

Current Biology

Climate change shifts the timing of nutritional flux from aquatic insects

Highlights

- Aquatic insect emergence is advancing much more rapidly than bird breeding timing
- Aquatic insects have more n-3 LCPUFAs than terrestrial insects
- The seasonal availability of key fatty acids is thus shifting with climate change
- Birds are increasingly at risk of experiencing nutritional phenological mismatch

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In brief

Compared with terrestrial insects, emergent aquatic insects are rich in omega-3 long-chain polyunsaturated fatty acids. Shipley et al. show that aquatic insect phenology is advancing more rapidly than bird phenology. Consequently, birds that rely on aquatic insects for fatty acids are likely to encounter nutritional mismatches with climate change.



Article

Climate change shifts the timing of nutritional flux from aquatic insects

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SUMMARY

Climate change can decouple resource supply from consumer demand, with the potential to create phenological mismatches driving negative consequences on fitness. However, the underlying ecological mechanisms of phenological mismatches between consumers and their resources have not been fully explored. Here, we use long-term records of aquatic and terrestrial insect biomass and egg-hatching times of several co-occurring insectivorous species to investigate temporal mismatches between the availability of and demand for nutrients that are essential for offspring development. We found that insects with aquatic larvae reach peak biomass earlier in the season than those with terrestrial larvae and that the relative availability of omega-3 long-chain polyunsaturated fatty acids (n-3 LCPUFAs) to consumers is almost entirely dependent on the phenology of aquatic insect emergence. This is due to the 4- to 34-fold greater n-3 LCPUFA concentration difference in insects emerging from aquatic as opposed to terrestrial habitats. From a long-sampled site (25 years) undergoing minimal land use conversion, we found that both aquatic and terrestrial insect phenologies have advanced substantially faster than those of insectivorous birds, shifting the timing of peak availability of n-3 LCPUFAs for birds during reproduction. For species that require n-3 LCPUFAs directly from diet, highly nutritious aquatic insects cannot simply be replaced by terrestrial insects, creating nutritional phenological mismatches. Our research findings reveal and highlight the increasing necessity of specifically investigating how nutritional phenology, rather than only overall resource availability, is changing for consumers in response to climate change.

INTRODUCTION

Climate change is causing phenological mismatches between consumers and the availability of resources ranging from zooplankton to mammals because organisms at lower trophic level often advance their annual life cycles at a faster rate than do consumers at higher trophic levels.^{1–4} Climate change is shifting optimal conditions for events such as reproduction and migration, which often occur only during a brief period throughout the year.⁵ For many species, fitness is determined by matching reproduction with pulsed ephemeral resource availability,^{5,6} and fitness decreases when periods of peak life-history demand become decoupled from highs in resource availability.^{7,8} However, increased resource availability alone may not necessarily translate into

increased fitness, as resources vary in energetic and nutritional content, both of which can drive fitness variation in consumers.^{9–12} Shifts in the timing of life-history stages and the availability of resources that contain certain critical nutrients during key life stages can lead to nutritional phenological mismatches.^{13,14} For example, limitation of specific nutrients and compounds, such as omega-3 long-chain polyunsaturated fatty acids (n-3 LCPUFAs) can decrease consumer growth and reproductive output.^{13,15–17} Elemental nutrients, such as calcium and iron, as well as organic compounds such as fatty acids, carbohydrates, proteins, and vitamins are often especially important during specific life stages, such as development or in preparation for migratory journeys, when animals are putting on large amounts of biomass and developing organs.^{18,19} Thus, it is critical that we



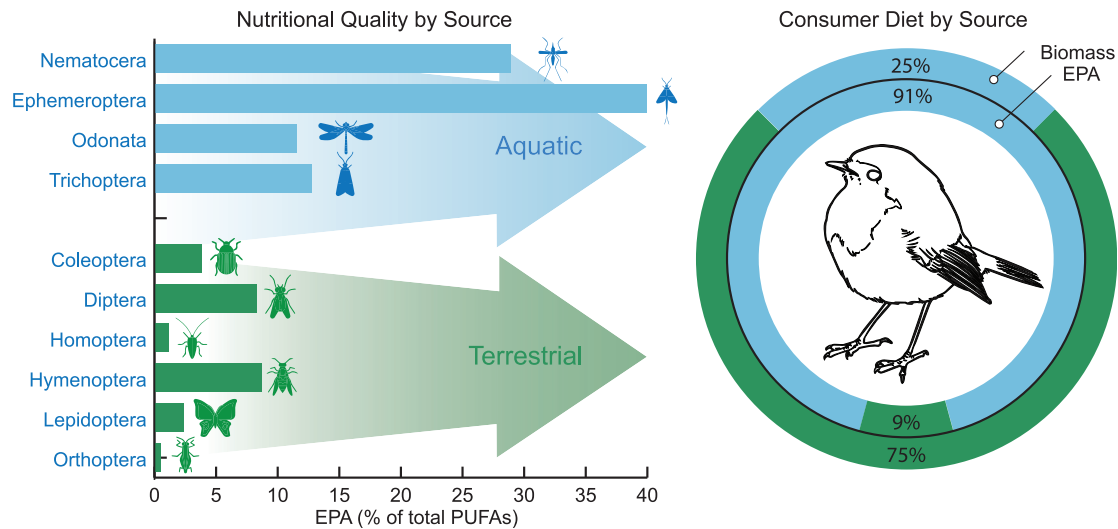


Figure 1. Ecosystem differences in quantity versus nutritional content of exports

