WILDLIFE BIOLOGY

Short communication

Swift sampling of farmland aerial invertebrates offers insights into foraging behaviour in an aerial insectivore

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The common swift *Apus apus* is an obligate aerial, migratory, insectivorous bird, that has experienced significant declines in the UK since the 1990s. Reductions in the availability of prey during their summer breeding season in the UK are likely to be a key factor in this decline. This short communication aims to contribute new insights into the current foraging behaviours of adult swifts feeding their nestlings, as a means of provoking new conversation and stimulating further work. Food bolus samples are small ball-like structures containing the insect prey that is regurgitated to nestlings. Boluses from adult swifts provisioning their nestlings were collected incidentally at a breeding colony in Suffolk, UK. These were taxonomically identified and compared to corresponding daily insect catches from a nearby Rothamsted Insect Survey suction trap operating within the foraging area of common swifts. There was a distinction between the contents of the bolus samples and the suction-trap samples, whereby larger-bodied aerial invertebrates appeared in greater numbers in bolus samples. This was evidenced by the relatively high numbers of agriculturally important species, pollen beetles, and cabbage stem flea beetles in bolus samples compared to low numbers in suction traps. Smaller invertebrates such as aphids (Aphididae), parasitoid wasps (Hymenoptera), and thrips (Thysanoptera) were not frequent in the bolus samples, relative to the high numbers identified from the suction-trap catch. These results are discussed in relation to swifts providing a pest suppression service, potential impacts of pesticides, and how selective foraging may both buffer and facilitate the challenges swifts face in a modern agricultural landscape.

Keywords: common swift, diet, invertebrates, agriculture, pest control, pesticide impacts

Introduction

The expansion and intensification of agriculture is believed to have driven the decline of many taxa associated with farmed landscapes (Donald et al. 2001, Green et al. 2005, Chaudhary et al. 2016). Farmland bird species are experiencing population

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declines globally, although the severity varies depending on species and region (Newton 2004, Nebel et al. 2010, Vickery et al. 2014, Bowler et al. 2019). In the UK, common swifts *Apus apus* (hereafter swifts) have suffered some of the most severe declines, with a 58% decline between 1995 and 2018 reported (Woodward et al. 2020). The main drivers of their decline are unclear; however, loss of nesting sites, poor summer climate, and a decline in their insect prey are likely to have contributed (British Trust for Ornithology 2023). Similar patterns of decline have been observed in other UK aerial insectivorous species, such as barn swallows *Hirundo rustica* and house martins *Delichon urbichon*, supporting the theory that declines in insect prey are contributing to declines (Møller 2019, Tallamy and Shriver 2021). This short communication adds data and insights on swift breeding season foraging, and prey composition related to insect availability.

Swifts are migratory birds that arrive and breed in the UK in spring, usually utilising structures such as residential buildings or farm outbuildings as nest sites (Dulisz et al. 2022). Swifts are exclusively insectivorous, consuming flying insects while airborne at heights ranging between six and 30 m (Lack and Owen 1955). Swifts arrive in the UK from their winter range in Sub-Saharan Africa in spring, followed by an incubation period of three to four weeks before eggs hatch. Adult swifts therefore typically only have time to raise a single brood, unlike other aerial insectivores which have multiple broods. The timing, as well as abundance, of insect prey is therefore critical for successful fledging of young (Visser et al. 1998).

Swift nestlings are fed by both parents in the form of a food bolus (a regurgitated ball-like structure containing insect prey), which varies in size and insect composition depending on prey availability and brood size (Lack and Owen 1955, Martins and Wright 1993). The protein and nutrient-dense diet afforded by insectivory is crucial for the development of their young (Razeng and Watson 2015). Links between population declines in insects and in swifts have been anecdotally linked; however, the scientific evidence in limited. Recently, Finch et al. (2023) found no association between temporal declines in aphid biomass and breeding success or survival of swifts, despite aphids being an apparent key food source for swifts. Instead, weather was found to be a stronger correlate of variation in swift demography, with higher precipitation associated with smaller brood size, higher nest failure, and lower first-year survival. In this short study, we also use the Rothamsted Insect Survey data, as were used in Finch et al. (2023), to compare the diet of swifts to local aerial insect density and composition.

Whilst the feeding ecology of swifts is evidently important for their breeding success and population trajectories, their diet may also provide a key service on farmland in the form of insect pest suppression. This has been studied and quantified in other parts of the world and in other aerial insectivores (Boyles et al. 2011, Orłowski et al. 2014, Nyffeler et al. 2018), but swifts' contribution to pest management in the UK is not well understood and is therefore likely to be undervalued. Data collected by Lack and Owen (1955) indicated a preference for foraging over low-lying agricultural landscapes, suggested by the volume of aphids in bolus samples. As pressure increases for nature-friendly agricultural practices, such as alternative strategies to chemical insecticides, expanding our understanding of the capacity of natural predators to provide such a service is essential, particularly in light of the population declines of insectivores. In addition, the impacts of chemical insecticide use on swifts foraging over agricultural landscapes will be important to monitor, as studies have linked insecticide exposure to poor chick health and survival in other farmland bird species (Boatman et al. 2004, Hart et al. 2006).

