

Hatching in dabbling ducks and emergence in chironomids: a case of predator–prey synchrony?

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Abstract It has been hypothesized that dabbling ducks (*Anas* spp.) time breeding to coincide with annual regional peaks in emerging dipterans, especially Chironomidae, which are important prey for newly hatched ducklings. However, this hypothesis has never been evaluated in a replicated lake-level study, including year effects in emergence patterns. We collected duck and invertebrate data from 12 lakes during the nesting seasons 1989–1994 in a watershed in southern Finland. The oligotrophic study lakes are typical of the boreal Holarctic, as are the three focal duck species: mallard *Anas*

platyrhynchos L., widgeon *Anas penelope* L and teal *Anas crecca* L. Hatching of ducklings showed a clear peak in relation to ambient phenology (annual ice-out date of lakes), whereas chironomid emergence was more erratic and showed no clear peak at the lake level, although total watershed-level emergence was somewhat higher before and long after the duck hatching peak. Thus, we find no evidence that ducklings hatch in synchrony with abundance peaks of emerging chironomids. There was large within-year temporal variation in chironomid emergence among lakes, but this was not correlated with ambient temperature. The rank of individual lakes with respect to the abundance of emerging chironomids was consistent among as well as within years, a predictability that ought to make adaptive lake choice by ducks possible. On the lake level, there was a positive correlation between the total amount of emerging chironomids and brood use. We argue that emergence patterns of chironomids on typical boreal lakes are neither compressed nor predictable enough to be a major selective force on the timing of egg-laying and hatching in dabbling ducks. Despite spatial (among-lake) patterns of abundance of emerging chironomids being predictable within and among years, the observed pattern of brood use suggests that other factors, e.g. habitat structure, also affect lake choice.

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Introduction

Ecology abounds with examples of how predator life cycles are adapted to those of their prey. For example, abundance of crucial prey resources greatly influences what time of the year animals in seasonal environments reproduce (Daan et al., 1988). On top of such very broad adaptations to seasonality, some birds exhibit more fine-tuned timing, e.g. so that hatching or feeding of young is timed to distinct peaks in food abundance (Lack, 1950; more recent examples in Visser & Both, 2005). Dabbling ducks (*Anas* spp.) are among the birds hypothesized to time hatching so that ducklings have access to regional peaks in invertebrate food abundance (Rohwer, 1992; deSzalay et al., 2003).

Seasonality is indeed a strong and pervasive selective force, and females that successfully time breeding to a peak in food supply will have an evolutionary advantage (Daan et al., 1988), supposing that such resource peaks are predictable. Prey emergence peaks can occur at the same time each year, or they may possibly be predicted by seasonal cues such as ice-out date of wetlands. Neighbouring wetlands frequently differ in prey abundance; hence, there is also a selective advantage for breeding females to choose the most favourable lake locally, assuming that this relative quality, too, is reasonably predictable from one year to the next. Breeding ducks may be programmed to go to their natal lake (Pöysä et al., 1997), or they may choose lakes based either on previous experience (as a breeder or a duckling; Blums et al., 2002) or on ‘in situ sampling’ after returning in spring but prior to egg-laying. An example of such ‘in situ sampling’ is the immediate response to new beaver ponds by teal (Nummi & Pöysä, 1997).

During the first 2 weeks of life, *Anas* ducklings depend on protein-rich foods to grow and to survive. They then feed primarily on invertebrates found near or on the water surface or on emergent vegetation (Chura, 1961; Pehrsson, 1979; Hill et al., 1987; Gardarsson & Einarsson, 1997; King & Wrubleski, 1998; Nummi et al., 2000), and chironomids (Diptera, Chironomidae) typically make up a large part of the diet of young ducklings (Chura, 1961; Street, 1977). Mortality during this early stage is often very high and food shortage along with harsh weather have been shown to be primary determinants of duckling

survival and growth (Koskimies & Lahti, 1964; Street, 1977; Sjöberg et al., 2000; Gunnarsson et al., 2004). Some empirical studies show that hatching of dabbling ducks is synchronized to a peak in emerging insects (Danell & Sjöberg, 1977; Pehrsson, 1984). The idea of a strong synchrony between these taxa has become a widely held notion in waterfowl ecology, but the evidence to support it remains scarce.

