

Early breeding teal *Anas crecca* use the best lakes and have the highest reproductive success

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Teal (*Anas crecca*) broods were studied in 1988–2003 in a boreal watershed comprising 51 permanent wetlands. Brood size of near-fledged ducklings was negatively related to the hatching date, i.e. early pairs had higher reproductive success than late pairs. However, brood size of newly hatched ducklings was not related to the hatching date, implying that the advantage of early breeding is due to processes operating during the brood stage rather than during nesting. Half of the lakes never produced a brood, and among the 26 lakes that actually did, two ‘preferred’ lakes generated 44% of the broods and 55% of the near-fledged ducklings. Early broods were over-represented on such ‘preferred’ lakes, and late broods over-represented on ‘less preferred’ lakes. Our study suggests that lake selection and early nesting may have important fitness consequences in teal.

Introduction

One of the few ‘universal truths’ of temperate avian ecology is that early nesters in a given population have higher reproductive success than those nesting later in the season; i.e. that early breeding confers a fitness advantage (Daan *et al.* 1986, Dzus & Clark 1998, reviews in Rohwer 1992 and in Kokko 1999). A number of more or less mutually exclusive hypotheses have been put forward to account for this pattern, focussing

on such diverse aspects as egg formation, general energetics, incubation energetics, re-nesting capability, predator avoidance, nest site availability, and timing hatching to food abundance peaks (review in Rohwer 1992). Recent work has highlighted the evolutionary trade-off between higher production of young in early broods and the price their parents may pay by arriving when conditions are still poor, i.e. before the actual cost-minimizing date (Kokko 1999, Drent *et al.* 2003). Further, it may be that only good ter-

ritories/habitats can successfully support early nesters, and that such sites are generally favored by early breeders or first settlers. This point has theoretical (Fretwell & Lucas 1970) as well as some empirical support (O'Connor 1985) in the general literature on habitat selection.

In general terms, breeding success and reproductive output in temperate waterfowl have been documented in hundreds of papers (review in Batt *et al.* 1992), and there is also a fairly large number of studies addressing how different aspects of reproduction are affected by nesting date. A majority of the former favors the view that clutch size, nest success, and number of ducklings fledged all decline the later a clutch is initiated (e.g., Toft *et al.* 1984, Rohwer 1992, Rotella & Ratti 1992, Sayler & Willms 1997, Dzus & Clark 1998, Krapu *et al.* 2000, 2004, Blums *et al.* 2002). Supposing that these trends correlate positively with recruitment into the breeding population, there would be a general fitness advantage to early breeding in temperate waterfowl. However, the vast majority of studies supporting this pattern has been carried out in North American prairie habitats, where many nesting ponds are ephemeral or otherwise offer conditions that vary among years. Permanent wetlands in forested landscapes are perhaps home to the majority of breeding ducks throughout the Holarctic, but these habitats remain little explored in the context of reproductive success *versus* nesting date (but see Toft *et al.* 1984 and Milonoff *et al.* 1998). Considering this bias in geography and breeding habitat, we argue that there is still no general picture of how reproductive output in temperate waterfowl is related to the timing of nesting. This opinion is supported by the fact that some studies from the North American prairies have indeed failed to document any seasonal decline in nesting success and duckling survival (e.g. Klett *et al.* 1988, Mauser *et al.* 1994, Gendron & Clark 2002).

The teal–green-winged teal superspecies (*Anas crecca/carolinensis*) is one of the world's most numerous and widely distributed ducks (Delany & Scott 2002), breeding in prairie as well as in forest wetlands throughout the Holarctic. It is thus an excellent candidate for exploring general patterns in temporal effects on reproductive success. Despite this, very little has been

published about its general post-nest breeding ecology anywhere, e.g., patterns of duckling mortality and brood size of near-fledged ducklings (Hildén 1964, Cramp & Simmons 1977: p. 502, Danell & Sjöberg 1979, Fox 1986, Nummi & Pöysä 1995). There is only one study explicitly addressing temporal effects on breeding success (Toft *et al.* 1984), but it concerns newly hatched ducklings, which may be a less relevant measure of breeding success than older, near-fledged, ducklings.

Using teal data from a long-term waterfowl project conducted in a boreal watershed comprising permanent wetlands, we here test the following general predictions about nesting date and habitat selection: (1) early broods will produce more near-fledged birds than late broods, and (2) early broods will be over-represented on preferred lakes (i.e., those that most often have broods), and late broods will be over-represented on less preferred lakes.