Insect biomass flux from both aquatic and terrestrial ecosystems affects the availability to consumers, but differences in nutritional quality drive oversized impact from aquatic systems. For example, due to the order-of-magnitude higher concentrations of EPA in aquatic insects, a hypothetical consumer with a diet of 75% terrestrial insects still obtains more than 91% of all its dietary EPA from aquatic sources.

consider both the nutritional composition, as well as abundance of available resources to understand the character and impact of phenological mismatches.¹²

Although mismatches in the overall availability of foods can exert strong effects on offspring growth and survival,^{20–22} the nutritional composition of resources can exert equally strong effects on fitness.^{11,17,23} Insects and other animals are typically considered high-quality foods, especially compared with plant-based foods because they contain a substantial amount of both fat and/or protein²⁴ in addition to having low carbon:nitrogen and carbon:phosphorus ratios.²⁵ Consequently, cross-ecosystem subsidies of insects from aquatic to terrestrial food webs have typically been considered high-quality resources for both terrestrial and aquatic consumers,²⁶ particularly compared with subsidies of plant material from terrestrial to aquatic systems.^{27,28} However, insects with aquatic or terrestrial larval stages vary in nutritional quality because of a fundamental dichotomy in concentrations of n-3 LCPUFA at the base of aquatic and terrestrial food webs. Specifically, algae at the base of aquatic food webs are often rich in n-3 LCPUFA, and these compounds thus are often present at all trophic levels within aquatic food webs.²⁹ In contrast, terrestrial primary producers typically only contain shorter chain n-3 fatty acids such as α -linolenic acid (ALA).^{30–32} As a result, terrestrial insects have n-3 LCPUFA contents only 3%–25% those of aquatic insects of the same mass.³³ Thus, the availability of desirable fatty acids for insectivores is likely proportional to the relative availability of aquatic versus terrestrial insects (Figure 1).

There is evidence of widespread insect biomass declines,^{34–36} shifts in insect community composition,^{37–39} and advancing insect phenology (e.g., Thackeray et al.²) that are all likely to change seasonal patterns of nutrient availability from insects. However, the consequences of such shifts in nutrient availability for insectivorous consumers have been largely neglected. For example, increased water temperatures from climate change

are predicted to speed maturation and decrease adult size in aquatic insects,⁴⁰ where warming temperatures can result in aquatic insects rich in n-3 LCPUFA emerging 20–40 days earlier and 12% smaller than previously observed.⁴¹ Accordingly, if insectivores that are unable to synthesize these compounds in sufficient quantities, they will require n-3 LCPUFA directly from their diet.⁴² Species that require these compounds directly from diet are likely to experience fitness consequences from changes in the overall availability, taxonomic composition, and phenology of aquatic versus terrestrial insects. Such shifts in aquatic insect phenology and insect phenology generally are particularly relevant for species of insectivorous birds which have already experienced significant declines across both North America and Europe over the past three decades.^{43,44} For example, insectivorous bird populations have declined by 13%–28% across Europe,⁴³ making them one of the most rapidly declining feeding guilds, while insect abundance has also undergone similar declines, decreasing by more than 75% within some regions of Europe.^{36,45} Thus, for consumers that rely on insects as prey, the challenges of keeping pace with rapidly advancing insect life cycles are further intensified under conditions of reduced overall densities of insect prey and the timing of emergence of the most nutritionally rich of these.

RESULTS

We used nest-record data from the citizen-science programs Project Nestwatch⁴⁶ and Project MartinWatch to explore the relationship between shifts in the timing of breeding of multiple bird species and phenological shifts in local aquatic and terrestrial insect communities. We selected several predominantly insectivorous species (i.e., all species feed their nestlings insects) that are frequently found foraging at our field site (i.e., Barn Swallows [*Hirundo rustica*], Eastern Phoebe [*Sayornis phoebe*], and Purple Martins [*Progne subis*]) including several

Table 1. Polyunsaturated fatty acid content of aquatic and terrestrial insect orders and families

Taxon	Habitat	n	ALA ^a	EPA ^a	DHA ^a
Ephemeroptera	aquatic	54	23.38 ± 2.01	39.87 ± 6.29	0.04 ± 0.01
Nematocera	aquatic	592	27.04 ± 7.51	28.91 ± 5.50	3.26 ± 0.45
Odonata	aquatic	16	7.30 ± 1.08	11.35 ± 1.41	0.38 ± 0.22
Trichoptera	aquatic	161	9.32 ± 2.34	12.79 ± 0.84	0.11 ± 0.04
Coleoptera	terrestrial	20	10.06 ± 9.90	4.25 ± 2.90	0.00 ± 0.00
Homoptera	terrestrial	22	18.45 ± 8.76	1.14 ± 1.52	0.00 ± 0.00
Hymenoptera	terrestrial	24	37.30 ± 9.98	10.69 ± 2.78	0.00 ± 0.00
Other Diptera	terrestrial	92	11.84 ± 1.69	12.20 ± 1.20	0.01 ± 0.02
Habitat averages	aquatic	889	19.59 ± 2.44	15.22 ± 2.68	0.32 ± 0.10
	terrestrial	232	42.39 ± 10.95	4.31 ± 2.55	0.01 ± 0.01