Swifts are known to be selective in their choice of insect prey and have been observed discarding prey items, as well as exclusively catching drone bees when foraging around beehives (Lacey 1910, Lack and Owen 1955). Lack and Owen (1955) found that insects larger than 10 mm and smaller than 2 mm were rarely taken, and larger insects were preferred in fair weather conditions, when more were available. A similar preference for larger prey during the breeding season has also been shown in barn swallows, whereby high throughput sequencing of nestling faecal samples demonstrated a flexible diet, with preference for larger flies (Diptera) (Turner 1982, McClenaghan et al. 2019). However, modern diet analysis techniques are, to our knowledge, yet to be performed for the swift, and are limited to taxonomic work done decades ago.

Nest records and ringing, as is led in the UK by the British Trust for Ornithology (BTO), provide valuable and detailed data on breeding success (e.g. hatching and fledging rates) and phenology (e.g. arrival date to breeding sites). In this study, additional data through incidental sampling of swift boluses were collected during this routine ringing. By comparing the abundance and composition of insects in swift boluses to temporally matched local aerial abundance and composition, this study aims to: 1) provide an up-to-date insight into the aerial insects selected by adult swifts provisioning their young, and 2) discuss the implications of (1) in the context of swift reproduction, pest suppression, and risk of pesticide exposure.

Material and methods

Study site

Swift bolus samples were collected during routine ringing at Brewery Farm, Suffolk, UK (52°11′26.2″N, 01°05′47.8″E), in June and July 2022. The site is a swift breeding colony, with 10 breeding pairs in 2022, nesting in nest boxes on farm buildings. The farm comprises 200 acres of land, primarily farmed 'for nature' with cereal cropping, mainly wheat. At the time of sampling, the farm was under the agri-environment scheme mid-tier stewardship, now known as Mid-Tier Countryside Stewardship. This means that the farm was subsidised to protect and enhance the natural environment, specifically through planting of large areas of nectar mix, wildflower mix, and winter bird food, which provides an area that is beneficial to wildlife (GOV UK. 2024). Such habitats

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have been shown to improve insect and farmland bird populations (Bright et al. 2015, Panassiti et al. 2023). There are extensive areas of scrub and woodland habitat, along with three small ponds. The wider habitat around Brewery Farm is mostly arable, dominated by arable landcover (77% of a 5 km radius), followed by improved grassland (14% of a 5 km radius) (Marston et al. 2022). In 2022, no insecticides were applied over the 200 acres at Brewery Farm.

Bolus collection

Swift ringing in 2022, as part of the BTO Bird Ringing Scheme, provided the opportunity to collect a total of three samples, on three separate occasions. Each year, all nestlings are ringed at approximately 10–14 days after hatching, once their eyes are open, before fledging. Two of the three bolus samples were collected from the same nest box on two occasions, and the other from a different nest on a single occasion. Both nests had three nestlings ringed in 2022.

Ringing of nestlings takes place in warm, dry conditions, to increase the chance of the adult birds being out foraging, to minimise distress. During ringing, if adult birds return to the nest, they are caught to be ringed or their current ring is checked. This is when incidental sampling of boluses occurred, as adult birds were unable to feed nestlings, so instead they regurgitated the boluses elsewhere. This happened on most ringing incidences; however, the three samples for this study were collected when sample bottles were available. Bolus samples were stored in a 95% ethanol and 5% glycerol solution. The invertebrate composition of the boluses were identified to family level and, where possible, to genus and species for some invertebrates. The invertebrate data were then compared with the data from nearby suction-trap sampling.

Suction-trap sampling

Rothamsted Insect Survey runs a network of 12.2-m-tall suction traps across the UK, primarily to sample aphids (Aphidae) of agricultural significance. The suction-trap network is the most comprehensive, standardised long-term monitoring and surveillance of invertebrate activity in the world (Harrington et al. 2013). Samples are collected at the same time daily (10:00), resulting in a 24-h catch period for each sample. Aphids and non-aphid bycatch of other flying invertebrates are stored in an archive, consisting of samples from 1974 onwards.

The habitat around Brewery Farm is similar to Booms Barn suction trap (52°15′38.5″N, 00°34′06.4″E) and is dominated by arable landcover (75% of a 5 km radius), followed by improved grassland (11% of 5 km radius) (Marston et al. 2022). In addition, suction-trap samples are deemed to be representative of an area with a radius of 80 km (50 miles) (Taylor 1979), and therefore representative of the aerial invertebrates available for swifts foraging at Brewery Farm, which is 45 km from Brooms Barn. The landcover at this wider landscape (45 km radius) is also similar between the areas surrounding Brooms Barn and Brewery Farm, both of which are dominated by arable farmland (66 and 60%, respectively) followed by improved grassland (16 and 17%, respectively).

