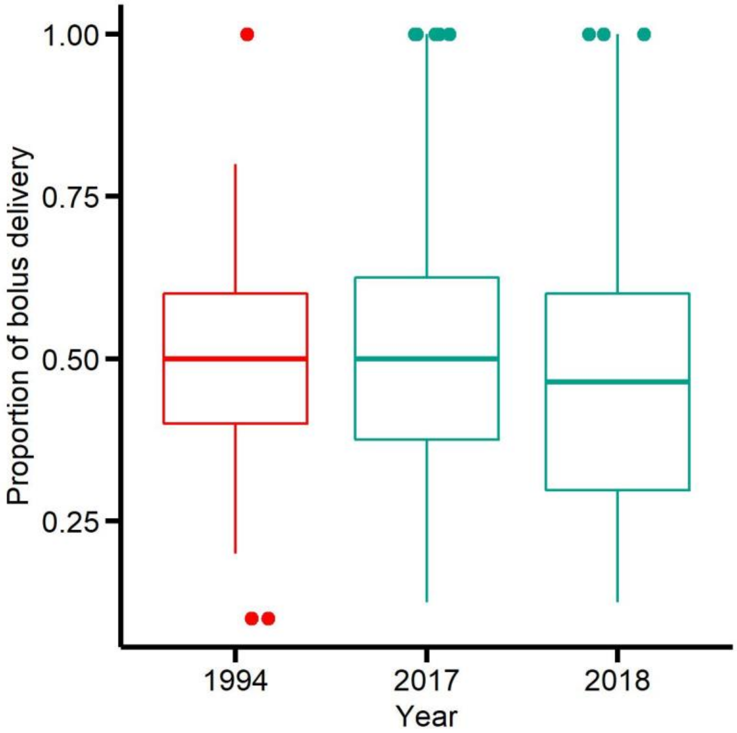

Figure 3.2. **Number of boluses collected per nest visit in 1994, 2017 and 2018 with 1.5 IQR.**