^aValues presented as mean ± SE for mg fatty acid methylated esters (FAMES) g⁻¹ dry mass

documented competitors for nest sites (i.e., Eastern Bluebirds [*Sialis sialis*], Tree Swallows [*Tachycineta bicolor*], and House Wrens [*Troglodytes aedon*]) to understand the long-term phenological trends in reproductive timing using bootstrapped linear models. We coupled this bird phenology dataset with a unique long-term dataset of daily insect abundance from Ithaca, NY (42.5043°N, -76.4659°W, daily sampling between April and July from 1989 to 2014: 3,646 unique sampling days) to examine insect biomass and nutrient availability from aquatic and terrestrial sources spanning 25 years. Insects were counted and placed into 2-mm size bins and categorized into one of 12 aquatic or terrestrial insect orders resulting in a total of 613,868 identified insects. We combined daily size counts with allometric equations for each insect order or sub-order (Table S1) to estimate daily availability of insect dry mass from aquatic and terrestrial habitats. The daily insect dry biomass per order was then merged with data on taxon-specific LCPUFA concentrations (Table 1) to determine the daily nutrient flux (i.e., mass of nutrient available per unit of time) from each of the taxonomic groups and habitats. Finally, we quantified seasonal changes in insect emergence by investigating (1) long-term seasonal trends in insect availability using an autoregressive generalized additive mixed model (GAMM) and (2) recent phenological shifts in insect availability by splitting the dataset into early (i.e., first 10 years of dataset) and late (i.e., last 10 years of dataset) periods.

Phenological differences drive seasonal availability of resources

The breeding season of insectivorous birds occupying similar ecoregions (Eastern Great Lakes and Hudson Lowlands and the Upper Appalachian Plateau) within 150 km of our insect sampling site in Ithaca, NY, spanned ~13 weeks from mid-April (start of breeding season for Eastern Bluebird) to mid-July (end of the breeding season for Purple Martin) (Figure 2A). During the bird breeding season, the seasonal flux of aquatic insects increases more quickly and peaks earlier than that of terrestrial insects, which tend to gradually increase throughout the season (Figure 2B). This phenological asynchrony between aquatic and terrestrial insect emergence translates into stark seasonal differences in the n-3 LCPUFA flux for insectivorous consumers (Figure 2C). For example, the export of the n-3 LCPUFAs

eicosapentaenoic acid (EPA; 20:5n-3) and docosahexaenoic acid (DHA; 22:6n-3) are typically more than an order of magnitude greater from aquatic versus terrestrial habitats at the study site (Figure 2C). This difference in EPA and DHA flux between these two groups of insects can be explained by their nutritional content rather than differences in total insect biomass. The total mass of daily observed emergences of aquatic and terrestrially insects are much more comparable (Figures 2B and 2C) than are their nutrient compositions: aquatic insects on average contain 27 times more DHA and four times more EPA than their terrestrial counterparts per mass (Table 1). Such nutritional differences can be even more pronounced among specific insect orders.

Asynchronous rates of advancement shift peak availability to consumers

Although spring insect emergence is advancing from 3–12 days over our study period in both aquatic and terrestrial communities, it is outpacing the rate of laying advancement of insectivorous birds (Figure 3A), such as Eastern Bluebirds (−2.9 days), Eastern Phoebe (−1.9 days), House Sparrows (−5.6 days), House Wrens (−2.8 days), Tree Swallows (−2.8 days), and Purple Martins (−6.7 days) from 1989–2014 (Figures 3A and S4; Table S4). Daily mean temperatures during this time have on average have warmed 0.24°C during our analysis window; however, this varies considerably from week to week (Figure 3B). There was little evidence for land use change over our study period, as the local region has some of the lowest rates of land use conversion in the Eastern United States.⁴⁸ Local data on Barn Swallow breeding timing were only available for 2008–2014 (i.e., at the end of our insect dataset); thus, we were unable to determine that species' long-term trends in the region. However, other recent studies from nearby Maritime Canada have observed similar if not greater rates of advancement for Barn Swallows (−2.2 days per decade) in addition to Cliff and Tree Swallows.⁴⁹ The availability of both aquatic (Figure 3C) and terrestrial insects (Figure 3D) inconsistently advanced throughout the breeding cycle over the 25-year record, with estimated advancement varying from 7 to 23 days throughout the season when using quantiles of daily sampled biomass as an indicator of annual insect phenology.