Suction-trap samples from Brooms Barn were identified to family level, with agriculturally important pest insects identified to species. R programming software ver. 4.0.5 was used to produce the donut plots using the 'Tidyverse' package (Wickham et al. 2019, www.r-project.org). Some families within orders, such as Neuroptera and Thysanoptera, were excluded from the donut plots as there were too few individuals to improve the visualisation.

Results

A total of 4198 invertebrates were collected and identified to a minimum of family level for the suction traps and swift boluses. The suction traps collected a total of 3122 invertebrates, and the swift boluses contained a total of 1076. Invertebrates from ten orders were identified across the whole study: ten in suction-trap samples and five in swift bolus samples (Fig. 1, Supporting information). A total of 82 families were identified; 77 in suction-trap samples and 38 in bolus samples.

Divergence of swift and suction-trap samples

The largest disparities between the suction-trap catch and the invertebrates caught by swifts was the percentage of thrips (Thripidae), pollen beetles (Nitidulidae), leaf beetles (Chrysomelidae), and aphids (Fig. 2). A total of 860 thrips (Thysanoptera) were caught in the suctiontraps during the sampling days, accounting for 28% of the total suction-trap catch, whereas swifts caught none (Fig. 2). Similarly, a total of 315 aphids (10%) were captured in the suction traps, whereas only 14 (0.01%) were captured by swifts over the three sampling days. A large percentage of Scathophagidae (Diptera) and small parasitoid wasps (Braconidae, Ceraphronidae, Chalcididae, Pteramalidae, Trichogrammatidae) (Hymenoptera) were also found in traps compared to bolus samples (Fig. 2, Supporting information)

Agriculturally important invertebrates

A total of 374 pollen beetles (*Meligethes aeneus*: Nitidulidae) were identified in the first swift bolus sample from 28 June 2022, whereas only seven pollen beetles were collected in the suction trap on the same day (Fig. 2, Supporting information). During the last sampling event (18 July 2022), 128 (45%) cabbage stem flea beetle (*Psylliodes chrysocephalus*: Chrysomelidae) were caught by the swift, whereas just six (2%) were caught in the suction trap (Fig. 2, Supporting information). Aphids made up a small percentage of the swift bolus samples with only 11 (1.9%), 0 (0%), and 3 (1%) aphids identified over the three bolus sampling periods sequentially (Fig. 2, Supporting information). During the same sampling periods, the suction trap caught 146 (25%), 142 (8.7%), and 27 (3%), respectively.

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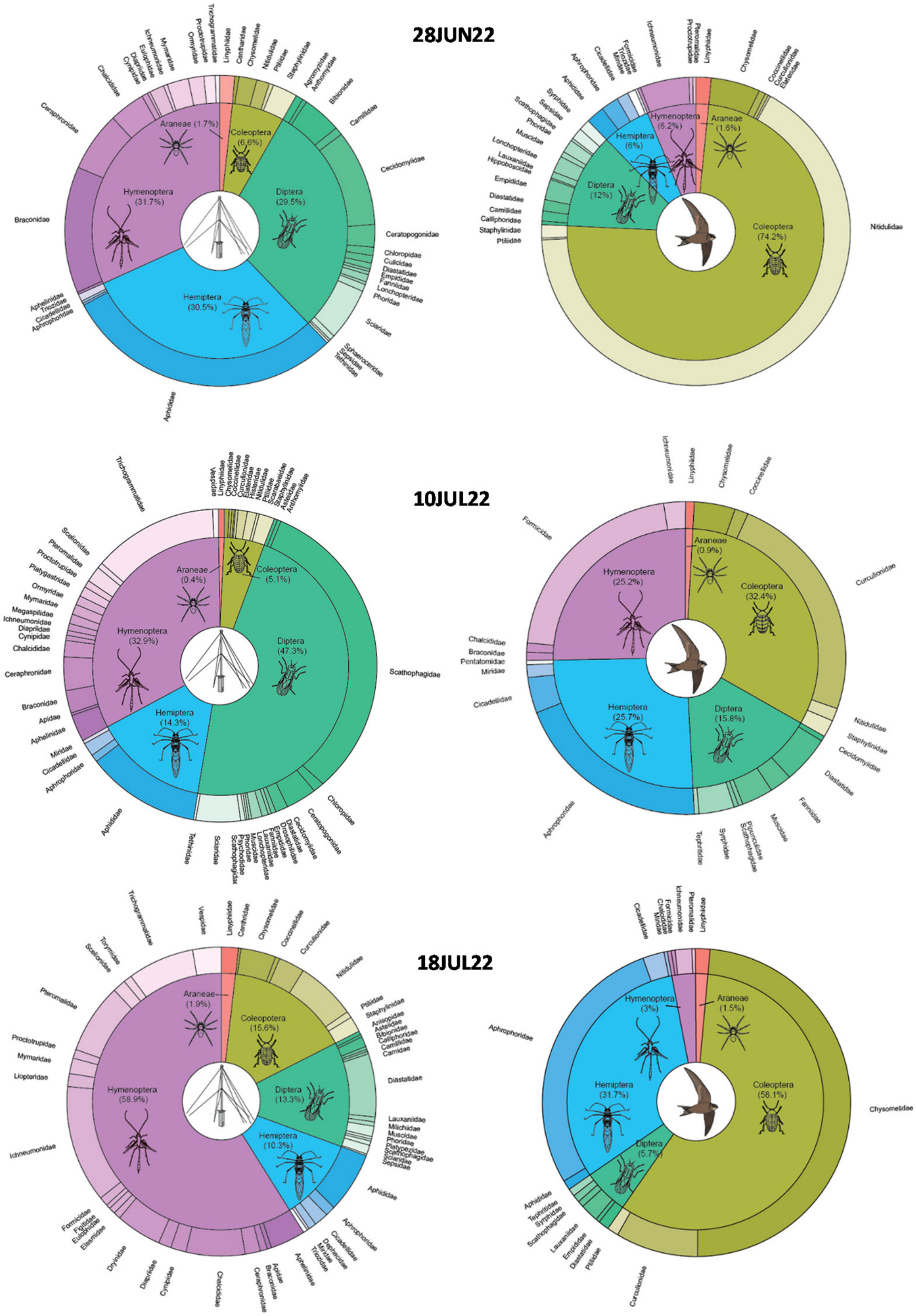