Chironomids sometimes emerge from wetlands in great numbers during fairly short periods (Oliver, 1971). Some of the lakes showing a strong peak in chironomid emergence are very productive, which can be a result of natural changes, e.g. pulses following damming by beavers (Nummi & Hahtola, 2008), or due to anthropogenic influences such as flooding (Danell & Sjöberg, 1977). A distinct peak in chironomid emergence may also be a reflection of low species diversity; individuals of the same species generally emerge fairly synchronously, but different species may have different emergence peaks (Wiederholm et al., 1977; Jónsson, 1987). Some of the studies demonstrating a clear peak in chironomid emergence concern arctic wetlands where, due to short summers, there is a temporally compressed period during which chironomids can swarm (Oliver, 1971; Danks & Oliver, 1972). Most lakes in the boreal Holarctic are mesotrophic or oligotrophic and support fairly low densities of emerging insects as well as duck broods. Hence, the hypothesis that hatching of ducklings and chironomid emergence are synchronized deserves to be assessed using a larger sample of lakes and one that is more representative of the boreal biome.

The issue of chironomid-duckling timing unites old and new paradigms in ecology. Seasonal cycles and timing adaptations were central in evolutionary ecology in the 1970s; the issue of predator–prey synchrony has prevailed in population ecology for decades (Bonsall & Hassell, 2007), and more recently, there has been concern that co-evolved temporal adaptations may become ‘mismatched’ due to different effects of climate change on different taxonomic groups (Visser & Both, 2005; Drever & Clark, 2007). Accordingly, changed temperatures and onset of seasons may alter the time when invertebrates emerge, and if dabbling ducks cannot adapt their schedule to such changes, then reproduction will be less successful and

populations may decline. The annual development of invertebrates is primarily determined by water temperature (Danks & Oliver, 1972) and is therefore likely to respond directly to a change in climate. The breeding period of dabbling ducks, however, may not be as easily adapted to seasonal changes in food abundance at the breeding site. One important reason is that any such adaptation has to be traded off against selective pressures acting in other biomes and at other times of the annual cycle (Arzel et al., 2007, 2009).

We here present the first replicated lake-level, multi-year study of chironomid emergence and breeding dabbling ducks. The study setting and its lakes are representative of vast areas of the Holarctic, and similarly, the three focal species of dabbling duck have a wide geographical range in Eurasia and North America. We test the following predictions based on the hypothesis that hatching of *Anas* ducklings is timed to chironomid emergence: (i) there is a predictable annual peak in chironomid emergence during the breeding season of waterfowl, and (ii) hatching of dabbling ducks is synchronized to such a peak. We also test the related assumptions that (iii) lake-level chironomid abundance in relation to that of nearby lakes is predictable among years and within season, and (iv) brood use is positively correlated with lake-level chironomid abundance.

Methods

Study area

The study was done from 1989 to 1994 in an oligotrophic mid-boreal 39 km² watershed at Evo, in Häme, Finland (61°10' N, 25°05' E). Boreal evergreen forest covers most of the watershed, the remainder comprising lakes (ca. 10% of the area) and mires. Agriculture and human settlement are very limited, and eutrophication impact on wetlands is negligible. Lakeshores are generally steep with sparse emergent vegetation (mainly sedges *Carex* spp.), although a few wetlands are more mesotrophic with narrow stands of horsetails (*Equisetum* spp.), cattails (*Typha* spp.) and reed (*Phragmites australis*). Located in a continental cool climate, all wetlands freeze over in winter and are colonized anew each spring by long-distance migrating ducks. The 51 permanent lakes and ponds in the watershed have been subject to comprehensive ecological studies of waterfowl, fish and beavers (Nummi & Pöysä, 1993; Rask et al., 2001; Elmberg et al., 2003; Nummi & Hahtola, 2008). For the present study, we used data from 12 of these lakes, with the explicit objective that they should be representative of the study area as well as of boreal forest areas throughout the Holarctic. Size of the study lakes ranges from 0.6 to 37.1 ha (shoreline lengths in Table 1). Weather data were