We found no evidence for a loss of total annual biomass for either aquatic or terrestrial insects from 1989–2014

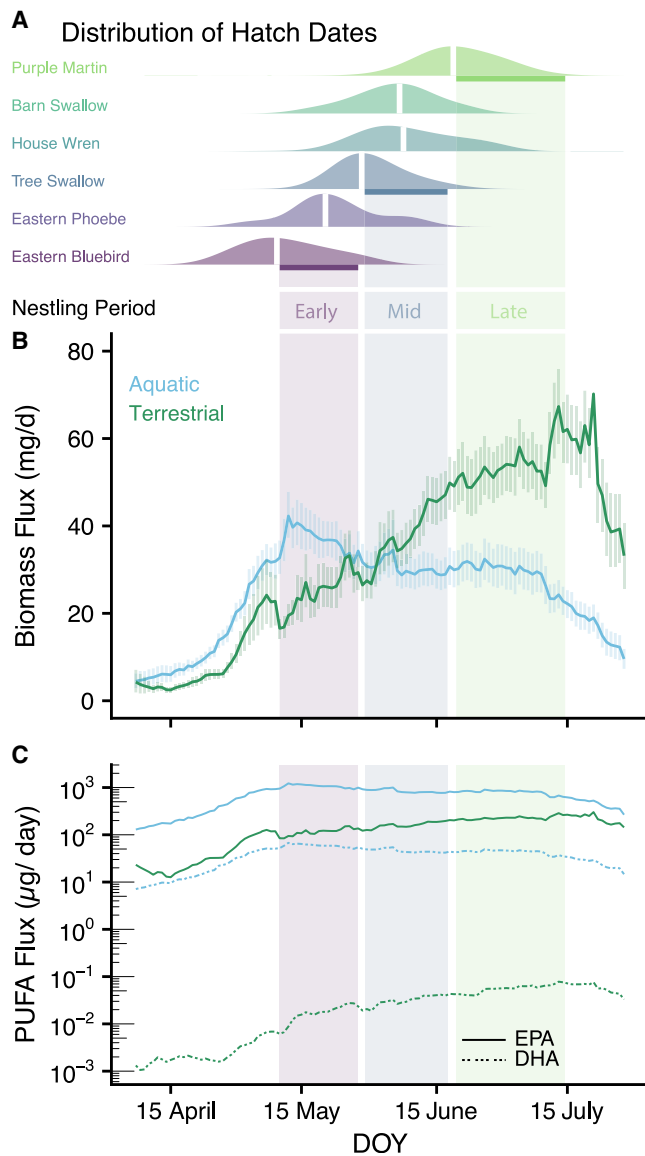


Figure 2. Breeding phenologies of insectivorous birds and seasonal changes in aquatic-terrestrial insect flux

(A) In Ithaca, NY, the timing of reproduction varies considerably between species and spans over 13 weeks (egg hatch dates of first attempts depicted). Density plots are based on recorded hatch dates and the period of average offspring provisioning⁴⁷ is the colored horizontal line.

(B) Aquatic (blue) increases more rapidly and peaks earlier than terrestrial insect flux (green), which tends to increase more linearly over the sampled time. Daily averages and 95% confidence intervals calculated using a non-parametric bootstrap between 1989 and 2014 are shown.

(C) The availability of nutrients such as EPA or DHA depends almost entirely on aquatic insect biomass (blue lines), as the concentration of n-3 LCPUFAs is often more than an order of magnitude greater than in terrestrial insects (green lines). See also Figures S1 and S2 and Tables S1 and S2.

(autoregressive moving average GAMM, $R^2 = 0.01$; Table S2). However, in both the aquatic and terrestrial insect time series there were proportional increases in total biomass in the first half of the sample season. Specifically, when comparing the two time periods (1989–1998 and 2005–2014), we found a

32.1% increase in total aquatic and 12.9% increase in total terrestrial biomass emerging before 1 June (Figures 3B and 3C) and corresponding declines of 26.7% and 37.5% after 1 June for aquatic and terrestrial insects, respectively (Figures 3C and 3D). In other words, late season biomass production appears to have shifted to earlier in the season resulting in a more punctuated and short-lived pulse of insect emergence (autoregressive moving average GAMM, tensor smooth [week * year], aquatic $R^2 = 0.39$, terrestrial $R^2 = 0.57$, Figure S3; Table S3). The initial spring samples collected each year had consistently higher biomass from 2005 to 2014, whereas samples from later in the season were associated with decreases in overall abundance in both aquatic and terrestrial insects. For example, the biomass of emerging small Nematocera increased by 27% in the early season from 1989 to 1998 compared with 2005 to 2014, whereas they decreased in the late season (after 1 June) by ~41% over the same time span. In addition, throughout the season, we observed decreases in the availability of Ephemeroptera and Trichoptera, although these taxonomic groups tend to be relatively rare and make up less than 1% of the total biomass at our insect sampling site.

In summary, the advancing phenology of insect emergence translates into an increasingly punctuated period of high insect availability at our study site, creating an ever-more elusive target for consumers such as aerial insectivores that must synchronize their reproduction with peak energetic and nutrient availability. Most notably, these asynchronous seasonal shifts in insect availability have resulted in decreases in n-3 LCPUFA export from aquatic ecosystems later in the season.