Figure 1. Results from suction-trap samples (left) and the common swift bolus samples (right). Percentages within each donut plot are a percentage of total catch for each order of invertebrates, and families are shown as relative percentages identified in each group.

Swift reproduction

In 2022, 21 swifts successfully fledged from ten nest boxes on the study site. Two nests failed due to either egg infertility or eggs being left for too long, leading to eggs chilling past the minimum survival threshold. For comparison, in 2021, 25 swifts fledged; and in 2023, 23 swifts fledged at this site. Date of fledging was not recorded in 2022.

Weather conditions

Meteorological data confirmed that weather conditions were similar at Brooms Barn and Brewery Farm on all three days of sampling (POWER 2023; Supporting information). Conditions were similar across sampling periods, as time of ringing usually favoured was when adults were more likely to be out foraging (i.e. dry, warm conditions),

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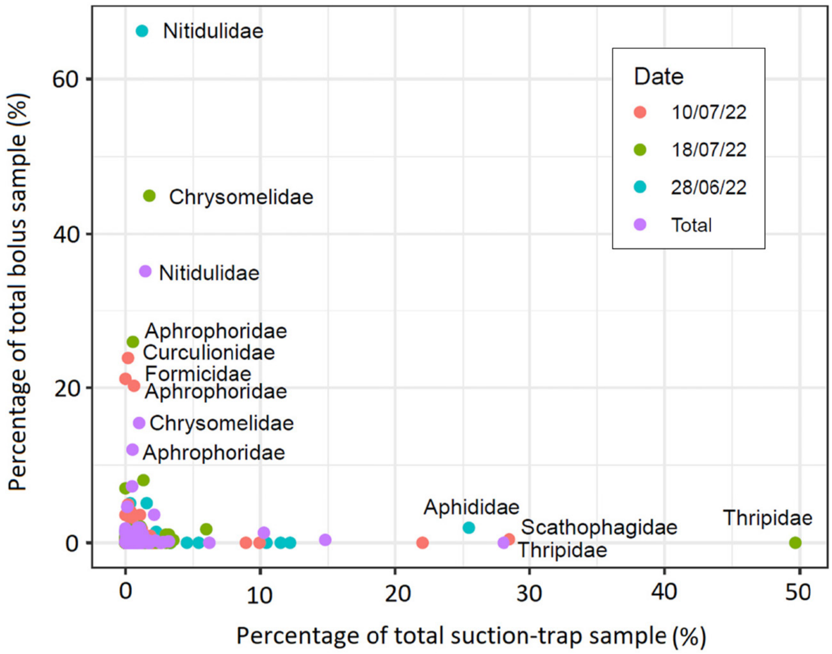

Figure 2. Comparison between the suction-trap samples and bolus samples, shown as a scatter plot, whereby each point on the plot is a family of invertebrate found on that day and each axis is a sample type. Points further to the top left and bottom right corners signify families that were found at a relatively high percentage in one sample compared to the other.

to minimise stress to adult birds during ringing of their nestlings.

Discussion

The opportunity presented by incidental sample collection during routine ringing has afforded a novel insight into the diet of swift nestlings, comparative to insect prey availability. There was a distinction between the swift and suction-trap samples (Fig. 2), suggesting possible prey selectivity by swifts gathering food for their broods.