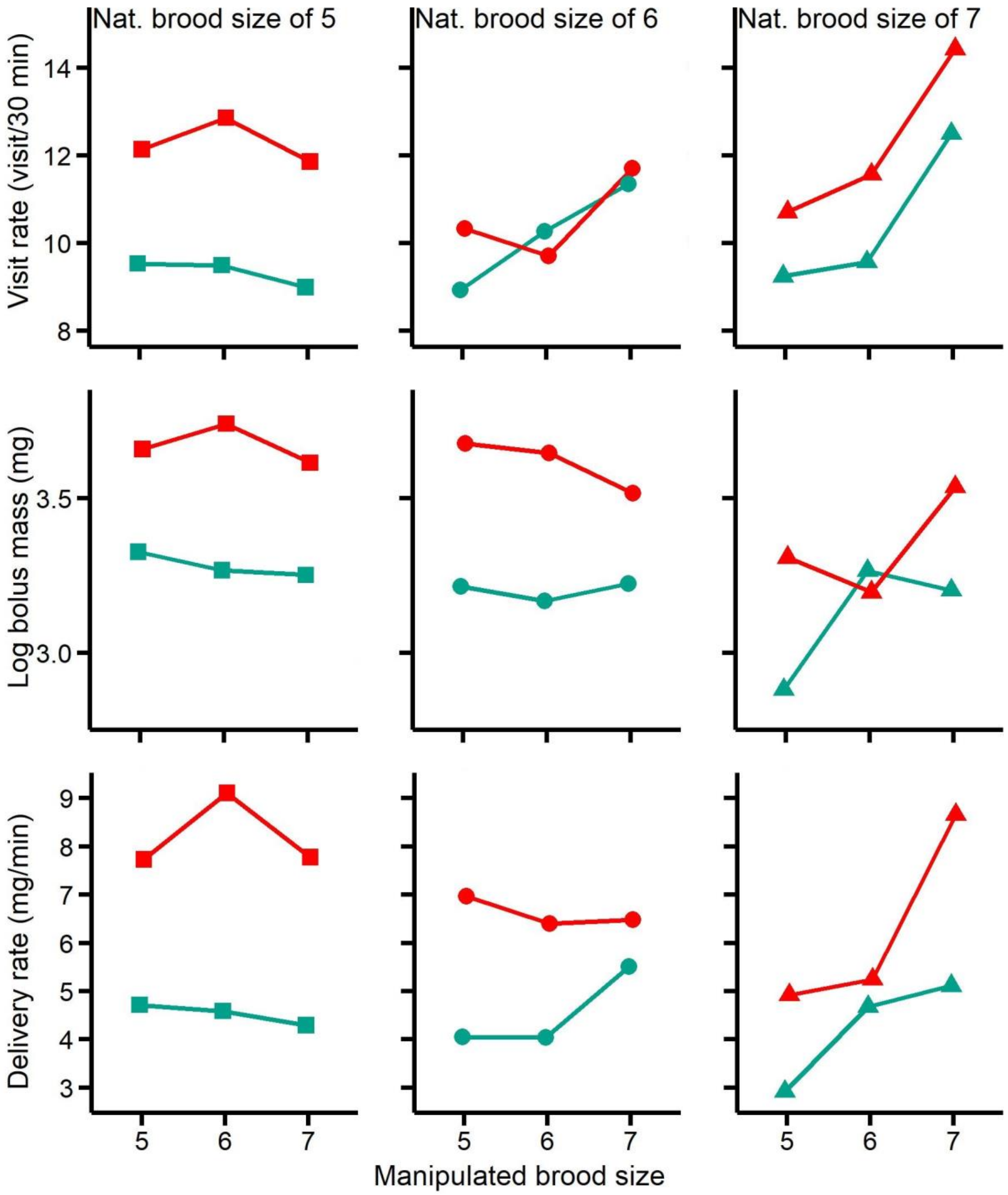

Figure 3.3. **Average visit rate, natural log bolus mass and delivery rate in response to manipulated brood size in 1994/1995 (red) and 2017/2018 (blue). Natural brood sizes of 5 (square), 6 (circle) and 7 (triangle) are represented in each column.**

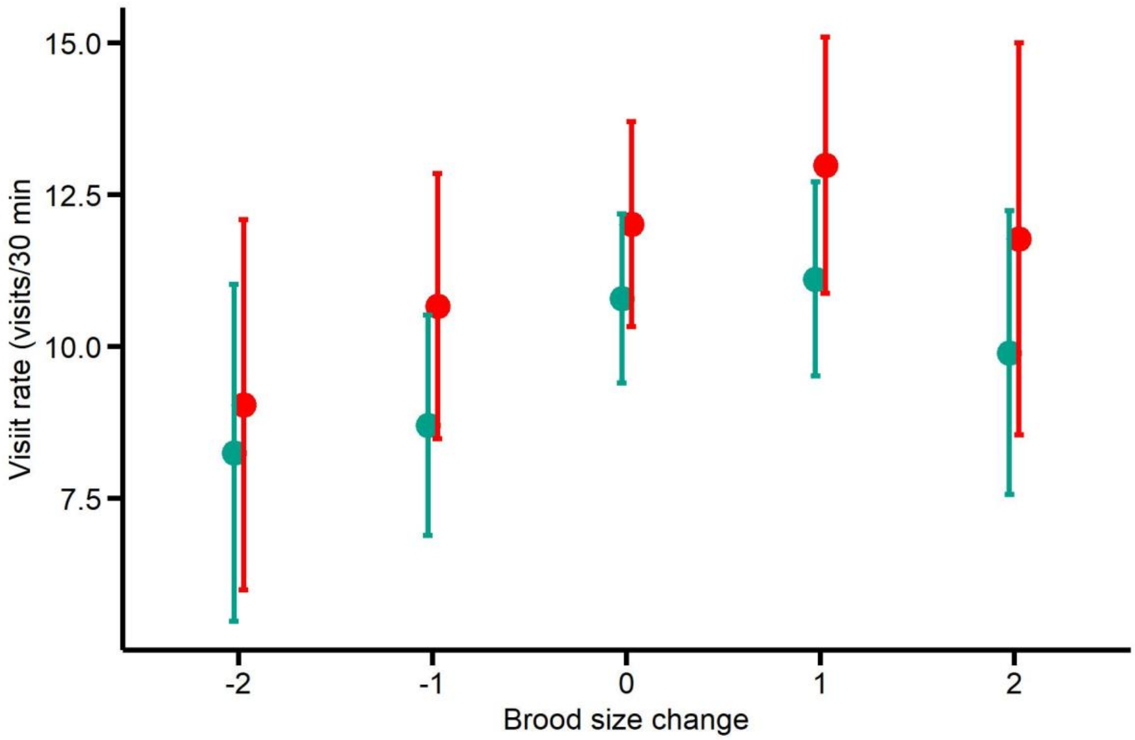

Figure 3.4. Visit rate relative to the change in brood size for the 1994/1995 (red) and 2017/2018 (blue) time periods with 95% confidence interval. Estimated marginal means are calculated after controlling for the effects of initial brood size, period and day of year from the linear mixed effects model.