Table 1 Perimeter length and annual brood production of study lakes

Lake	Shoreline length (m)	1989	1990	1991	1992	1993	1994	Broods/km shoreline	Luxuriance score
Vähä Vehkajärvi	1,069	§†	††	§¶††	†	¶		9.35	3.84
Saarisjärvi	1,973	†		§†	§			2.02	4.49
Iso Vehkajärvi	3,528	§¶¶	§¶¶	¶	¶¶	§¶¶	†¶¶	4.25	5.37
Tekumi/Saukonlammi	361	†						2.78	2.10
Iso Ruuhijärvi	1,780			†				0.56	0.98
Keskinen-Mustajärvi	801	†						1.25	0.86
Rahtijärvi	2,110	†						0.47	2.06
Majajärvi	1,138							0.00	0.72
Ylinen-Rautjärvi	3,537	†						0.28	1.66
Pitkänjärvi	2,311							0.00	−1.82
Iso Valkjärvi	763				†			1.31	−2.97
Vähä Valkjärvi	613							0.00	−2.37

Brood symbols: § = mallard, † = teal, ¶ = widgeon. Luxuriance scores for shoreline vegetation are from Nummi & Pöysä (1993)

obtained from the meteorological station at the Evo Game Research Station (see Paasivaara & Pöysä, 2007).

Waterfowl counts

Wetland use and breeding success were assessed by five waterfowl brood counts during the main hatching and brood-rearing period in June and July. We used the seven age classes (1A, 1B, 1C, 2A, 2B, 2C and 3) of Pirkola & Högmander (1974) to assess duckling development, which was subsequently used to back-calculate the hatching date of each brood. Shoreline vegetation of the study lakes is generally sparse, but in order to ascertain that no broods were missed, we used combined point and round counts, as described in Nummi & Pöysä (1995). Observed broods were easily told apart as they were different species and/or age; moreover, most lakes with successful breeding had only one brood per year. For the rank correlation (see results), absolute brood number was transformed to a density index (broods/km shoreline).

Emerging chironomids

The relative abundance of insects emerging from their pupal stage was measured by floating emergence traps composed of a funnel with the wide end in the water and an open, net-covered bucket above water (Danell & Sjöberg, 1977; Nummi & Pöysä, 1993). In each lake, two traps were placed 2–3 m apart in a section of the shoreline with the most ‘lush vegetation’, and two traps were placed in an area with sparse vegetation. Most of the shoreline in the study lakes has sparse vegetation; hence, the ‘lush vegetation’ sampled represents the locally superior foraging microhabitats for dabbling ducks. Traps were placed ca 1 m from the shore, and they were emptied every week. Since emergence traps were continually in operation during the annual study period, which generally lasted from late May to July, emerging insects accumulated between the occasions when traps were emptied, and no peak was therefore missed.

By numbers, chironomids and a very few similar-sized Diptera made up 94% of the invertebrate catch. These other Diptera were pooled with the chironomids for the analyses in this study (henceforth collectively called “chironomids”). The remaining

invertebrate catch consisted of Trichoptera, Ephemeroptera and Odonata, and these were left out of the analysis.

Chironomid larvae stay dormant as long as ice covers lakes (Jónasson, 1970). In order to make the among-year analysis phenologically comparable, emergence was examined in relation to days after ice-out rather than by calendar date. For this, we used ice-out dates from Lake Rautjärvi in the middle of the study area (see Elmberg et al., 2005; Heikki Koivunen, unpublished data). In our study area, ice-out date may differ somewhat in a given year between nearby lakes due to size and hydrology, but it is correlated within a region. For example, the regression of ice break-up dates between two lakes 30 km apart (ca. 80–100 km from our study area) was $Y = 1.0064X - 0.95$; $r^2 = 0.936$; $n = 40$ years (1961–2000), the average yearly difference between the lakes being less than 1 day (Korhonen, 2005, Fig. 11). In general, in Korhonen’s (2005) data, the correlation of ice break-up dates of lakes less than 50 km apart is $r^2 > 0.90$. Hence, we are confident that using the ice-out date from only one lake does not cause serious errors in our analyses.

Data analysis

The influences of weather and ice-out date on chironomid emergence were explored in two complementary ways. First, we performed an analysis of covariance (ANCOVA) in which weather and ice-out date were included as covariates and year as a factor. As the data were not normally distributed, not even after traditional transformations, we used rank-transformed data (emergence, weather and ice-out date) in the ANCOVA as suggested by Conover & Iman (1981) (RT-1 type ranks where all of the observations are ranked together). Second, we used Spearman’s rank correlation to assess the relationship between emergence and weather and ice-out date within each year separately. Average weekly air temperature was used as a weather index, since both day and night temperatures affect water temperature. Days since ice-out were matched with the weekly values of emergence. Spearman’s rank correlation was also used to assess the association between lake level brood density and chironomid abundance. We used a rank concordance test to study the predictability of emergence among and within years; in other words, (1) will a breeding lake with plenty of

food also be good next year? (2) is it possible for the female to estimate how good a potential rearing lake will be later in summer by ‘sampling it’ in the early season?