Prey selection

Pollen beetles *Meligethes aeneus* (2–3 mm, (CABI. 2019)) and cabbage stem flea beetles *Psylliodes chrysocephala* (3–5 mm, (CABI. 2021)) were found in percentages higher than the availability suggested by the suction-trap catches. These findings are in support of Turner (1982) who found that swifts accept insects between a body size of 2 and 10 mm. However, few aphids were caught by swifts despite these being within the same size category as both *M. aeneus* and *P. chrysocephala*, and the high numbers recorded in the suction traps at the same time. This could suggest that swifts appear to be selecting for prey in high abundance and/or within close proximity to the nesting sites. This may represent a hunting strategy of gathering the highest biomass in the shortest amount of time. Indeed, the abundance of beetles over oilseed rape crops (a major source of both pollen and cabbage stem flea beetles) is often substantial and may indicate the behaviour of the bird to seek out crops as foraging habitat. This behaviour may also be considered as volume-concentrated searching (VCS), whereby complex aerial movements are concentrated to areas of dense prey, and is known to be used by swifts in agricultural landscapes (de Margerie et al. 2018). However, three boluses cannot represent the broader behaviours of swifts in the area, and further investigation is required to properly test the hypothesis that swifts forage for prey that is in high abundance.

Agriculturally important invertebrates

The presence of such a high percentage of crop pest species (aphids, pollen beetles, and cabbage stem flea beetles) in bolus samples also supports the notion that swifts can provide a valuable service in UK farmland. Whilst there has been work done to understand and quantify the value of farmland birds and other natural predators of pests, such as bats, more research is needed to account for swifts (Boyles et al. 2011, Whelan et al. 2015, Zhang et al. 2018).

Conversely, some invertebrate taxa found in the swift boluses may themselves be considered as beneficial to agriculture. Pollen beetles, for example, are regarded as pests in the spring on oilseed rape crops; however, adult beetles feeding on pollen in the summer can result in useful pollination (Williams 2010). Even so, summer numbers of pollen beetles have been found to be correlated with the abundance of beetles in the following spring, and therefore crop damage (Shortall et al. 2023).

Previous researchers have suggested that aphids are a crucial food source for swifts and other insectivorous farmland

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birds (Lack and Owen 1955, Cucco et al. 1993, Orłowski and Karg 2013, Cristiano et al. 2018). Our findings suggest that this is not always the case. The swifts whose three boluses were sampled in this study did not catch many aphids relative to the aphid abundance in the suction trap. This could suggest less reliance on aphids than once thought. Finch et al. (2023) highlighted that there was no association between aphid biomass and swift demography, despite the marked declines of aphid biomass across most of southern and eastern England since the mid-1970s.

Pesticide concerns

The high percentage of crop pests in the bolus samples also raises concerns for the impacts of pesticides, as pollen and stem flea beetles are among the most commercially significant pests of oilseed rape, frequently controlled by spray applications. Pesticide use has been hypothesised as a key driver of avian decline, through direct exposure and reduced prey availability (target and non-target species) (Hallmann et al. 2014, Poisson et al. 2021).

Pesticides picked up in the environment have shown to impact nestling survival: directly, such as impacts on egg thickness and resultant risk from predators (Cox 1991, Fry 1995, Mitra et al. 2011), and indirectly through reduced prey availability for foraging birds (Brickle et al. 2000, Boatman et al. 2004). A long-term study between 1944 and 1992 (48 years) on guano of chimney swift *Chaetura pelagica* found that large increases of dichloro-diphenyl-trichloroethane (DDT), a once widely used insecticide, were correlated with an increase in Hemipteran prey and a decrease in Coleopteran prey, significantly shifting the swift's diet and specifically the ratios of different nutrients in the diet (Nocera et al. 2012). Additionally, sub-lethal effects on both target and non-target invertebrates have been shown to affect flight and locomotion performance (De França et al. 2017). As a result, affected invertebrates would generally be easier to catch on the wing and therefore are likely to be selected over non-exposed invertebrates (Desneux et al. 2007, Jung et al. 2018).

Prey diversity

Invertebrates from five orders and 38 families were identified in the swift bolus samples. This diversity of prey may buffer swifts from future change in any single insect group (McClenaghan et al. 2019, Finch et al. 2023). The number of studies reporting long-term change in the abundance and phenology of insect taxa is growing in the UK; many of such taxa are found here and in other studies to be consumed by swifts (Shortall et al. 2009, Sanders et al. 2019, van Klink and Bowler 2019, Bell et al. 2020). An ability to be adaptable to shifts in aerial invertebrate composition is therefore likely to be advantageous to breeding swifts, particularly as long-distance migrants are at potentially increased risk of mismatch, if arrival time at breeding sites no longer coincides with beneficial foraging conditions (Møller et al. 2008, Newson et al. 2016). A greater sampling effort would be required to infer more about the variability and adaptability of swifts more generally.