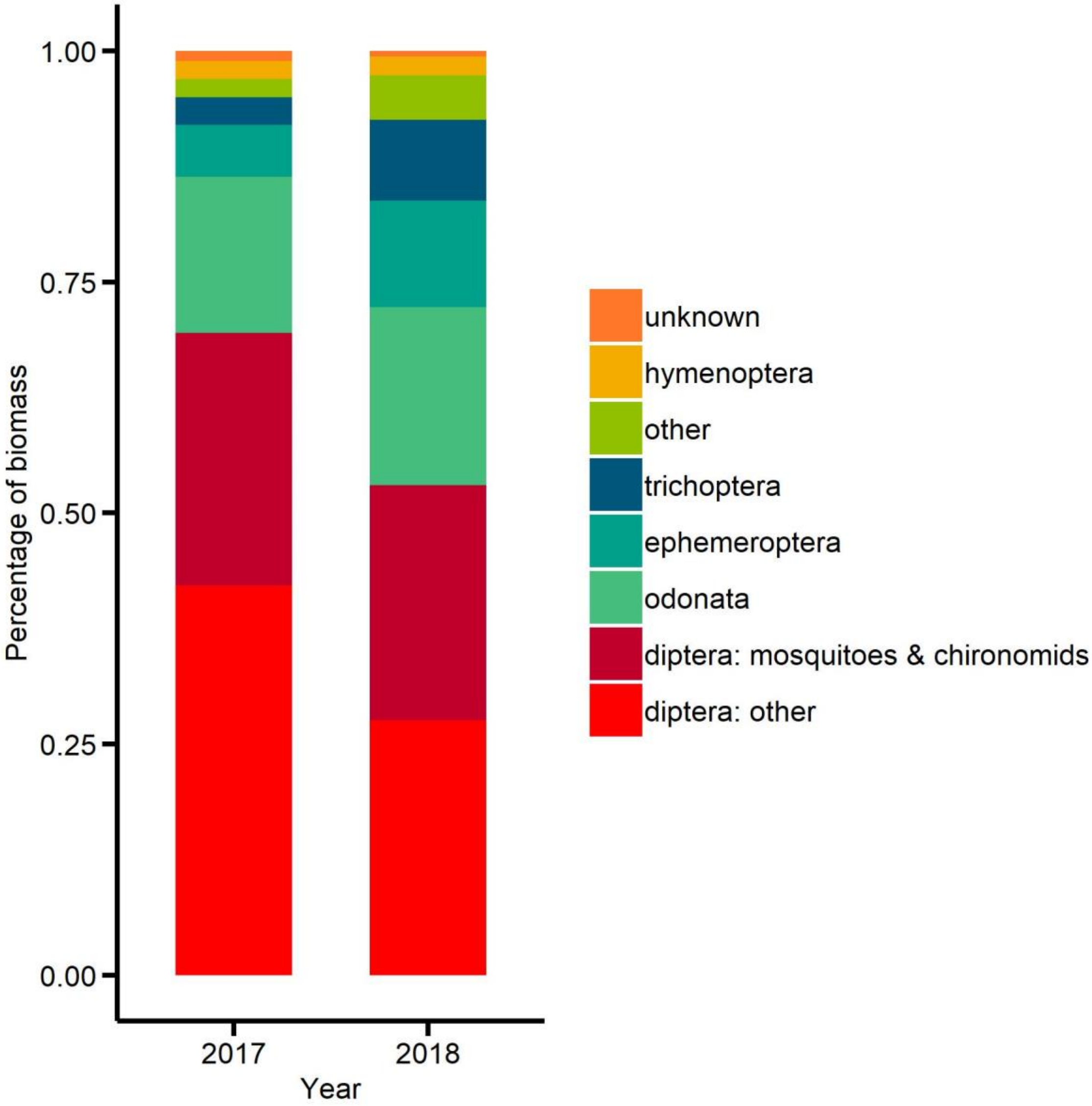

Figure 3.5. **Composition all boluses collected in 2017 and 2018 by taxonomic order. All groups were identified to the order level, but mosquitoes and chironomids were distinguished as a sub-category of diptera.**

