Experimental evidence for a mismatch between insect emergence and waterfowl hatching under increased spring temperatures

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Abstract. By combining a large-scale experimental assessment on timing of insect emergence with long-term monitoring of waterfowl hatching date, we here show that insect emergence is mainly driven by temperature, whereas there is only a weak effect of increasing spring temperatures on inter-annual variability in observations of waterfowl chicks. Hence, a change in timing of the mass-emergence of insects from lakes and wetlands, which is the crucial food source for waterfowl chicks, will likely result in a consumer/resource mismatch in a future climate change perspective. Specifically, we experimentally show that a moderate increase in temperature of 3°C above ambient, expected to occur within 25–75 years, leads to a considerably (2 weeks) earlier, and more pronounced, peak in insect emergence (Chironomus sp). Moreover, by utilizing long-term Citizen Science databases, ranging over several decades, we also show that common waterfowl species are unable to significantly adjust their reproduction to fit future temperature increase. Hence, based on our data we predict a future mismatch between insect emergence and waterfowl species basing their reproduction on temperature. This will have a profound impact on reproductive success and population dynamics of many aquatic birds, as well as on freshwater biodiversity.

Key words: Chironomus; citizen science; climate change; crowd sourcing; hatching; insect emergence; mismatch; waterfowl.

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INTRODUCTION

There are few doubts that on-going climate change will affect consumer-resource relations in most biomes (Estes et al. 2011, Hansson et al. 2013). Specifically, spring, with its rapidly increasing temperatures, is a critical period for consumers since those have to match the maximum abundances of their prey with their own reproduction in order to safeguard the survival and growth of their progeny. Many consumer species rely on a specific and predictable food resource during development, which may lead to a mismatch between the consumer and its prey if they are affected differently by temperature changes, such as in a climate warming scenario (Cushing 1990). Such an example is the almost complete reliance of newly hatched waterfowl chicks on animal (insect) food during their first weeks (Chura 1961, Brinkhof 1997). Emergence of insects, specifically chironomid larvae, in lakes and wetlands during
spring, is generally an immense and reliable food source. Moreover, since chicks of most waterfowl species, irrespective of their diet as adults, are dependent on animal proteins during their first weeks, this resource constitutes a major bottleneck for population growth (Nummi et al. 2000, Gunnarsson et al. 2004). Since emergence of chironomids, which generally constitutes the majority of the food intake by waterfowl chicks (Dessborn et al. 2009), is temperature dependent (Learner and Potter 1974), both the timing and magnitude of emergence may change in a future climate change scenario, potentially creating a severe consumer/resource mismatch.

Individual female waterfowl may be able to adjust laying date, and thereby the hatching of chicks, suggesting that there may be a plasticity in laying date (Oja and Poyya 2007, Drever et al. 2012). It is yet unknown if this plasticity is sufficient to meet future changes in temperature elevation, or if there will be a mismatch between hatching and resource supply. Therefore, we here address the question whether present variance in hatching phenology can meet future environmental changes with respect to the bottleneck of food supply for waterfowl chicks. Most studies on insect emergence are performed in natural systems using emergence traps and although such studies are important, experimental studies specifically addressing insect emergence in a standardised and replicated way are crucial for a general understanding and firm conclusions. In order to provide such data we performed a replicated enclosure study with elevated temperatures as a way to estimate the magnitude and timing of insect emergence from lakes and wetlands in the future. We combined the insect emergence studies with a database analysis of waterfowl observations in order to assess the hatching phenology of some common waterfowl species and their ability to adjust to predicted future temperature changes.