Limitations

Since swifts collect diurnal invertebrates during daylight foraging trips, and the suction trap continuously samples over a 24-h period, strict comparisons between the two sample types must be treated with caution (Lack and Owen 1955). However at 12.2 m, the suction trap is well within the foraging arena of swifts (Lack and Owen 1955). Breeding swifts are also known to feed close to their colonies and nests (Lack and Owen 1955), supporting the assumption that swifts sampled in this study will have been foraging well within the 80-km representative range of the suction trap located 45 km from the nest sites.

Also, the nature of non-invasive incidental sampling meant that only three bolus samples were analysed and more samples would be required to conduct a statistical analysis to draw stronger conclusions on diet. The samples were also taken from a single farm that practices 'nature friendly' methods of farming, and whilst the swifts may have foraged beyond the farm boundary, it would be useful to sample at more intensive agricultural systems.

Conclusion

Whilst this short communication is a small insight into how swifts are foraging in modern agricultural landscapes, it has contributed new data to an otherwise scarce and largely outdated field. This study has also highlighted key areas of discussion and gaps in our understanding in a difficult study system. Notably, the apparent preference for large prey and insects of high economic interest (i.e. pest species), as well as the unexpected lack of aphids as a key part of the diet, have contributed new knowledge. It is envisaged that this straightforward comparison will stimulate further research to expand our understanding of the foraging ecology and its application to the future conservation of common swifts in agricultural landscapes.

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Permits – Catching of birds for ringing was conducted by fully licensed ringers in the Brewery Farm Ringing Group (https://breweryringing.uk), and in accordance with British Trust for Ornithology ringing protocol. Catching was carried out under permit no. A4686 and no. C6928.

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Author contributions

Hannah Romanowski: Conceptualization (equal); Investigation (equal); Methodology (equal); Project administration (equal); Writing – original draft (lead); Writing – review and editing (lead). **Kelly Jowett**: Conceptualization (equal); Data curation (equal); Investigation (equal); Methodology (equal); Project administration (equal); Writing – original draft (lead); Writing – review and editing (lead). **Dion Garrett**: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Chris Shortall**: Conceptualization (equal); Investigation (equal); Methodology (equal); Project administration (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

Data are available from the Rothamsted Repository: https://doi.org/10.23637/rothamsted.99011 (Romanowski et al. 2024)

Supporting information

The Supporting information associated with this article is available with the online version.

References

Bell, J. R., Blumgart, D. and Shortall, C. R. 2020. Are insects declining and at what rate? An analysis of standardised, systematic catches of aphid and moth abundances across Great Britain. – Insect Conserv. Divers. 13: 115–126.

Boatman, N. D., Brickle, N. W., Hart, J. D., Milsom, T. P., Morris, A. J., Murray, A. W. A., Murray, K. A. and Robertson, P. A. 2004. Evidence for the indirect effects of pesticides on farmland birds. – Ibis 146: 131–143.

Bowler, D. E., Heldbjerg, H., Fox, A. D., de Jong, M. and Böhning-Gaese, K. 2019. Long-term declines of European insectivorous bird populations and potential causes. – Conserv. Biol. 33: 1120–1130.

Boyles, J. G., Cryan, P. M., McCracken, G. F. and Kunz, T. H. 2011. Economic importance of bats in agriculture. – Science 332: 41–42.

Brickle, N. W., Harper, D. G., Aebischer, N. J. and Cockayne, S. H. 2000. Effects of agricultural intensification on the breeding success of corn buntings *Miliaria calandra*. – J. Appl. Ecol. 37: 742–755.

Bright, J. A., Morris, A. J., Field, R. H., Cooke, A. I., Grice, P. V., Walker, L. K., Fern, J. and Peach, W. J. 2015. Higher-tier agri-environment scheme enhances breeding densities of some priority farmland birds in England. – Agric. Ecosyst. Environ. 203: 69–79.

British Trust for Ornithology. 2023. BirdFacts. – https://www.bto.org/understanding-birds/birdfacts/swift#:~:text=The%20reasons%20for%20these%20losses,loss%20of%20suitable%20nesting%20sites.

CABI. 2019. *Meligethes aeneus* (rape beetle). CABI compendium. – CAB International.

CABI. 2021. *Psylliodes chrysocephala* (cabbage stem flea beetle). CABI compendium. – CAB International.

Chaudhary, A., Pfister, S. and Hellweg, S. 2016. Spatially explicit analysis of biodiversity loss due to global agriculture, pasture and forest land use from a producer and consumer perspective. – Environ. Sci. Technol. 50: 3928–3936.

Cox, C. 1991. Pesticides and birds: from DDT to today's poisons. – J. Pestic. Reform 11: 2–6.

Cristiano, L., Lantieri, A. and Noano, G. 2018. Comparison of pallid swift *Apus pallidus* diet across 20 years reveals the recent appearance of an invasive insect pest. – Avocetta 42: 9–14.

Cucco, M., Bryant, D. M. and Malacarne, G. 1993. Differences in diet of common (*Apus apus*) and pallid (*A. pallidus*) swifts. – Avocetta 17: 131–138.