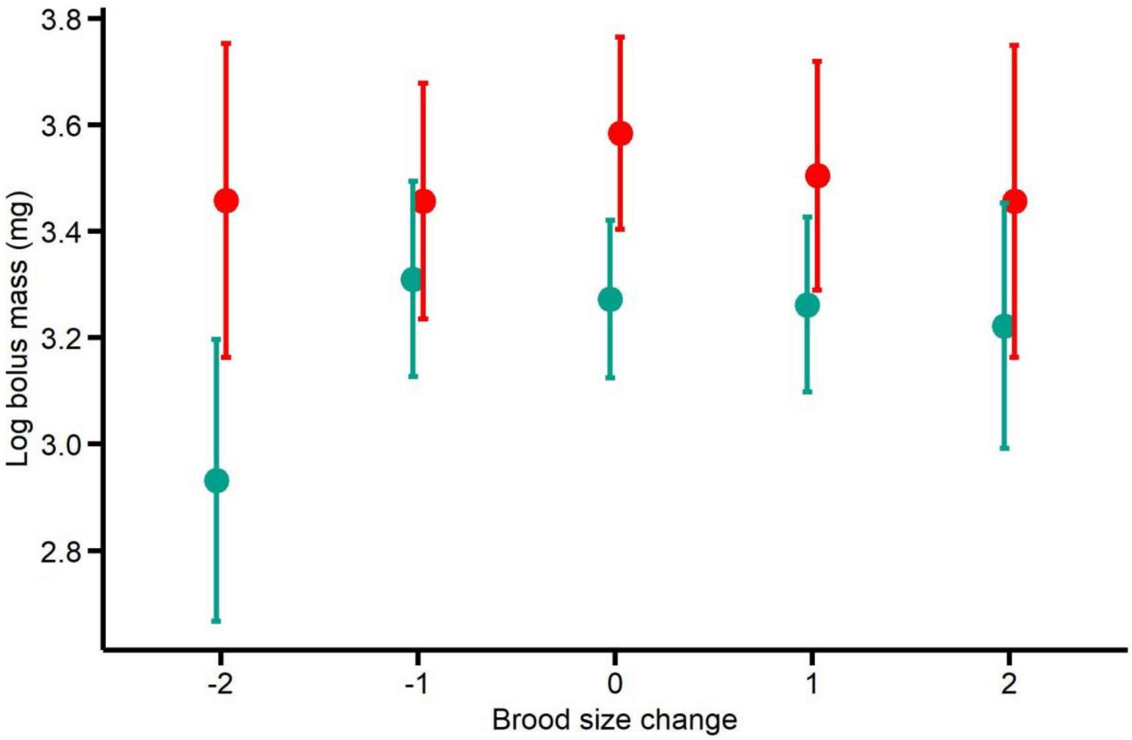

Figure 3.6. Log bolus mass relative to the change in brood size for the 1994/1995 (red) and 2017/2018 (blue) time periods with 95% confidence interval. Estimated marginal means are calculated after controlling for the effects of initial brood size, period and day of year from the linear mixed effects model.