**Methods**

The experiment addressing insect emergence consisted of 24 insulated cylindrical polyethylene containers, with an inner diameter of 0.74 m and a volume of 400 L. The containers were placed outdoors, close to the Ecology Building at Lund University (52°42’ N, 13°12’ E). Sediment, which contained chironomid larvae, was gathered from the nearby Lake Kränkesjön (55°42’ N, 13°28’ E), and thoroughly mixed before spreading a 5 cm thick layer in each enclosure. Lake water was then carefully added to each container. Twelve containers were used to mimic today’s situation (Controls; C-treatment), whereas in another treatment ($n = 12$) we elevated the temperature with 3°C above ambient (T-treatment) in accordance with conservative predictions from IPCC (Christensen et al. 2007). Hence, we aimed to mimic a situation predicted to occur during the lifetime of the coming human generation, i.e., during the period between 2040 and 2090. Each container was aerated using aquarium pumps and distilled water was added to compensate for evaporation. The experiment started 25 March and ended 20 June 2010.

Temperature was controlled by a computerised system measuring the average temperature in control treatments using temperature sensors (National semiconductor LM335AZ), which adjusted the temperature every 10 second in each of the heated enclosures to 3°C above the mean temperature of the control enclosures. Temperature was elevated using 150-W aquarium heaters in each of the heated containers. Each individual heater was on until the water temperature exceeded the desired temperature and then off until the temperature dropped below the desired temperature (for details, see Nicolle et al. [2012]). This means that the temperature was instantly (every 10 sec) adjusted at 3°C difference between control (C) and temperature treatment (T), thereby comparing today’s situation with a future spring scenario (Fig. 1). Mature chironomid pupae first emerge from the sediment to the water surface and then the adult insect fly away, leaving the pupae skin floating at the water surface. Chironomid emergence was therefore quantified by picking pupae skins from the surface of each container twice a week. The pupae were counted and determined to taxa and here we focus on the dominant genus Chironomus, which constituted >90% of the number of hatched insects.

Observations of waterfowl chicks were retrieved from the national Swedish database Svalan (http://www.artportalen.se/birds/) which is based on laymen reports (mainly bird watchers). The website was developed and is main-
tained by the “ArtDatabanken” (the Swedish species information centre), which is a part of the Swedish University of Agricultural Sciences (SLU). Registered users can report their observations directly on the website. In our analysis we have focused on mallard (Anas platyrhincos) and Eurasian coot (Fulica atra; onwards denoted coot). A considerable part of the populations stay in southern Sweden year around, whereas some migrate short distances, generally to continental Europe, during winter. We extracted the first three observations of broods for each year from 2000 to 2013 (n=14) from the database and then calculated the mean first observation for each year. Mean values of three observations was used in order to reduce the impact of occasional very early observations. If three observations were not registered observations from that year was removed from the data set, leading to only 11 years of observation for coot. Using Citizen Science, or “crowd-sourcing” has been increasingly acknowledged as a way to retrieve data which would otherwise not be possible to gather (Cooper et al. 2010, Dickinson and Bonney 2012, Rowland 2012). A main advantage is the rare opportunity to retrieve large numbers of observations, although there are always risks in using common databases. Such risks include that the quality of the data provided may vary among observers. Moreover, the data gathering is not standardized and may also potentially be biased towards more often reporting extreme events and taxa than more ordinary observations. In order to minimize the risks we focused on two very common, easy recognisable species, mallard (Anas platyrhincos) and coot (Fulica atra). Moreover, the mallard duckling counts in our study are based on over 4000 observations, whereas the studies of coot include observations of more than 2500 chicks. In addition, it may be argued that field ornithologists, which are the main contributors to this database, are generally skilled when it comes to bird species identification. Hence, the data reported to this database may constitute some of the more reliable “crowd sources”. Despite the considerable variation in sample size (number of observations per year) there was no effect of sample size on mean date of first observation (r = 0.097 and 0.000 for mallard and coot, respectively).