Compensatory flux from terrestrial ecosystems is not nutritionally equivalent

Aquatic insects have an outsized nutritional impact on consumers in terrestrial ecosystems and offsetting their losses would require orders of magnitude increases in export from terrestrial insects (Figure 4). For example, a 20- to 34-fold increase in the biomass of EPA-poor terrestrial taxa, such as Hemiptera, would be required to offset losses of EPA-rich aquatic taxa, such as Ephemeroptera or Nematocera. However, insectivorous consumers such as birds are unlikely to be able to increase their foraging and food intake at rates required to compensate for this loss (Table 1) because they are limited not only in the amount of time they can spend foraging, but also physically in terms of their maximum gut capacity and processing rates^{50,51} and, in the case of flying birds, their overall mass.⁵² In contrast, the loss of EPA-poor terrestrial taxa, such as many Coleoptera, could easily be offset nutritionally by a more reasonable 13% increase in Nematocera or other aquatic taxa. Thus, from the nutritional perspective of consumers, changes in insect community composition and phenology can have equal or even greater impacts than losses of biomass alone. While losses of EPA and/or DHA-rich taxa are likely to be most problematic for consumers that require n-3 LCPUFA directly from diet, species that can synthesize their n-3 LCPUFA will also incur additional energetic costs of synthesis if they lose dietary sources of these compounds.⁴² Freshwater ponds, lakes, estuaries, and wetlands around the globe have been modified and degraded by increased human activity for decades, and biodiversity and abundance of key animals are declining often at a faster rate

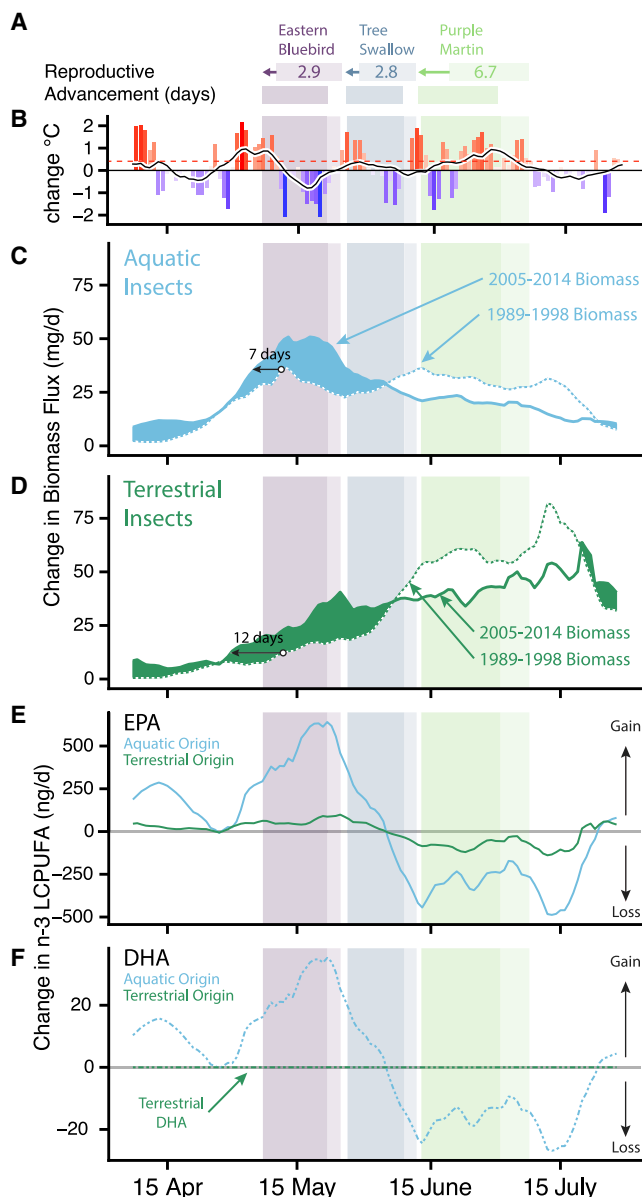


Figure 3. Absolute changes in reproductive timing, insect emergence, and n-3 LCPUFA availability

(A) Three of the study species have significantly advanced reproduction over the last 25 years, with two others (Eastern Phoebe and House Wren, not depicted) showing non-significant trends toward earlier breeding. The lighter shaded region depicts the model estimate for chick provisioning from the beginning (1989) and the darker from the end of our time series (2014).

(B) There is uneven spring warming in the region, with a seasonal average increase of 0.24°C between 1965 and 2014 (dashed red line). The black line is difference in 7-day mean temperature between 1965–1998 and 2005–2014, and the bars denoting the daily difference between these time periods.

(C) Mean daily aquatic insect emergence between 1989–1998 (dashed line) and 2005–2014 (solid line). The solid blue area represents an increase, and white a decrease, of insect emergence over time.

(D) Mean daily terrestrial insect emergence between 1989–1998 (dashed line) and 2005–2014 (solid line). The solid green area represents an increase, and white area a decrease of insect abundance over time.

than those in adjacent terrestrial habitats.⁵³ Coupled with the additional threats posed by climate change, these dramatic differences in nutritional output highlight the importance of conserving nutrient hotspots that are key sources of nutritional diversity across the landscape.