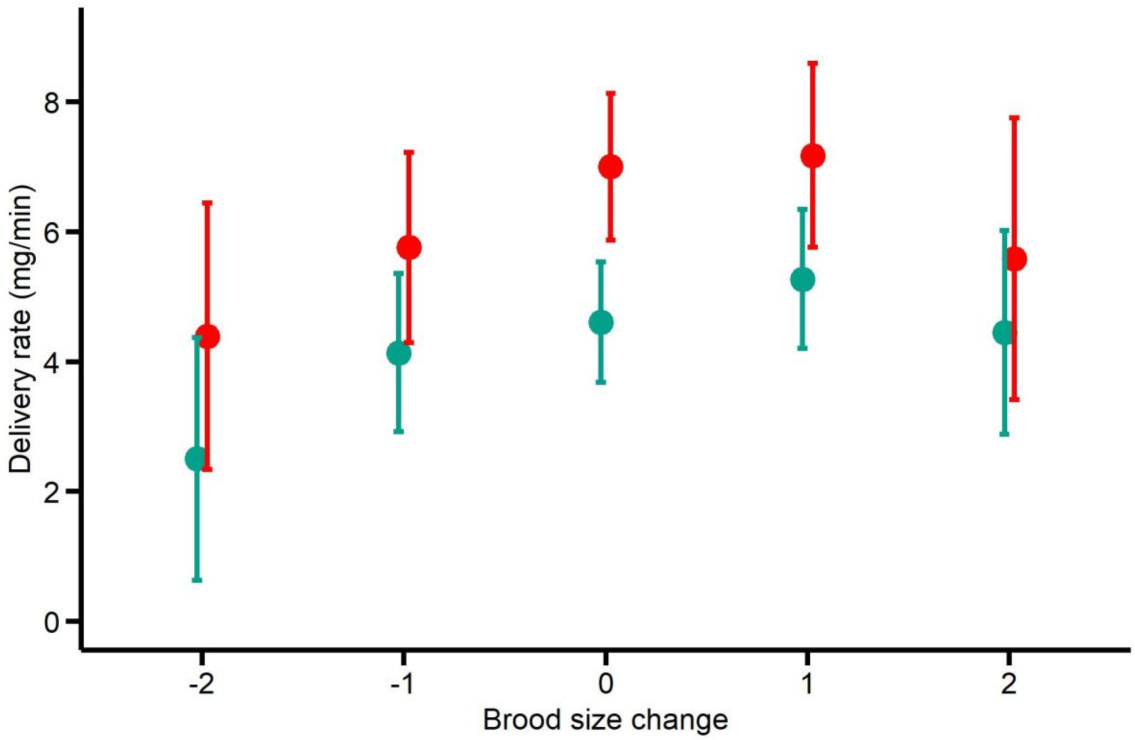

Figure 3.7. Delivery rate relative to the change in brood size for the 1994/1995 (red) and 2017/2018 (blue) time periods with 95% confidence interval. Estimated marginal means are calculated after controlling for the effects of initial brood size, period and day of year from the linear mixed effects model.