Methods

Study area

This study was carried out in 1988–2003 in an oligotrophic watershed (area 39 km²) at Evo in southern Finland (61°10'N, 25°05'E). All 52 permanent lakes and ponds within the watershed were included, except for one with obvious human disturbance (lake Kaitalammi at the Evo Game Research Station). The total lake area is 290 hectares and the total shoreline length is 50 775 m (mean lake area 5.6 ha, range 0.1–49.5 ha, only nine lakes larger than 10 ha). Boreal evergreen forest covers most of the watershed, with lakes and mires being mixed in. Agriculture and human settlement are very limited and local, hence also lake eutrophication and vegetation change. Lakeshores are generally steep with little emergent vegetation (mainly sedges *Carex* spp.), although a few lakes are more mesotrophic with narrow stands of horsetail (*Equisetum* spp.), cat-tail (*Typha* spp.), and reed (*Phragmites australis*). Located in a continental cool climate, all wetlands are frozen over from November to late April, and they are “colonized anew” each spring by long-distance migrating ducks. We regard

the waterfowl populations in the watershed as closed during the breeding season, with negligible immigration and emigration of adults and broods. However, broods may sometimes move between adjacent lakes within the watershed (*see below*).

Waterfowl counts

Each year breeding success was monitored by five brood counts in June–July (combined point and round counts as described in Nummi & Pöysä 1995). We used the seven age classes (1A, 1B, 1C, 2A, 2B, 2C, and 3) of Pirkola and Högmänder (1974) to assess duckling development, i.e. a combination of schemes in Gollop and Marshall (1954) and Linkola (1962). Keeping broods separate was generally simple in the field, and subsequent brood history reconstruction was similarly straightforward because: (a) pair counts done earlier in the season showed that most lakes had only one or no nesting pairs, (b) most lakes had sparse aquatic and shoreline vegetation, making underestimation of brood number unlikely, (c) most lakes with successful breeding had only one brood each year, (d) duckling number and age in combination made confusion of broods unlikely in the few instances when there were two or more broods on a lake, and (e) many broods were on lakes that were isolated from other lakes with a brood, i.e. there were no or only empty lakes in between. The very few cases in which there were several broods of the same age on a lake or on a neighboring lake were left out of the study.

Although the duration of the flightless period in teal ducklings may vary (Pirkola & Högmänder 1974 *versus* Glutz von Blotzheim 1990), we used the mean of 36 days of the former authors to estimate the average duration of each age class at five days. This, in turn, was used for each observation of a brood to back-calculate the hatching date, assuming that all broods were mid-class when observed. Accordingly, a 1C brood seen on 22 June, was estimated to have hatched 5 + 5 + 2.5 days earlier, i.e. on 10 June. When ducklings approach fledging in age class 3, ageing becomes more imprecise, hence the analyses below refer only to ducklings in age

classes 1A–2C. We used counts of ducklings in age classes 2A–2C to estimate fledging success, although the former are still pre-fledglings. This is justified by the fact that many previous studies have shown that duckling mortality is very limited after the first 10 days of life, and by our own observation that brood size did not change much after age class 1A (*see below*).

Prediction 1: early broods produce more fledglings than late

For this analysis we used data only from years with three or more broods observed in age class 2A–2C. This left us with data from 40 broods from 1988, 1989, 1991, 1992, 1994, 1995, 1998, 1999, and 2001. We used only the first sighting of each brood, and we then z -standardized the Julian hatching date and brood size within years to compensate for differences among years in the relative earliness of spring.

Prediction 2: early broods will be over-represented on preferred lakes

Lakes were ranked according to how many broods were produced on them over the 16 years. Those that never had a brood were excluded from the analysis. Remaining lakes were divided into two categories, each representing roughly half of the broods recorded: ‘preferred’ and ‘less preferred breeding lakes’ (*see Results and Table 1*). Estimated hatching dates were then compared within each year and between lake categories with a multiple-year pair-wise test, making it unnecessary to compensate for extreme weather events and other phenological variation among years.

Statistical procedures

Some broods were observed more than once, that is in two or more age classes. Data from such repeated sightings were used to calculate the age-class specific brood size and hatching date (Tables 2 and 3), but in all tests we used only data from the first sighting of each brood in order

not to violate statistical independence. Tests were run with the SPSS 11.0 and SYSTAT 10.0 statistical software packages. All significance levels are for two-tailed tests.

Results

General

Of the 51 lakes in the watershed, 25 never had a teal brood over the 16 breeding seasons. On the other 26 lakes a total of 95 broods were recorded, but there were only three lakes on which more than five broods were produced over the years. Thirty-three broods were seen twice, 11 three times, and 3 four times. Seven broods were observed in age class 3 only, reducing the sample available for the subsequent analyses to 88 broods (Table 1).