DISCUSSION

The phenology of aquatic and terrestrial insect communities drives the seasonal availability of n-3 LCPUFA, which are important nutrients for a diversity of consumers reliant on insects,^{33,54,55} including avian aerial insectivores.^{11,14,56} We find that the peak biomass of aquatic insect emergence tends to occur earlier in the season and then declines in total output, whereas terrestrial insect biomass progressively increases throughout our observed season. More importantly, EPA and DHA availability is almost entirely driven by the phenology and biomass of aquatic taxa due to the order-of-magnitude differences in n-3 LCPUFA content between aquatic and terrestrial taxa (Figure 2C). However, even for generalist insectivorous consumers where fitness is not limited by n-3 LCPUFA availability, seasonal changes in insect abundance are likely to negatively affect species where reproductive timing and success are also shaped by overall energetic availability.⁵⁷

Most notably, we find that the phenological advancement of aquatic and terrestrial insect communities associated with warming early spring temperatures is asynchronous across the season and appears decoupled from the reproductive phenologies of the birds and, thus, from the demands of insectivorous consumers during reproduction. In addition, both aquatic and terrestrial insect emergence appear to be becoming more punctuated and concentrated earlier in the spring (Figures 3 and S3), driving changes in timing and peak availability of n-3 LCPUFA. The earliest breeding insectivores, such as Eastern Bluebirds, now enjoy greater overall availability of EPA and DHA-rich aquatic insects, whereas mid- to late-breeding species such as Tree Swallows and Purple Martins are experiencing dramatic losses in the availability of these nutrients. Breeding Bird Survey data show that all three swallow species in our study area (Lower Great Lakes/St. Lawrence Plain) have undergone population declines from 1966 to 2015, whereas Eastern Bluebirds, Eastern Phoebes, and House Wrens have either stable or increasing populations.⁴⁸ Thus, understanding the sources of regional swallow declines,⁴⁹ including the phenological nutritional mismatches we document here, is of crucial importance for conservation.

Due to the n-3 LCPUFA richness of aquatic insects, the potential for compensation of n-3 LCPUFA lost from aquatic insects by increased abundance of terrestrial insects is very limited for EPA and practically non-existent for DHA. Certain aquatic taxa, such as Ephemeroptera, Plecoptera, and Trichoptera (EPT), are

(E) Increased emergence of aquatic and terrestrial insects between 1989–1998 and 2005–2014 translates to increased EPA availability early and decreasing availability late in the reproductive season.

(F) Similarly, increased emergence of aquatic and terrestrial insects between 1989–1998 and 2005–2014 translates to increased DHA availability early and decreasing availability late in the reproductive season. See also Figures S1–S4 and Tables S3 and S4.

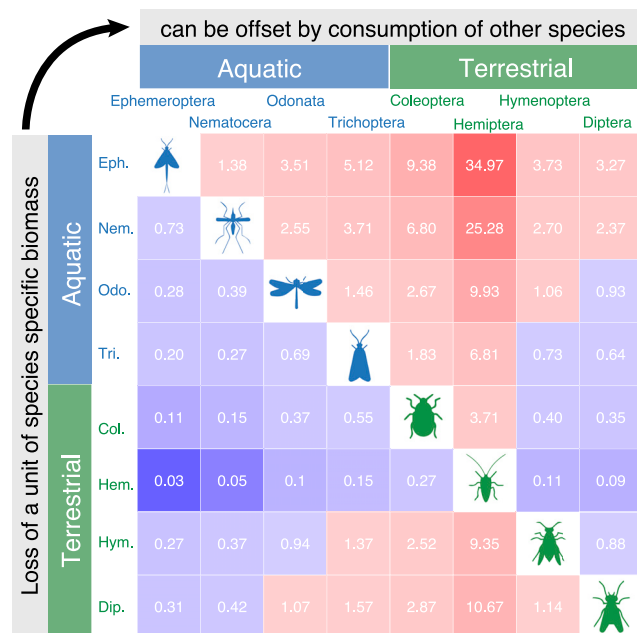


Figure 4. Required increase in aquatic and terrestrial insect biomass to offset hypothetical losses of EPA

Aquatic taxa are rich in EPA, and for example, the loss of Ephemeroptera biomass requires more than a 34-fold increase in EPA-poor terrestrial taxa such as Hemiptera. In contrast, loss of terrestrial insects could be offset by marginal gains in aquatic insect abundance. Numbers are based on the values in Table 1, which provide the mass-specific content of EPA for each of the insect orders.

particularly rich in n-3 LCPUFA. The relatively large body sizes of these aquatic insects also make them preferred food items for many species of birds.^{58–62} Unfortunately, EPT taxa are especially sensitive to anthropogenic disturbances like increased agricultural intensification and urbanization.^{63–65} As a consequence, EPT taxa are some of the first species to be lost from local food webs following disturbance and exposure to agricultural pesticides,⁶⁶ and their nutritional contributions to consumers cannot be readily offset by conservation of terrestrial systems alone (Figure 4).