Results

The total number of dabbling duck broods on the 12 study lakes ranged from three to ten per year, and they comprised 13 widgeon (*Anas penelope*), 7 mallard (*Anas platyrhynchos*) and 15 teal (*Anas crecca*) broods (Table 1). A few lakes hosted most of the broods, whilst a few were without throughout the study (Table 1). There was a general annual hatching peak for dabbling duck broods, but it was rather prolonged and occurred 36–56 days after ice-out (pooled data for all years; Fig. 1). Mean hatching date for the three duck species differed somewhat, with mallard being the earliest and teal the latest.

Pooled over years and lakes, and when related to annual ice-out date, chironomid emergence was fairly even over the annual study period (Fig. 1). When plotted against calendar date instead, chironomid

emergence appeared more erratic, whereas duckling hatching showed an even more well-defined peak (neither shown), though still without any connection to chironomid emergence.

By pooling chironomid emergence for all lakes and years, some information may be lost, though, e.g. lake-level peaks may be masked. To examine the possible occurrence of emergence peaks at the lake level, we used data from the most productive lake in terms of chironomid emergence to illustrate annual fluctuations in the latter. However, we did not find any indication that hatching of ducklings was synchronized to chironomid emergence in this case, and there were no regularly occurring peaks in the latter (Fig. 2).

There is a general trend of increasing water temperature from May through late July in the study area. However, an ANCOVA including weekly temperature and days after ice-out as covariates and year as a factor revealed that weekly temperature ($F = 0.35$, $P = 0.55$) did not affect weekly emergence levels of chironomids, whereas days after ice-out ($F = 3.77$, $P = 0.053$) had some impact and year ($F = 3.55$, $P = 0.004$) had a strong impact on

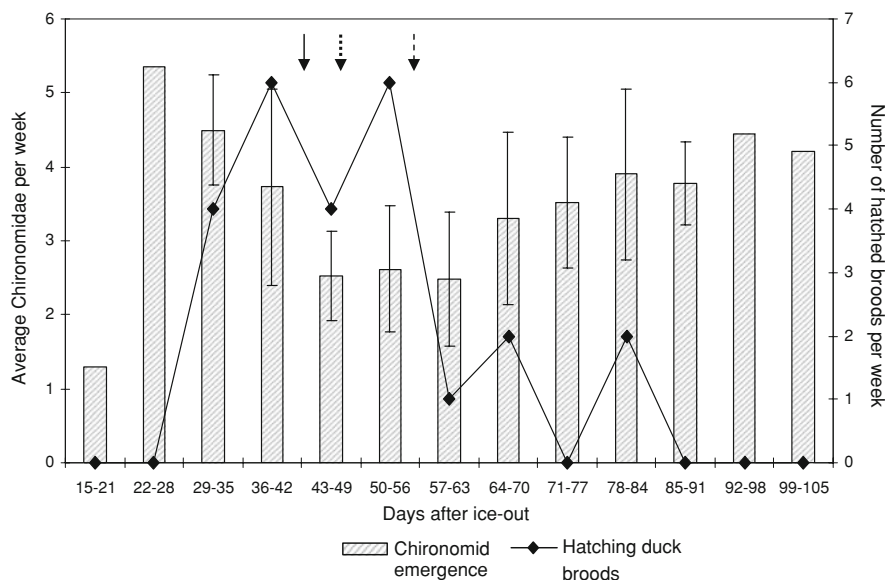


Fig. 1 Hatching of duck broods and abundance of chironomids emerging from their aquatic phase in relation to the number of days after ice break-up. *Left y-axis*: mean emerging Chironomidae per lake and trap pooled over all six study years. *Right y-axis*: total number of *Anas* broods hatched per week based on back-calculation of age determination of ducklings

(data for all 6 years and all three duck species pooled). *Error bars* (S.E.) represent between year variation of weekly values and are missing from early and late periods due to small sample size. The *arrows* represent the species specific average brood hatching days after ice out: →, Mallard; --→, Teal; ···→, Widgeon

