

Why are there so many empty lakes? Food limits survival of mallard ducklings

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Abstract: Food is an important factor affecting survival in many bird species, but this relationship has rarely been explored experimentally with respect to reproductive output of precocial birds. In a field experiment we tested the hypothesis that food abundance limits reproductive output in breeding dabbling ducks. On 10 oligotrophic lakes in northern Sweden we introduced one wing-clipped female mallard (*Anas platyrhynchos* L., 1758) and a brood of 10 newly hatched ducklings, and survival was monitored for 24 days. Food was added ad libitum at five of the lakes, but not at the other five. Duckling survival was best modelled to include a treatment effect, with higher survival on lakes with food added, and a negative effect of harsh weather. As expected, duckling survival increased nonlinearly with age. Only one female remained on control lakes after 24 days, whereas four remained on lakes with food added. This is the first experimental demonstration that food may limit survival and reproductive output in breeding precocial birds. We argue that food limitation may be one reason why duckling mortality is high and why many lakes throughout the Holarctic have no breeding dabbling ducks.

Résumé : La nourriture est un facteur important pour la survie de plusieurs espèces d'oiseaux, mais sa relation avec le rendement reproductif des oiseaux nidifuges n'a que rarement été explorée expérimentalement. Une expérience sur le terrain nous a permis de vérifier l'hypothèse selon laquelle l'abondance de la nourriture contrôle le rendement reproductif chez les canards barboteurs en période de reproduction. Nous avons introduit une femelle à ailes écourtées du canard colvert (*Anas platyrhynchos* L., 1758) ainsi qu'une couvée fraîchement éclos de 10 canetons dans 10 lacs oligotrophes du nord de la Suède et nous avons noté leur survie pendant 24 jours. Nous avons ajouté de la nourriture à volonté dans cinq des lacs, mais pas dans les cinq autres. Notre modélisation optimale de la survie des canetons inclut un effet du traitement expérimental avec une survie accrue dans les lacs approvisionnés et un effet négatif des conditions climatiques rigoureuses. Comme prévu, la survie des canetons augmente de façon non linéaire avec l'âge. Au bout de 24 jours, il ne restait qu'une seule femelle sur les lacs témoins, alors qu'il y en avait quatre sur les lacs approvisionnés. C'est une première démonstration expérimentale que la nourriture peut contrôler la survie et le rendement reproductif chez les oiseaux nidifuges en période de reproduction. Nous croyons que la carence de nourriture peut être l'une des causes de la forte mortalité des canetons et de l'absence de reproduction de canards barboteurs dans de nombreux lacs de la région holarctique.

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Introduction

Population size is limited by factors such as food, nest sites, predation, weather, competition, and disease (Wiens 1984; Martin 1987; Newton 1998; White 2001). Food effects may be direct through starvation, or indirect through increased predation as a result of changed behaviour and exposure (Jansson et al. 1981; Newton 1998). However, it is often difficult to assess the importance of food abundance to population limitation, as its impact may differ between indi-

viduals, age classes, spatial scales, and even be time-delayed (Newton 1980; Martin 1987; Newton 1998). Nevertheless, reviews by Martin (1987) and Newton (1998) support the idea that there is a general and causal link between bird productivity (young raised per pair) and food supply.

A common way to study the topic is to provide additional food to closed or semi-closed populations, and then compare survival or reproductive rate between experimental and control sites (Boutin 1990). This approach has many advantages, the most obvious being that limiting factors can be

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more easily separated and their relative importance assessed. In this way, survival of prefledged birds in several genera has been shown to be limited by food (reviewed by Newton 1998). However, these studies exclusively concern altricial birds (or the altricial stage in semi-precocial birds (Brinkhof and Cavé 1997)), whereas experimental evidence for food limitation in precocial birds is still lacking (Newton 1998, p. 150; but see Swennen 1989). This lack is a major shortcoming when it comes to understanding the general role of food limitation to avian breeding success, as altricial and precocial birds represent radically different evolutionary strategies of food provisioning for young.

There is a well-documented positive association between food abundance, duckling growth, and survival in dabbling ducks (Street 1977; Johnson et al. 1992; Cox et al. 1998), although predation and adverse weather may also affect breeding success (Solman 1945; Koskimies and Lahti 1964; Talent et al. 1983; Cox et al. 1998). Duckling survival is a key factor in the overall breeding success of ducks, which in turn is a driving force in their population dynamics (e.g., Johnson et al. 1989). Most of the mortality in ducklings occurs during the first 2 weeks in life (Talent et al. 1983; Hill et al. 1987; Orthmeyer and Ball 1990; Rotella and Ratti 1992; Mauser et al. 1994), which is also the period when they entirely rely on high-protein invertebrate prey (e.g., Chura 1961). Despite the evidence that food abundance affects duckling performance, there is no experimental study addressing whether the former may actually limit survival and reproductive success in dabbling ducks.