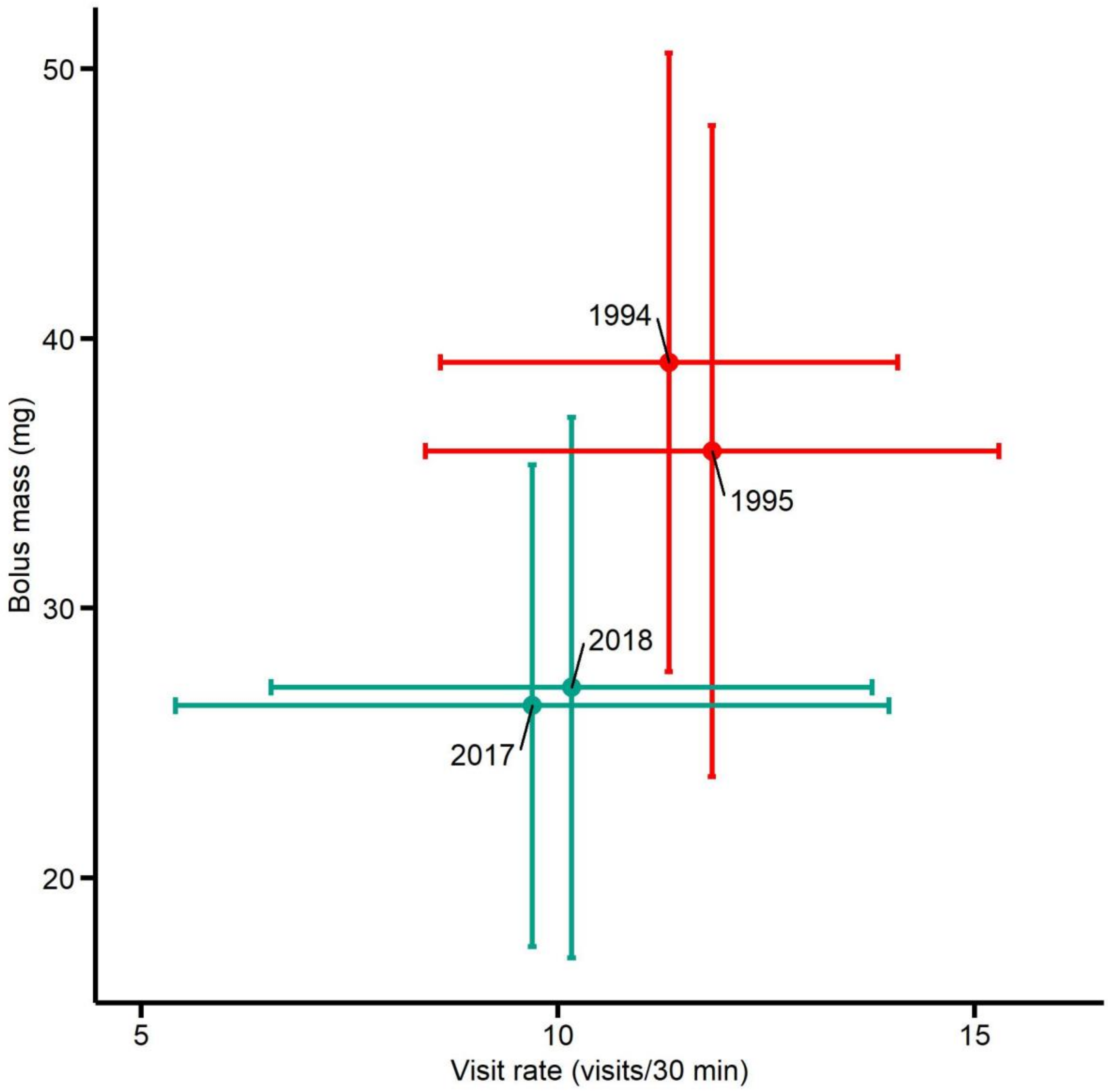

Figure 3.8. Relationship between mean bolus mass and visit rate for 1994, 1995, 2017 and 2018. Points show means and bars standard deviations. Means are calculated from all observations collected and do not control for brood sizes or experimental manipulations.

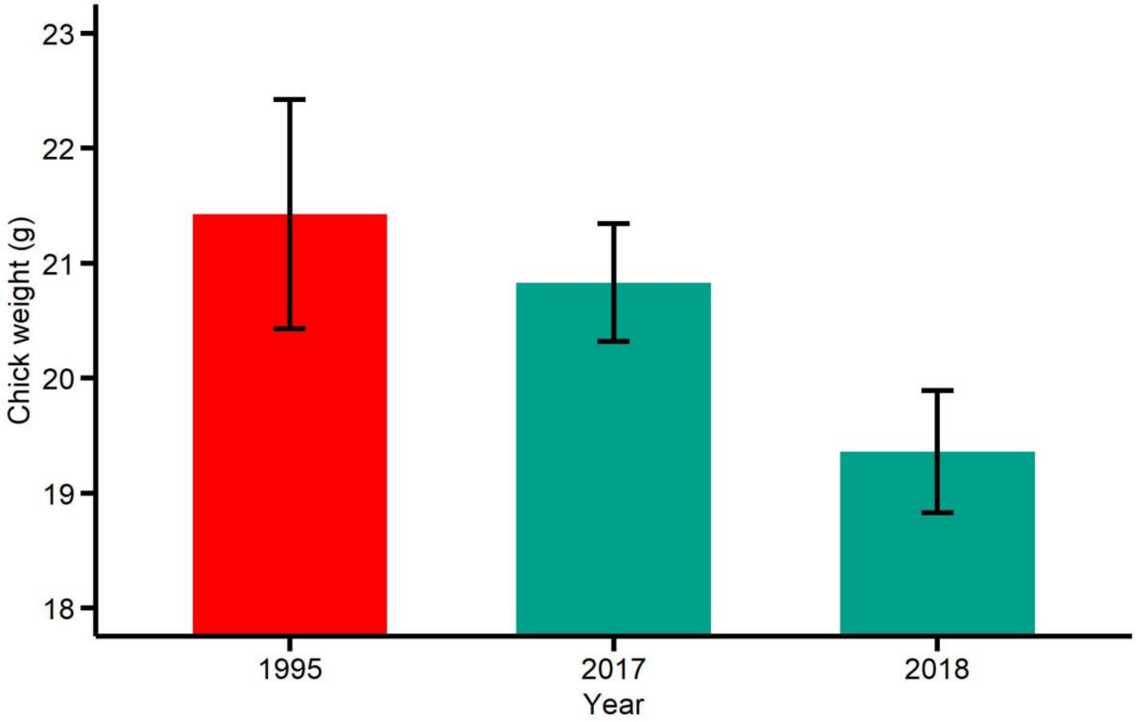

Figure 3.9. **Estimated marginal means of average chick weights in a nest at day 12 in 1995, 2017 and 2018 adjusted for clutch size and experimental nests with 95% confidence intervals.**