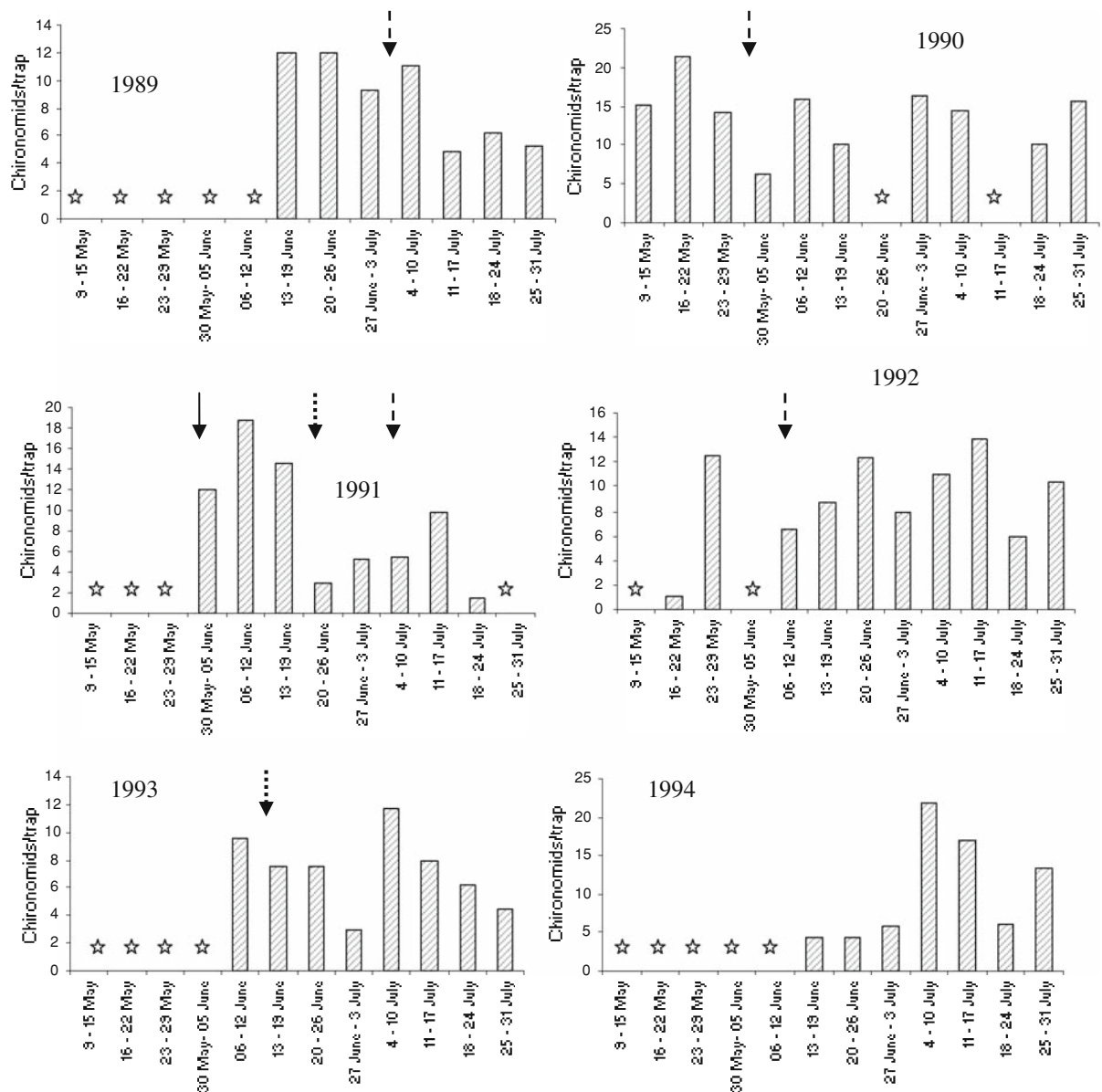


Fig. 2 Annual patterns of weekly chironomid emergence in Vähä Vehkajärvi, the most productive lake in terms of broods/km shoreline and with respect to chironomid emergence. The arrows represent hatching of single broods by species: →, Mallard; --→, Teal; ···→, Widgeon. Stars represent periods when

no emergence sampling was carried out. In 1992, data are missing from June 5th due to broken traps. Annual ice out dates: 25 April 1989; 17 April 1990, 3 May 1991, 5 May 1992, 3 May 1993, 29 April 1994

weekly emergence levels of chironomids (ANCOVA, full model $r^2 = 0.038$, $F = 3.17$, $P = 0.003$). On an year-by-year basis, there was a positive correlation between mean catch and average air temperature in only one year, and moreover, there was no consistency in sign (Spearman rank correlation: 1989: $r_s = -0.66$, $P = 0.16$; 1990: $r_s = 0.32$, $P = 0.37$;