De França, S. M., Breda, M. O., Barbosa, D. R., Araujo, A. M. and Guedes, C. A. 2017. The sublethal effects of insecticides in insects. – In: Shield, V. D. C. (ed.) Biological control of pest and vector insects. InTech, pp. n 23–39.

de Margerie, E., Pichot, C. and Benhamou, S. 2018. Volume-concentrated searching by an aerial insectivore, the common swift, *Apus apus*. – Anim. Behav. 136: 159–172.

Desneux, N., Decourtye, A. and Delpuech, J. M. 2007. The sublethal effects of pesticides on beneficial arthropods. – Annu. Rev. Entomol. 52: 81–106.

Donald, P. F., Gree, R. E. and Heath, M. F. 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. – Proc. R. Soc. B 268: 25–29.

Dulisz, B., Stawicka, A. M., Knozowski, P., Diserens, T. A. and Nowakowski, J. J. 2022. Effectiveness of using nest boxes as a form of bird protection after building modernization. – Biodivers. Conserv. 31: 277–294.

Finch, T., Bell, J. R., Robinson, R. A. and Peach, W. J. 2023. Demography of common swifts (*Apus apus*) breeding in the UK associated with local weather but not aphid biomass. – Ibis 165: 420–435.

Fry, D. M. 1995. Reproductive effects in birds exposed to pesticides and industrial chemicals. – Environ. Health Perspect. 103: 165–171.

GOV UK. 2024. Guidance: countryside stewardship: get funding to protect and improve the land you manage. – https://www.gov.uk/guidance/countryside-stewardship-get-funding-to-protect-and-improve-the-land-you-manage.

Green, R. E., Cornell, S. J., Scharlemann, J. P. and Balmford, A. 2005. Farming and the fate of wild nature. – Science 307: 550–555.

Hallmann, C. A., Foppen, R. P., Van Turnhout, C. A., De Kroon, H. and Jongejans, E. 2014. Declines in insectivorous birds are associated with high neonicotinoid concentrations. – Nature 511: 341–343.

Harrington, R., Taylor, M. S., Alderson, L. J., Shortall, C. R., Kruger, T., Izera, D., Verrier, P. J. and Pickup, J. 2013. The Rothamsted insect survey: gold standard aphid monitoring. – NJF Rep. 9: 7–12.

Hart, J. D., Milsom, T. P., Fisher, G., Wilkins, V., Moreby, S. J., Murray, A. W. A. and Robertson, P. A. 2006. The relationship between yellowhammer breeding performance, arthropod abundance and insecticide applications on arable farmland. – J. Appl. Ecol. 43: 81–91.