Overall, our analyses reveal a new dimension of phenological mismatch, one that is related to the spatiotemporal variation in nutritional quality of resources and is highly relevant for fitness variation in consumers.²⁹ Insectivores are largely defined by their foraging strategy rather than their reliance on a single dietary taxon. Thus, seasonal nutritional availability for generalist insectivores in terms of n-3 LCPUFA is largely driven by the phenology of aquatic systems. Nutritional phenological mismatches are of particular concern for aerial insectivores because this entire group of birds, including several of the species we focus on here, is already experiencing declines across both North America and Europe.^{43,44} While the causes of these declines are likely complex and multifaceted,⁶⁷ changes in the phenology and availability of insects are likely to have widespread effects across this group of birds. Aerial insectivores and other insect predators are now chasing a moving resource target that, even when matched in time, may provide them with more limited resource availability due to declines in insect abundance as well as

more limited resource quality due to losses of nutritionally critical taxa. Our results suggest that even if some consumers can match the pace of advancement of certain lower trophic level species, they may still find themselves facing lower quantities of the most nutritionally important resources.

Our findings point to the critical importance of examining changes in insect availability and phenology simultaneously and translating such changes into the currencies that are most relevant for consumer fitness. Recent studies have demonstrated that aquatic and terrestrial resources, including emerging aquatic and terrestrial insects, are not nutritionally substitutable for many consumers, such as insectivorous birds.^{11,14,42} Here, for the first time, we show that shifts in the relative availability and phenology of aquatic and terrestrial insects in response to a changing climate are likely to have major fitness consequences for the breeding success of aerial insectivores, especially those that breed in middle or late season that rely on specific nutrients directly from diet.

STAR★METHODS

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2022.01.057>.

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AUTHOR CONTRIBUTIONS

Conceptualization, J.R.S., C.W.T., C.W., C.H.G., and B.M.; resources, D.W.W., M.K., D.M.-C., T.P.P., and M.M.-R.; formal analysis, J.R.S., C.W.T., C.W., and B.M.; original draft, J.R.S., C.W.T., C.W., C.H.G., and B.M.; all authors contributed to reviewing and editing of the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Custom analysis and associated data	This manuscript	https://doi.org/10.5061/dryad.cfxpnvx6k
Software and algorithms		
R Project for Statistical Computing	https://cran.r-project.org	N/A
Other		
Observational data on birds	Project Nestwatch	https://nestwatch.org/nw/public/export
Observational data on Purple Martins	MartinWatch	https://doi.org/10.5061/dryad.msbcc2fwq
Daily ambient temperature data	NOAA	https://www.ncdc.noaa.gov/cdo-web/datatools
Land Use Change	USGS	https://doi.org/10.3133/pp1794D
PUFA Concentration data	Manuscript	https://doi.org/10.5061/dryad.crjdfn34q

RESOURCE AVAILABILITY

Lead Contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Ryan Shipley (ryan.shipley@eawag.ch).

Materials availability

This study did not generate unique new reagents.

Data and code availability

Fatty acid concentration data have been deposited at Dryad and are publicly available as of the date of publication. In addition, this paper analyzes existing, publicly available data. The accession numbers for all of the datasets are listed in the [key resources table](#).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Insect Activity Data

We used a 12-m tall Rothamsted aerial insect vacuum sampler at the Cornell Experimental Ponds near Ithaca, New York (42.5043°N, –76.4659°W) to collect insect samples from 1 April to mid-summer, the end of the Tree Swallow breeding season, spanning 25 y from 1989 to 2014, with the sampler inoperable in 1996 and 2004. The insect sampling schedule typically started on 1 April and continued daily through the end of July. The sampler was operated from 1 h after sunrise to 1 h before sunset and samples were collected once per day. All insect sampling methods are subject to some extent of taxonomic or habitat sampling bias, and our 12m vacuum sampler likely captures certain taxa more frequently than others. However, because our insect data were collected using the same methods over 25 years, these biases should be consistent through time and our data should be representative of the phenological changes that are of interest in this study, even if certain taxa are consistently not captured. Although the insects used by the birds are undoubtedly quite diverse, the activity of many insects is affected by variation in ambient temperatures (although see the study conducted by Heinrich and Esch⁶⁸), and the 12m height of the sampler is based on Rothamsted research to provide a regional measure of insect activity free of local irruptive effects. Thus, it provides a uniform integrated daily measure over the entire study period of the numbers and activity levels of insects in the study area. Within each daily sample, individual insects were classified into 1 of 8 insect orders (Table 1) and then grouped into 2 mm size bins, resulting in a total of 613,868 total insect samples in the dataset.

METHOD DETAILS

Insect Classification and Estimates of Biomass

Insects were classified into aquatic or terrestrial based on the habitat of the juvenile stage, however some of the orders contain species that span both habitats. Insects that are classified as aquatic possess a strictly aquatic juvenile stage at the order, suborder, or family level (Nematocera, Odonata, Ephemeroptera, and Trichoptera), thus our estimates are conservative for overall aquatic insect emergence. Due to the irruptive nature of some species, we transformed outlier values by truncating them at the 99th percentile, which involved only 6 daily observations of Hymenoptera and Nematocera over 25 years. In these cases, the sampled daily

emergence was more than several orders of magnitude greater than the emergence the day before or after the outlier event. We then used previously published length-mass regression equations to estimate the total daily biomass for each sample insect order. (Table S1). The equations take the form of a power function to predict mass based on measured linear dimensions –

$$M = aL^b$$

where M is the insect dry mass, L in the body length (mm), and a and b are order specific constants.