The chicks of mallard and coot are strongly dependent on insect protein during their first weeks in life (Nummi and Pysa 1993, Brinkhof 1997), specifically coot chicks which, despite

Fig. 1. Mean temperature fluctuations during spring in experimental enclosures at ambient temperature (open symbols) and elevated according to a climate change scenario of 3 degrees increase in temperature (filled symbols). Each treatment was replicated 12 times.
adults almost exclusively utilise vegetative food, rely to more than 70% on insects (Brinkhof 1997). We restricted the observations to Scania, which is the southernmost region of Sweden and includes the area where our chironomid emergence experiment was performed. The region lacks major variations in altitude and is climatologically even, suggesting that the phenology within the region is relatively similar. The mean temperature in April (daily means of hourly measurements) was retrieved from the Swedish Hydrological and Meteorological Institute (SMHI) at the station #5343 Lund (www.smhi.se).

All field data were gathered according to Swedish law, which also states that no specific permissions are required for the type of studies performed and for the localities visited. The field or laboratory studies did not involve endangered or protected species and no live animals were captured or injured during our studies, and therefore no ethical permissions were required.

RESULTS

The total number of chironomid pupae emerged during the season (mean ± SD; 20 April–20 June 2010) was 114.1 ± 38.0 pupae m⁻² at ambient temperatures (C) and 119.2 ± 40.4 pupae m⁻² at elevated temperatures (T), that is, there was no difference in the total number of pupae emerging from the different treatments (t₂₂ = 0.31; p > 0.10; n_c = n_T = 12). In contrast, the timing of the emergence differed considerably between treatments (Fig. 2). Before 23 April only occasional pupae emerged in any of the treatments. However, already 27 April the mean emergence rates were between 10 and 15 midges m⁻² day⁻¹ in the elevated temperature treatments, but this emergence lasted only about 10 days (Fig. 2). In the controls the emergence started about two weeks later, i.e., about 4 May, and the emergence rates were rarely above 6 individuals m⁻² day⁻¹ (Fig. 2). In contrast to the temperature elevated treatments, the first emergence period lasted for almost a month (Fig. 2). Both treatments had a second, less pronounced,
emergence peak of the same species (*Chironomus* sp.), which occurred between 20 and 25 May in the temperature elevated treatment, and about 1–2 weeks later at ambient temperatures (Fig. 2).

There are observations of mallard ducklings already in mid-April, but the main period for first observations of chicks is during the first weeks in May (Fig. 3). Coot are somewhat later
with reproduction and there are only occasional observations of chicks in late April, whereas the major period for first observations of chicks is the second half of May (Fig. 3). The earliest first observations of mallard ducklings is 12 April (years 2002 and 2004) and the latest 25 May (2001), i.e., a variation of about a month. Similarly, the earliest first observation of coot chicks is 27 April (2012) and the latest first observation 19 May (2006). The range in April mean temperatures is 6.0–10.3°C. However, despite a considerable variation in mean April temperatures among years in date of first mean observation of chicks, mallards only adjust this date when April mean temperatures are lower than about 7°C (Fig. 4). In years when April temperatures were higher than 7°C the first observations of hatchlings of both mallard and coot changed little despite a temperature range of between 7°C and 10.3°C (Fig. 4). Long term monitoring data from Lake Krankesjön, situated within the investigation area, show that water and air temperatures are closely correlated: \( r = 0.95; t_{81} = 28.67; p < 0.001. \)

**DISCUSSION**

Emergence of insects, such as chironomids, generally occurs during a period lasting several weeks in spring and it has been argued that many waterfowl species adjust their hatching of chicks to this period (Danell and Sjöberg 1977).

**Fig. 4.** Day (day 1 is 1 April) of first observation (mean of the three first observations each year) of newly hatched chicks in relation to the April mean temperature, i.e., the period when the female develop and incubate the eggs. The upper panel shows mallard, *Anas platyrhynchos*, at April mean temperatures below 7°C (filled symbols) and for temperatures above 7°C (open symbols). The lower panel shows the same metrics for coot, *Fulica atra.*
This synchrony has, however, been questioned since the hatching of waterfowl chicks shows a clear phenology based on ice-out, whereas emergence of chironomids is more erratic (Dessborn et al. 2009). Hence, as the insect emergence occurs over an extended period in spring there might, at the present climate regime, be food enough for chicks irrespective of hatching date. However, as an effect of on-going climate change the pattern of insect emergence may, as shown here, change considerably leading to a mismatch between emergence of insects and feeding opportunities, and thereby survival, for the newly hatched waterfowl. During the first two weeks of their life chicks almost exclusively feed on invertebrate food, and the mass-emergence of insects is the absolutely most important food source (Chura 1961, Nummi and Poyya 1993, Brinkhof 1997). Mortality is often high during these first weeks in life (Brinkhof 1997, Nummi et al. 2000, Gunnarsson et al. 2004) and is generally directly related to the amount of insects available (Brinkhof 1997).