1991: $r_s = -0.62$, $P = 0.10$; 1992: $r_s = 0.01$, $P = 0.98$; 1993: $r_s = 0.81$, $P = 0.02^*$; 1994: $r_s = 0.68$, $P = 0.09$). Similarly, there was no consistent pattern amongst the annual correlations between mean catch and days after ice-out (Spearman rank correlation: 1989: $r_s = 0.09$, $P = 0.44$; 1990: $r_s = -0.22$, $P = 0.06$; 1991: $r_s = -0.15$, $P = 0.17$;

1992: $r_s = 0.13$, $P = 0.20$; 1993: $r_s = 0.25$, $P = 0.01^*$; 1994: $r_s = 0.15$, $P = 0.19$).

In many landscapes rich in wetlands, lakes with abundant invertebrate prey are regularly favoured by breeding ducks for brood rearing (Danell & Sjöberg, 1982a; Nummi & Pöysä, 1995; Nummi & Hahtola, 2008). Indeed, we found a general positive correlation between brood density and number of emerging chironomids on the lake level (data pooled for all years for each lake; $r_s = 0.613$, $P < 0.05$, $n = 12$), although lakes with the highest density of broods were not always the most productive in terms of chironomid emergence (cf. Figs. 3, 4; Table 1).

The relative quality of the Evo study lakes with respect to chironomid emergence was predictable among years in the sense that a certain lake kept its rank relative to other lakes (Kendall's $W = 0.60$; $P < 0.001$; cf. Figs. 3, 4). Similarly, prey abundance early in a specific season was a good predictor of a lake's quality as a duckling foraging site later in the same season. In other words, study lakes generally kept their rank also within seasons (Kendall's W ranging from 0.41 to 0.65; $P < 0.001$ in all cases, $n = 6$ years and 12 lakes per year).

Discussion

We found that the three studied species of dabbling ducks had a fairly prolonged hatching peak when watershed-level data were related to ambient

phenology on an annual basis. However, there was no corresponding peak in chironomid emergence, but rather a seasonal pattern of moderately higher values in early spring and mid-summer. Neither of these periods of higher abundance overlapped with the period when most ducklings are 1–14 days old, i.e. when they are in their most sensitive period and hypothesized to benefit from a chironomid emergence peak (Danell & Sjöberg, 1977). Lake-level emergence patterns showed much variation within and among years, but again with no obvious peaks, including in the lakes producing the most broods (Fig. 1). However, chironomids may be available in the vegetation for some time after having emerged (Danell & Sjöberg, 1982b).

The hatching of broods appears to occur around the same time each year, as the peak was more pronounced when using calendar dates instead of days after ice-out. This indicates that, rather than being dependent on the spring conditions on the breeding ground, dabbling ducks largely time their nesting to cues related to photoperiod. In this study, teal has the latest hatch dates, which is probably due to re-nesting after initial clutch failures.

Looking at annual lake-level data, there was great fluctuation in chironomid emergence, but these fluctuations were not influenced by weekly changes in air temperature. Water temperature and light intensity are primary determinants of development speed of chironomid larvae (Danks & Oliver, 1972; Learner & Potter, 1974; Hodkinson et al., 1996). Shading, wind

Fig. 3 Between-year variation in mean chironomid emergence (animals per trap and week) in lakes that produced on average at least 0.3 duck broods per km shoreline. In 1989, Vähä Vehkajärvi was flooded by a beaver dam, which explains the increase in emergence the following year