Although ageing ducklings in the field is a widely used and generally accurate procedure,

Table 1. Number of pre-fledgling teal (*Anas crecca*) broods recorded in different lake categories in the Evo watershed in 1988–2003. Median, earliest, and latest estimated hatching date for broods in each category are given below.

Year	On preferred lakes	On less preferred lakes	Annual total
1988	2	5	7
1989	3	9	12
1990	1	2	3
1991	2	6	8
1992	3	4	7
1993	2	0	2
1994	3	4	7
1995	3	3	6
1996	4	1	5
1997	4	2	6
1998	3	2	5
1999	3	3	6
2000	1	2	3
2001	2	2	4
2002	3	0	3
2003	1	3	4
Grand total	40	48	88
Median	10 June	16 June	
Earliest	26 May	24 May	
Latest	13 July	14 July	

reliability of age class estimates is a conceivable bias in a study of this type. However, there was no indication of such a problem, as age classes did not differ in terms of the estimated hatching date (data in Table 2; ANOVA using only the first sighting of each brood: $F = 0.66$, $N = 84$, $df = 5$, $P = 0.66$). Brood size changed remarkably little with increasing age (Table 3), indicating that virtually all mortality occurred very soon after hatching.

Prediction 1: early broods produce more fledglings than late

Our data supported this prediction; i.e., brood size in age class 2A–2C was negatively correlated with hatching date ($r = -0.43$, $P < 0.01$,

Table 2. Mean hatching date for teal (*Anas crecca*) broods in different age classes in the Evo watershed 1988–2003 as estimated by backdating. N refers to the total number of broods sighted, i.e., some broods were seen more than once and thus contributed with data in more than one age class. However, each ageing event was independent of any previous sighting of a brood.

Age class	Mean hatching date	SD	$N_{\text{sightings}}$
1A	18 June	9.4	14
1B	16 June	11.9	15
1C	13 June	11.1	37
2A	14 June	11.3	23
2B	15 June	11.1	21
2C	14 June	11.4	14

Table 3. Brood size in teal (*Anas crecca*) in different age classes. N refers to the total number of broods sighted, i.e., some broods were seen more than once and thus contributed with data in more than one age class. Sample size differs in age class 2A as compared with that in Table 2 because one brood was aged but not all ducklings in it were positively seen.

Age class	Mean brood size	SD	$N_{\text{sightings}}$
1A	7.1	2.6	14
1B	5.2	1.9	15
1C	5.5	2.3	37
2A	4.9	2.4	22
2B	5.4	2.3	21
2C	5.2	2.6	14

$N = 40$; Fig. 1). This result did not change when brood size data were not standardized ($r = -0.39$, $P < 0.02$, $N = 40$). The pattern of early broods producing more fledglings was consistent also on a yearly basis in the sense that the correlation coefficient was negative in eight out of nine years and zero in the ninth (sign test: $P = 0.04$).

Prediction 2: early broods will be over-represented on preferred lakes

The two most productive lakes together had 44% of the broods and 55% of the ducklings aged class 2A or older: lake 'Vähä Ruuhijärvi', which had at least one brood in 15 out of 16 years, and lake 'SO:n allas' which had at least one brood in 14 years. In the following, these two comprise 'the preferred lakes' (Table 1). Twenty-four lakes had at least one brood in one to five years, and they are collectively referred to as 'less preferred'. The only brood that moved from a less preferred lake to a preferred lake was excluded from the analysis below. No brood moved from a preferred lake to another, whereas 10 broods moved from a less preferred lake to another, further indicating the lower status of the latter.

There were 14 breeding seasons with at least one brood in each category i.e. 'preferred' and 'less preferred' lakes (1993 and 2002 did not meet this criterion). The earliest brood to hatch anywhere was observed on one of the 'preferred' lakes in 10 out of 14 years. We also ranked all broods in a given season according to the estimated hatching date and calculated the mean rank of the hatching date for the two lake categories. In a year-by-year pair-wise comparison, broods on 'preferred' lakes hatched earlier than broods on 'less preferred' lakes, i.e. the median of ranks of the former were lower (Wilcoxon signed rank test: $T = 9.5$; $P < 0.05$, $N = 14$ years).