Fatty Acid Concentration Data

We quantified the fatty acid contents for each insect samples by extraction as fatty acid methylated esters (FAMES) that were analyzed by gas chromatography (GC) and compared to internal standards of known concentration. A detailed description of the entire extraction/analysis process is provided in Martin-Creuzburg et al.⁶⁹ We measured the concentration of α -linolenic acid (ALA, 18:3n-3), eicosapentaenoic acid (EPA, 20:5n-3), and docosahexaenoic acid (DHA, 22:6n-3) from insects that were representative for each of the sample orders in the long-term daily dataset (Table 1). We averaged these samples to obtain an estimate of the concentration of these 3 compounds (ALA, EPA, and DHA) per g insect dry mass in each insect taxon. We then multiplied taxa specific PUFA concentration estimates with the daily insect emergence dry mass for each taxon to determine the total PUFA emergence from each of the insect orders and habitat realms (aquatic or terrestrial).

Timing of Reproduction Data

Individual nest records were obtained from the Cornell Lab of Ornithology's Nestwatch Program and from Project Martinwatch. From an original 13,204 records within 150 kilometers of the Ithaca, NY field site (Figure S2) – we maximized nest record precision by removing 1.) inaccurate location data and 2.) implausible records such as negative egg or chick counts. This left us with a total of 11,970 records from 1986 to 2020 for 7 representative species. 6 of the selected species (Eastern Bluebird *Sialis sialis*, Eastern Phoebe *Sayornis phoebe*, House Sparrow *Passer domesticus*, House Wren *Troglodytes aedon*, Purple Martin *Progne subis*, and Tree Swallow *Tachycineta bicolor*) have sufficient regional nest records to estimate the seasonal timing of reproduction relative to insect emergence and the change over time. Despite insufficient records to identify a temporal trend, we retained the Barn Swallow (*Hirundo rustica*) to place its reproductive life history within context of the insect emergence phenology and has been the subject of multiple nearby studies adjacent to our sample region.

Regional Temperature Data

We downloaded daily temperature measurements from within 25km of the field site from 1890 – 2020 using the package 'rNOAA' in R.⁷⁰ We averaged the daily minimum (nighttime) and maximum (typically daytime) temperature records to obtain a daily estimate for daily mean temperature. We then split the dataset into two sets, one from 1965 – 1998 and the other from 2005 – 2014 to document the timing and extent of temperature change trends across the annual reproductive season. We included data before 1989 to get a more robust estimate of the typical seasonal temperature to compare with more recent data from 2005 – 2014.

QUANTIFICATION AND STATISTICAL ANALYSIS

Analysis of Daily Insect Emergence

Short-term weather events can have profound effects on the daily flight activity of aerial insects,⁷¹ thus we applied a 7-day rolling median to minimize the effects of inclement daily weather events on sampled insect biomass. We then resampled measured daily capture records from the first ten years of the time series (1989-1998) and the second half (2005-2014) using a non-parametric bootstrap 1,000 times to obtain a mean and 95% confidence intervals for the daily estimate during each of these time periods.

Changes in Land Cover

We compared data from the USGS reanalysis of LANDSAT (<https://doi.org/10.3133/pp1794D>) and more recent land use classification data downloaded from the Multi-Resolution Land Classification Consortium (<https://www.mrlc.gov>). The USGS reanalysis document compares data from 1973 – 2000 and we collected data from the National Land Cover dataset for the years of 2001, 2004, 2006, 2011, and 2013. We then created spatial buffers at distances of 250, 1000, and 2500 meters from the insect sampler to sample different land use categories to calculate percent land use change.

Model construction and evaluation

We used generalized additive mixed models (GAMM, mgcv package in R⁷²) with an autoregressive moving average error structure to test for differences in the annual phenology as well as changes in overall annual biomass sampled for each of the taxa of interest. Due to the nature of insect samples being either zero or positive values, we modeled these data using a Tweedie distribution with p ranges from [1, 2], where 1 is a Poisson process and 2 is gamma distributed. To test for differences between taxa within a season as well as changes over our time series, we used a GAMM with a tensor product smooth between sampled insect mass and year for each taxa. To simplify the calculation of a tensor product smooth⁷³ between annual emergence trends of different insect taxa and the between year trends that occurred from 1989 – 2014, we resampled weekly capture records from each year using a non-parametric bootstrap

1,000 times to obtain a mean and 95% confidence intervals for each week within each year using the R package 'hmisc'.⁷⁴ We checked for the fit of models using the function 'gam.check' within mcgv and used the R package 'sjPlot' to visualize coefficients and model results.⁷⁵

To determine whether there was a significant trend in hatch dates over the time series, we used a generalized linear model ('lm' in base R) and calculated confidence intervals using a bias-corrected and accelerated bootstrap (BCA) by resampling the individual hatch dates 1,000 times using the R package 'boot'.⁷⁶ We inspected for evidence of temporal autocorrelation using the function "acf" in R. For all models, we evaluated the fit by examining the residual versus fitted values and qq-plot for departures from normality, and we visually inspected for equal variance using a spread location plot. We also checked for influential outliers in the data using a scale-leverage plot.