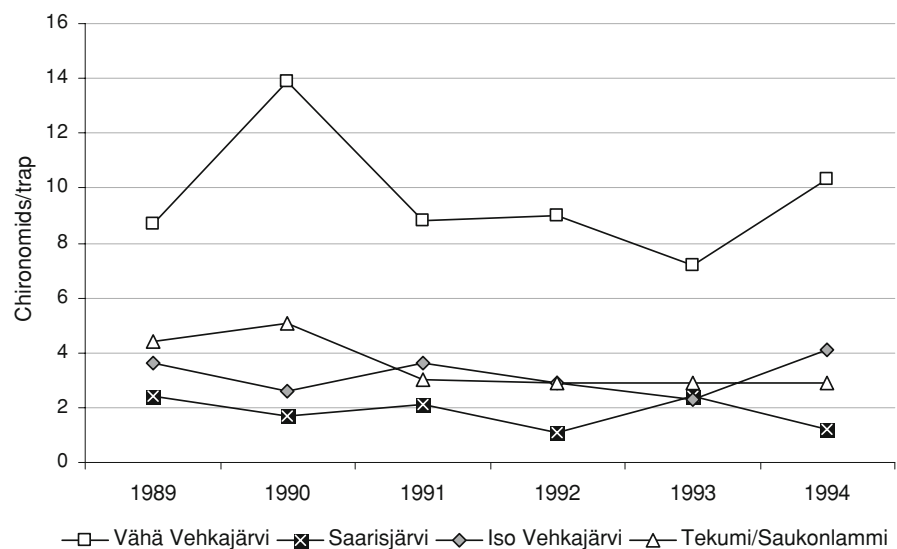
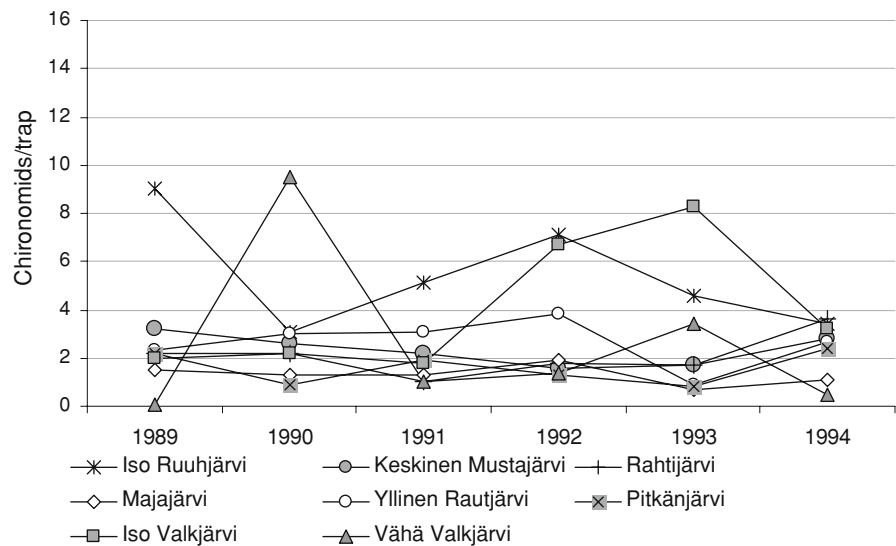


Fig. 4 Between-year variation in mean chironomid emergence (animals per trap and week) in lakes with less than 0.3 broods per km shoreline. Iso Ruuhijärvi had beavers prior to 1989 (1984–1988). In Iso Valkjärvi, half the lake suffered from fish death between 1991 and 1992. In Vähä Valkjärvi, the fish population recovered from acidification only in 1992



exposure, bottom topography and depth of individual lakes can therefore have a strong impact on emergence patterns (Armitage, 1971; Danks & Oliver, 1972). Some of these factors can rapidly alter conditions for developing chironomids and ultimately affect the number emerging, thus increasing fluctuations within a year and reducing predictability of annual peaks (Sjöberg & Danell, 1983, Fig. 2). It seems very unlikely that among-lake and between-year variation in temporal emergence patterns can be predicted by dabbling duck females about to lay eggs, thus making it difficult to time hatching to optimal food resources on an annual basis.

Yet, timing of hatching does have strong fitness consequences in dabbling ducks (Rohwer, 1992; Dzus & Clark, 1997; Hoekman et al., 2004). Elmberg et al. (2005) found that early breeders of teal in the present study area generally had higher reproductive success. Street (1977), on the other hand, demonstrated that mallard ducklings in a gravel pit system in Britain had very low survival if they hatched before the annual peak in invertebrate emergence. Ducklings are further sensitive to harsh weather (Koskimies & Lahti, 1964; Gunnarsson et al., 2004), putting a likely penalty on early hatching due to the higher chances of experiencing episodes of inclement ambient conditions. Timing of hatching may also be constrained by female condition prior to egg-laying; that is, her ability to accumulate energy reserves may be limited by conditions at wintering and migration sites (Arzel et al., 2006). Hence, optimal timing has

to be considered from a total fitness perspective that includes the costs for females as well as the factors that may influence survival of nests and ducklings (Rohwer, 1992; Kokko, 1999). Even if hatching and chironomid emergence synchrony were the main determining factor affecting duckling survival, other factors influencing breeding ducks may lead to suboptimal timing.