The chironomids in the temperature elevated treatment of our experimental study showed two maxima in emergence rate, one large around 25 April (80% of the emergence) and a smaller (20% of the emergence) about a month later (Fig. 2). In a future perspective most waterfowl chicks will fail to track the main emergence peak in April. However, they may still benefit from the second, much lower, peak of chironomids, although this is unlikely to keep the populations of waterfowl at their present levels, since chick survival is strongly affected by insect availability (Brinkhof 1997, Winkler et al. 2002).

It may be hypothesized that waterfowl should show plasticity in egg laying date in response to spring temperature, i.e., also hatching date of chicks may be temperature dependent. Such adjustments to temperature changes have been shown for many organisms (Stenseth et al. 2002), and if this is valid also for waterfowl we should expect earlier hatching in years with higher, than with lower, temperatures. Our data show that although there is a considerable variation in first chick observation, this variation is only weakly related to mean temperatures above 7°C in April, which is the month when the female is developing and laying eggs. This suggests that at April mean temperatures above 7°C temperature is a weak predictor of hatching day, which has also been found with respect to other species, such as great tit (Parus major; Visser et al. 1998). On the other hand, ectothermic organisms, like insects, are able to rapidly adjust their development and emergence to the prevailing temperatures, whereas homoeothermic organisms, such as waterfowl, are less likely to evolutionary respond to such changes (Buse et al. 1999, Winkler et al. 2002). However, some waterfowl, e.g., mallard, are often considered to be relatively flexible in their breeding time (Sjoberg et al. 2011, Drever et al. 2012). We show here that this is, at least partly, true since both mallard and coot seem to delay their breeding during very cold winters, but, in contrast, show negligible adjustments at temperatures above 7°C (Fig. 4). This means that although both mallard and coot seem to be able to adjust for cooler springs they are likely to mistime the main food resource for their progeny in a rising temperature scenario. We may therefore expect a mismatch between insect emergence and hatching of chicks, since the insect emergence show a strong, whereas waterfowl a negligible, adjustment to increasing temperatures. In broader context this likely leads to population declines in waterfowl, as has been found in e.g., pied flycatchers (Both et al. 2006). However, in both mallard and coot there are a few very early observations of chicks (Fig. 3), and we cannot rule out that these early hatchers will be favoured compared to those hatching later. If so, this will lead to a strong selection for a shift to an earlier hatching date in a future perspective, as early hatched chicks should be able to take advantage of the immense emergence of chironomids. It may also be argued that emerging insects use water temperature, whereas waterfowl may rely more on air temperature as a cue. However, air and water temperatures are tightly coupled, as suggested by data from our monitoring lake (Lake Krankesjöen; $r = 0.95$). Moreover, previous studies have shown that any difference between air and water temperatures is reduced by 50% within three days (Mooij et al. 2005). Hence, although we may expect a short lag phase between temperatures in air and water, they provide an identical cue for both insects and waterfowl.

We conclude that, given the present predictions for climate warming, the major food item
(emergence of chironomid larvae) for waterfowl chicks will appear more than two weeks earlier and show a far more distinct maximum than at present. On the other hand the reproduction of common waterfowl species, such as mallard and coot, show little adjustment to increasing temperatures. This implies that the majority of the newly hatched chicks will not be able to match the insect resource peak, likely resulting in a considerable reduction in waterfowl abundances and biodiversity.

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