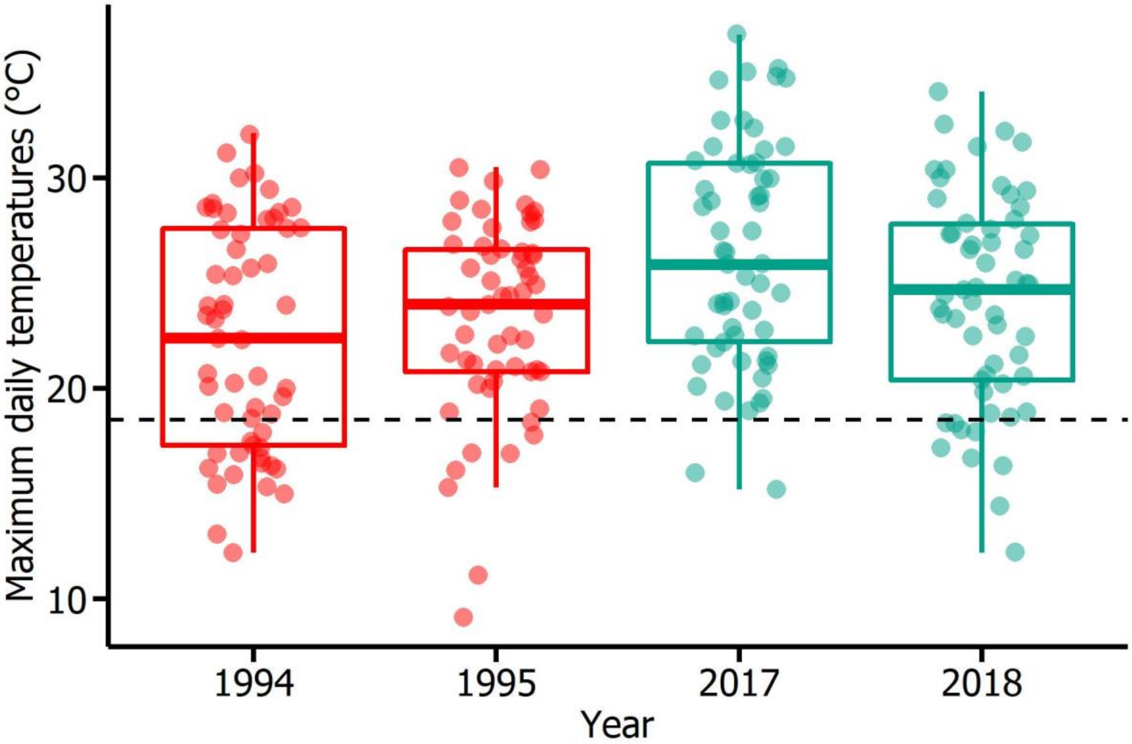

Figure 3.10. Maximum daily temperatures in june of each year with 1.5 IQR.

Chapter 4. Conclusion

4.1. Summary

In North America, population declines of aerial insectivores could be due to population declines of their insect prey, but the ability to test this hypothesis is limited by the lack of long-term data on insect abundance. I proposed that this knowledge gap could be mitigated by using historic data on the breeding performance and behaviour of aerial insectivores. I evaluated this idea by using nest monitoring data collected over the last 33 years at a single site in British Columbia, conducting a literature review, and examining changes in parental responses to a brood manipulation experiment.

In Chapter 1, I compiled nest monitoring data for a population of tree swallows breeding in nestboxes in Creston, BC since the late 1980s, and assessed whether breeding performance has declined over time. The long-term monitoring data indicated that average brood size was 18% lower, and average fledging success was 24% lower in 2008 to 2016 than in the late 1980s. However, I identified some issues with using this historical data; Field methods were not consistent and nest-box numbers varied over the years. Moreover, while breeding performance may have declined, productivity does not explicitly relate to population trends. Nonetheless, these results are consistent with the Breeding Bird Survey data that suggests that tree swallow populations have been declining over the last few decades (Sauer et al. 2017).

In chapter 2, I specifically explored the idea that brood size manipulation experiments (BSMEs) can be repurposed to assess long-term trends in bird feeding behaviour, thus insect availability. I conducted a scoping review of the literature to assess the number of studies on aerial insectivores that held the potential to be repurposed. As expected given the scarcity of replicated studies in ecology (Schnitzer and Carson 2016), I found that no BSMEs on aerial insectivores have ever been explicitly repeated at a same breeding site across many years. Two studies from the same location appeared similar enough in methodology to be considered replicates, but the earlier study did not provide the data in a format that would allow evaluation of whether parental responses to an enlarged brood have changed over time. I identified 33 BSMEs on aerial insectivores provisioning behaviour conducted between 1992 and 2016 that had the potential to be repurposed. Fourteen of these studies provided the data needed to calculate an effect size of a brood size enlargement on nest visit rates. Preliminary analyses of these studies found no evidence that the effect of the manipulation has changed over time. However, the methods used in these experiments were not consistent. Twenty-five of the studies on aerial insectivores provisioning behaviour could be replicated to directly test for changes over the years that would not be confounded by differences in effect size associated with differences in methods and location.