1903220x, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/wlb3.01294 by Test, Wiley Online Library on [30/05/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Jung, M., Kim, S., Kim, H. G. and Lee, D. H. 2018. Lethal and sublethal effects of synthetic insecticides on the locomotory and feeding behavior of *Riptortus pedestris* (Hemiptera: Alydidae) under laboratory conditions. – J. Asia Pac. Entomol. 21: 179–185.
Lacey, E. 1910. Swifts eating drones of the hive bee. – Br. Birds 3: 263.
Lack, D. and Owen, D. F. 1955. The food of the swift. – J. Anim. Ecol. 24: 120–136.
Marston, C., Rowland, C. S., O'Neil, A. W. and Morton, R. D. 2022. Land cover map 2021 (25m rasterised land parcels, GB). – Environmental Information Data Centre.
Martins, T. L. and Wright, J. 1993. Cost of reproduction and allocation of food between parent and young in the swift (*Apus apus*). – Behav. Ecol. 4: 213–223.
McClenaghan, B., Nol, E. and Kerr, K. C. R. 2019. DNA metabarcoding reveals the broad and flexible diet of a declining aerial insectivore. – Auk 136: 1–11.
Mitra, A., Chatterjee, C. and Mandal, F. B. 2011. Synthetic chemical pesticides and their effects on birds. – Res. J. Environ. Toxicol. 5: 81–96.
Møller, A. P. 2019. Parallel declines in abundance of insects and insectivorous birds in Denmark over 22 years. – Ecol. Evol. 9: 6581–6587.
Møller, A. P., Rubolini, D. and Lehikoinen, E. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. – Proc. Natl Acad. Sci. USA 105: 16195–16200.
Nebel, S., Mills, A., McCracken, J. and Taylor, P. 2010. Declines of aerial insectivores in North America follow a geographic gradient. – ACE 5: 1.
Newson, S. E., Moran, N. J., Musgrove, A. J., Pearce-Higgins, J. W., Gillings, S., Atkinson, P. W., Miller, R., Grantham, M. J. and Baillie, S. R. 2016. Long-term changes in the migration phenology of UK breeding birds detected by large-scale citizen science recording schemes. – Ibis 158: 481–495.
Newton, I. 2004. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. – Ibis 146: 579–600.
Nocera, J. J., Blais, J. M., Beresford, D. V., Finity, L. K., Grooms, C., Kimpe, L. E., Kyser, K., Michelutti, N., Reudink, M. W. and Smol, J. P. 2012. Historical pesticide applications coincided with an altered diet of aerially foraging insectivorous chimney swifts. – Proc. R. Soc. B 279: 3114–3120.
Nyffeler, M., Şekercioğlu, Ç. H. and Whelan, C. J. 2018. Insectivorous birds consume an estimated 400–500 million tons of prey annually. – Sci. Nat. 105: 1–13.
Orłowski, G. and Karg, J. 2013. Diet breadth and overlap in three sympatric aerial insectivorous birds at the same location. – Bird Study 60: 475–483.
Orłowski, G., Karg, J. and Karg, G. 2014. Functional invertebrate prey groups reflect dietary responses to phenology and farming activity and pest control services in three sympatric species of aerially foraging insectivorous birds. – PLoS One 9: e114906.
Panassiti, B., Wolfrum, S., Birnbeck, S., Burmeister, J., Freibauer, A., Morinière, J. and Walter, R. 2023. Insects benefit from agri-environmental schemes aiming at grassland extensification. – Agric. Ecosyst. Environ. 356: 108613.
Poisson, M. C., Garrett, D. R., Sigouin, A., Bélisle, M., Garant, D., Haroune, L., Bellenger, J. P. and Pelletier, F. 2021. Assessing pesticides exposure effects on the reproductive performance of a declining aerial insectivore. – Ecol. Appl. 31: e02415.
POWER project's daily agroclimatology archive. 2023. Power data access viewer. – https://power.larc.nasa.gov/data-access-viewer.
Razeng, E. and Watson, D. M. 2015. Nutritional composition of the preferred prey of insectivorous birds: popularity reflects quality. – J. Avian Biol. 46: 89–96.
Romanowski, H., Shortall, C. R., Jowett, K. and Garrett, D. 2024. Data from: Swift sampling of farmland aerial inverebrates offers insights into foraging behaviour in an aerial insectivore. – Rothamsted Research, https://doi.org/10.23637/rothamsted.99011.
Sanders, C. J., Shortall, C. R., England, M., Harrington, R., Purse, B., Burgin, L., Carpenter, S. and Gubbins, S. 2019. Long-term shifts in the seasonal abundance of adult Culicoides biting midges and their impact on potential arbovirus outbreaks. – J. Appl. Ecol. 56: 1649–1660.
Shortall, C. R., Moore, A., Smith, E., Hall, M. J., Woiwod, I. P. and Harrington, R. 2009. Long-term changes in the abundance of flying insects. – Insect Conserv. Divers. 2: 251–260.
Shortall, C. R., Cook, S. M., Mauchline, A. L. and Bell, J. R. 2023. Long-term trends in migrating *Brassicogethes aeneus* in the UK. – Pest Manage. Sci. 80: 2211–2494.
Tallamy, D. W. and Shriver, W. G. 2021. Are declines in insects and insectivorous birds related? – Condor 123: duaa059.
Taylor, L. R. 1974. Monitoring change in the distribution and abundance of insects. Rothamsted Research Experimental Station Report for 1973, Part 2. – Rothamsted Research, pp. 202–239.
Turner, A. K. 1982. Optimal foraging by the swallow (*Hirundo rustica*, L.): prey size selection. – Anim. Behav. 30: 862–872.
van Klink, R. and Bowler, D. 2019. Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. – World Acad. Sci. Eng. Technol. 13: 340–348.
Vickery, J. A., Ewing, S. R., Smith, K. W., Pain, D. J., Bairlein, F., Škorpilová, J. and Gregory, R. D. 2014. The decline of Afro-Palaearctic migrants and an assessment of potential causes. – Ibis 156: 1–22.
Visser, M. E., Noordwijk, A. J., Tinbergen, J. M. and Lessells, C. M. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). – Proc. R. Soc. B 265: 1867–1870.
Whelan, C. J., Şekercioğlu, Ç. H. and Wenny, D. G. 2015. Why birds matter: from economic ornithology to ecosystem services. – J. Ornithol. 156: 227–238.
Wickham, H. et al. 2019. Welcome to the tidyverse. – J. Open Source Softw. 4: 1686.
Williams, I. H. 2010. The major insect pests of oilseed rape in Europe and their management: an overview. – In: Williams, I.H. (ed.), Biocontrol-based integrated management of oilseed rape pests. Springer, pp. 1–43.
Woodward, I. D., Massimino, D., Hammond, M. J., Barber, L., Barimore, C., Harris, S. J., Leech, D. I., Noble, D. G., Walker, R. H., Baillie, S. R. and Robinson, R. A. 2020. BirdTrends 2020: trends in numbers, breeding success and survival for UK breeding birds. Research report 732. – BTO.
Zhang, H., Garratt, M. P. D., Bailey, A., Potts, S. G. and Breeze, T. 2018. Economic valuation of natural pest control of the summer grain aphid in wheat in South East England. – Ecosyst. Serv. 30: 149–157.

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