Discussion

Brood size in the youngest ducklings in Evo conforms well with that reported in comparable studies (age class 1A in Table 3 versus 6.2–8.3 ducklings in Linkola 1962, Hildén 1964, Toft *et al.* 1984, and Fox 1986). Mean brood size in

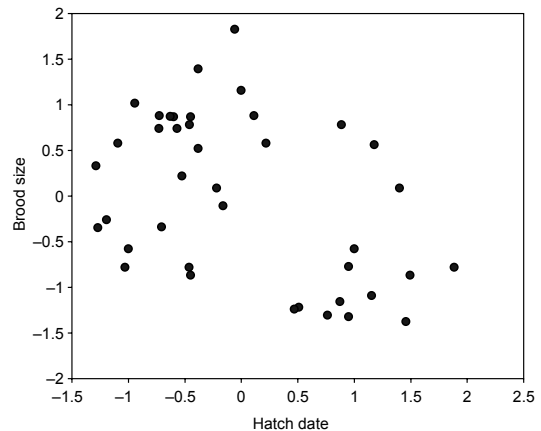


Fig. 1. Brood size of teal ducklings in age class 2A–2C decreased with advancing hatching date (Julian). Both axes show z-standardized values.

older ducklings (age classes 2B–2C in Table 3) was higher in Evo than previously reported in most studies of near-fledged and fledged teal (i.e., 3.4–4.8 ducklings in Hildén 1964, Danell & Sjöberg 1979, and Fox 1986, but 5.9 in Linkola 1962). Clutch size in teal generally ranges from 8 to 11 eggs (e.g., Linkola 1962, Cramp & Simmons 1977, Fox 1986, Glutz von Blotzheim 1990, Krapu *et al.* 2004), implying that factors reducing subsequent brood size chiefly operate either in the nest stage or on very young ducklings (age classes 1A–1B). Such a mortality pattern corresponds well to that found in congeneric species (e.g., Rotella & Ratti 1992, Mauser *et al.* 1994), and it is supported by our data. Agents known to have the potential to significantly affect survival of eggs and newly hatched young, in dabbling ducks as well as in other precocial birds, are predation, chilling, food shortage and disease (reviews in Batt *et al.* 1992 and Newton 1998).

Our study corroborates the general idea that early breeding, or some factor associated with it, leads to more fledged birds. In addition, we argue that the advantage of early breeding is due to processes operating during the later phases of the brood stage (age classes 1C–2C), as we found no relationship between hatching date and brood size in very young ducklings (standardized hatching date versus standardized brood size in age classes 1A–1B: $r = 0.08$, $P > 0.75$, $N = 19$). This pattern, too, persisted when brood size was not standardized ($r = 0.17$, $P > 0.50$).

Why early breeding teals in Evo produced more ducklings than late breeding ones is an open question. Within-season variations in abundance of high-protein insect food (cf. Danell & Sjöberg 1977 and Krapu *et al.* 2004; see Daan *et al.* 1986 and Rohwer 1992 for a general discussion) and in predation pressure are possible explanations, but we have no data to explicitly test this. Temporal decline in egg size and egg viability could produce the same pattern, but both seem unlikely in teal (cf. Rohwer 1992: pp. 502–507).

Half of the lakes in the Evo watershed did not have teal broods in any of the 16 study years, and 23 of the 26 lakes on which successful breeding was recorded were nonetheless without teal broods in 11 or more of the 16 seasons. This pattern of ‘vacant patches’ appears to be a common feature of breeding ducks in boreal biomes (cf. Danell & Sjöberg 1979, Decarie *et al.* 1995, Sjöberg *et al.* 2000). Our study generated two independent patterns (see Results) showing that the earliest clutches are produced in high-quality habitats (i.e., lakes), and we also show that early clutches produce more near-fledging young than late. Habitat selection is thus a process which may affect fitness considerably in boreal teal, as is, of course, age, physiological state, experience and other intrinsic factors. Teal in the Evo watershed also seem to meet the basic assumption of habitat selection models, i.e. that the habitats with the highest suitability are occupied first (Fretwell & Lucas 1970).

Our results agree with the patterns observed in mallards (*Anas platyrhynchos*) breeding in another part of southern Finland (Pöysä 2001) in the sense that the latter birds, too, preferred lakes on which breeding success was higher. However, in contrast to teal in Evo, Pöysä (2001) found that mallard pairs arriving from migration occupied preferred lakes and less-preferred lakes at approximately the same time, but he did not study lake occupation in relation to hatching date. Although high-quality and low-quality lakes were occupied at about the same time (Pöysä 2001), nest success may be higher at the former and, hence, re-nesting less frequent, resulting in earlier broods there. Further research on these aspects is needed in both species.

The main message from the present study — occupying the best lakes first and then nesting

early increases reproductive success in teal — is a novel finding for waterfowl in the boreal zone. This is thought-provoking also considering that it is often argued that weather has an overriding effect on duckling survival and even on breeding success in general in such settings (Sargeant & Raveling 1992, Krapu *et al.* 2000, 2004, Blums *et al.* 2002).

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