In chapter 3, I examined whether the exact replication of a BSME that measured parental nest visit rates, prey load sizes and prey delivery rates at a single site would provide insights into prey availability. I repeated an experiment conducted in southeast British Columbia from 1994 and 1995 on tree swallows. In both periods (1994/1995 and 2017/2018), parents responded to the brood size manipulation by reducing or increasing their nest visit rates and delivery rates when feeding a reduced or enlarged brood. Interestingly, parents with broods that were enlarged by 2 chicks (40%) did not increase their nest visit rates. Between periods, nest visit rates decreased by 10%, and bolus sizes decreased by 25%. I therefore found evidence that the provisioning performance of tree swallows has decreased in the last two decades. This finding suggests that insect availability has decreased, but could also indicate changes in prey composition or declines in parental foraging ability. I would have expected that reduced delivery rates in recent years would have inhibited the development of nestlings. However, chick growth appeared to be lower only in 2018, but not 2017. This mismatch between delivery rates and chick sizes in 2017 could be attributed to “good” yearly conditions where higher temperatures enhanced chick health and/or extended daily foraging hours, or where a diet composed of more flies and bigger prey items provided a higher-quality food.

4.2. Limitations

The careful replication of an experiment conducted in 1994/5 produced some interesting results. However, the original experimental design had four major limitations. Because I was constrained to follow the original protocol, I could not adapt the experiment to our specific question. Firstly, the most informative component of the original experiment the brood size enlargements were restricted to brood sizes of 5 and 6 as they were the only treatments involving enlarged broods. Ideal experiments for repurposing would enlarge nests of all brood size as to not only challenge parents of potentially lower quality. This also resulted in a small sample size of nests that experienced a considerable challenge (+2). Secondly, observations of feeding visits had to be recorded between day 4 and day 9 post-hatching, yet peak feeding demand occurs around day 13 (Morehouse and Brewer 1968, Leonard and Horn 2006, Lundberg and Alatalo 2010). That is when parents are most likely to experience a challenge. Therefore, there is a possibility that at the time of feeding observations, parents were not challenged enough to be affected by an increase in brood size. Thirdly, unlike the majority of BSMEs, our experiment involved a temporary manipulation where feeding behaviour was observed immediately after a change in brood size. Considering that visit rate varies in response to experimental increases in brood size (Murphy et al. 2000) or nestling begging intensity (Leonard and Horn 1996, 1998; Whittingham et al. 2003), I assumed that parents responded to these changes immediately after a brood manipulation. Nonetheless, there is no direct evidence that provisioning behaviour is affected over such a short time range. Finally, when conducted in the 1990s, this experiment measured the size distribution of the prey but did not report the types of prey times (Dyck 1995). This information would have enhanced our results regarding the changes in prey composition between the two time periods.

4.3. Future research

My scoping review identified 33 studies about the provisioning performance of aerial insectivores. I recommended replicating experiments to detect temporal trends in the responses to brood size manipulations, prioritizing studies that were conducted on swallows, swifts or nightjars, in North America more than 20 years ago. Most of the identified studies measured the rate of feeding visits, but few examined the mass or composition of the delivered food. Further research should be expanded beyond the scope of brood size manipulation experiments by conducting an expanded review that included non-BSME studies measuring load mass. Future work could also involve a more detailed meta-analysis that includes studies where costs to chicks were measured.

Further research could also examine the effects of different methodological parameters of BSMEs on the measured responses. Indeed, the methods used to perform BSME varied widely between studies. A better understanding of the repercussion of each methodological decision on the measured response could allow us to define an optimal method for BSMEs, i.e. a method that maximizes the challenge for the parents. Standard protocols for BSMEs would also allow for easier comparison between future studies.

My study was the first to repeat a BSME and compare the feeding behaviour of an aerial insectivore between several decades. Considering that aerial insectivore populations have declined across North America possibly due to declines in their prey, this experiment aimed to test the idea of repurposing past experiments to assess changes in flying insect availability. Results showed that parental provisioning behaviour may have changed at a breeding site. Further research should continue replicating studies on aerial insectivore feeding behaviour at various breeding sited to evaluate the generality of my findings and potentially generate a broad-scale assessment of insect availability across North America.

Our findings support the hypothesis of aerial insect declines and emphasize the need to investigate changes in aerial insectivore diets to understand declines in these bird populations. Considering the likely relationship between insect and aerial insectivore populations, conservation efforts should focus on preserving habitats rich in aquatic insects, the main prey of aerial insectivores (Michelson et al. 2018). This implies mitigating the consequences of agricultural intensification, the impacts of which have long been documented in birds (Donald et al. 2001, Ghilain and Bélisle 2008, Conover et al. 2014, Stanton et al. 2016).

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