Most chironomid species hatch and swarm during short seasonal intervals. However, different species have different swarming periods (Oliver, 1971; Learner & Potter, 1974; Wiederholm et al., 1977; Jónsson, 1987), and if a wetland is dominated by one or a few species, then a peak in total emergence is likely to be more evident. Many previous studies in which a temporal peak in insect emergence has been found were carried out in shallow ponds or flooded areas without fish (Danks & Oliver, 1972; Danell & Sjöberg, 1977). It is possible that such wetlands are dominated by a few species of chironomids, whereas most temperate lakes probably have more species, the hatching peaks of which overlap to produce a more even temporal emergence pattern.

Vähä Vekjärvi was flooded by beavers during the first year of the study. This may partly explain the increased levels of emerging chironomids in 1990 (Fig. 3). Recently flooded wetlands have a higher general production, resulting in a more distinct chironomid emergence peak (Danell & Sjöberg, 1977; Sjöberg & Danell, 1983; Nummi, 1992; Nummi & Pöysä, 1995).

Although we found no evidence of temporally predictable emergence peaks, relative lake quality with respect to chironomid emergence was highly predictable, within as well as among years. Hence, females in our study system ought to be able to make adaptive choices of nesting lake based on previous experience as well as on in situ sampling of benthic chironomid larvae after arrival in spring (Pöysä et al., 2000). Some of the lakes supporting broods did not have particularly high production of emerging insects. However, they did have quite high abundance of benthic invertebrates (Nummi & Pöysä, 1993), which are also known to enhance duckling survival (Cox et al., 1998; Nummi & Hahtola, 2008). Some of the most productive lakes in terms of chironomid emergence were not consistently favoured as brood-rearing habitats, and one of the lakes with broods was among the least productive (Saarisjärvi). In similar boreal lakes, Gunnarsson et al. (2004) were able to increase duckling survival by adding food, a result implying that overall food limitation may occur. In addition, we suggest that habitat structure may have influenced rearing lake choice in the present study, so that lakes with more vegetation may be favoured over those with just more food resources (Elmberg et al., 1993; Nummi & Pöysä, 1993). Indeed, brood density was positively correlated with an index describing lake-specific vegetation luxuriance ($r_s = 0.697$, $n = 12$, $P < 0.01$; data in Table 1). Note, though, that vegetation luxuriance and chironomid abundance were not correlated between lakes ($r_s = 0.154$, $n = 12$, $P > 0.5$); hence, each of them affected lake use by broods. This indicates that, from a duckling's point of view, a lake has to offer emergent vegetation as well as emerging chironomids to be truly attractive. We speculate that a causal link between these two patterns is that such lakes have chironomids as well as luxuriant vegetation from which insects can be gleaned by ducklings (cf. Danell & Sjöberg, 1982b). This view is supported by the fact that lakes with sparse shoreline vegetation did not have many broods although they sometimes had numerous insects (Vähä Valkjärvi (in 1990), Iso Ruuhijärvi).

Conclusions

Our study examined the relationship between chironomid emergence and hatching of ducklings in

lakes typical of much of the boreal region. We found no evidence for a predictable emergence peak, neither on lake nor on watershed level, even though hatching of ducklings was temporally concentrated. Our study is the first examining typical boreal wetlands; previous work focussed on recently flooded wetlands (Danell & Sjöberg, 1977; Sjöberg & Danell, 1983), wetlands in agricultural landscapes (Jacobsen, 1991) and gravel pits (Street, 1977). Even though our study area is limited to a small part of the boreal region, we argue that our choice of lakes and the study design comprising data from 12 wetlands over 6 years gives a representative picture of emergence and hatching patterns of chironomids and ducklings in similar systems. We did not find any convincing evidence that chironomid emergence is a major factor influencing the timing of hatching of dabbling duck broods; however, more studies are needed in other regions and biomes to establish the generality of our conclusions. We also argue that chironomid emergence in the studied system is not temporally predictable enough to invoke temporal adaptations of the timing of nesting in breeding dabbling ducks. However, spatial (among-lake) patterns of relative lake quality, based on chironomid emergence, were predictable within and among years.

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