A general observation in nemoral as well as in boreal areas throughout the Holarctic is that many seemingly suitable lakes lack breeding ducks (Danell and Sjöberg 1978; Toft et al. 1982; DesGranges and Darveau 1985; Blancher et al. 1992; Elmberg et al. 1997; Pöysä et al. 1998; Sjöberg et al. 2000). In an earlier experiment we found that duckling mass increased more on lakes with higher nutrient levels than on lakes with less nutrients, implying food limitation in this system (Sjöberg et al. 2000; see also Nummi et al. 2000; Pöysä et al. 2000). However, as food abundance was not explicitly measured or manipulated in that experiment, we did not obtain conclusive evidence of food limitation, in particular whether it affects survival.

We here test the hypothesis that food abundance may limit breeding success in mallards (*Anas platyrhynchos* L., 1758). This was done by manipulating food abundance at some lakes where broods were introduced. Based on previous studies, we predicted that survival of ducklings would be higher on lakes where food was added than on lakes where food abundance was not manipulated. In addition, we studied whether survival was negatively affected by harsh weather and whether duckling survival probability increases with age.

Materials and methods

Study lakes

Fieldwork was carried out from 8 June to 10 July 2002 in the province of Västerbotten, northern Sweden (64°N, 20°E). We selected 10 small (1.9–4.5 ha) oligotrophic lakes, all having fairly sparse aquatic vegetation and a similar roundish shape. Lakes were thus easily and reliably surveyed

from the shore. All lakes were surrounded by mixed coniferous forest and peatland, representing a very common lake type in the boreal biome throughout the Holarctic. To obstruct escape by introduced mallards (see below), no study lake was connected to other lakes by permanent creeks, and there were no adjacent lakes (<300 m).

Although no wild mallard broods were seen on the study lakes during the study period, all lakes were regarded as potential nesting sites for mallard, which is a common breeding species in the region. This assumption was based on an earlier study of habitat use by breeding ducks in the area (Danell and Sjöberg 1978) and on our own observations of waterfowl on the 10 study lakes. Teal (*Anas crecca* L., 1758) bred on two control lakes and on two experimental lakes. Common goldeneye (*Bucephala clangula* (L., 1758)) bred on one control lake and on one experimental lake, and single females were observed on some other study lakes. Single mallard hens without a brood were seen on several study lakes, but these could not be distinguished as either failed breeders or nonbreeders. A few individuals of the following species were seen occasionally: red-throated loon (*Gavia stellata* (Pontoppidan, 1763)), arctic loon (*Gavia arctica* (L., 1758)), horned grebe (*Podiceps auritus* (L., 1758)), whooper swan (*Cygnus cygnus* (L., 1758)), tufted duck (*Aythya fuligula* (L., 1758)), and white-winged scoter (*Melanitta fusca* (L., 1758)).

Experimental design

To ensure successful experimental treatment we used wing-clipped adult female mallards brought from a game farm situated 300 km farther southwest, but also in the boreal zone (transported and released according to permit A1-02 from The Research Animals Ethics Board at the Court of Appeal for North Sweden, Umeå). All had either been caught as wild birds less than a year before the experiment or they were daughters of wild females caught the previous season. The game farm is surrounded by a fence preventing ducks from escaping, but habitats inside include natural areas with ponds, shrubs, taller herbs, and grass. Mallards at this game farm thus forage as wild birds, although they receive supplementary food, especially in winter. Females constructed their own nest and laid eggs at the same time as non-captive local mallards (early May). As soon as a brood hatched the female and her ducklings were transported overnight to one of our experimental lakes (i.e., to an area and a site of which the female had no previous experience).

Brood size was standardized to 10 ducklings. This usually meant removal of ducklings from the brood, but in a few cases, a duckling was added to a brood. All ducklings added to an alien brood were accepted by the hen and her brood. For practical reasons it was not possible to do all introductions on the same night; hence, 1 week lapsed between the first and the last introductions. At release ducklings in all broods were 1–2 days old. We randomly selected five of the lakes (mean size 2.8 ha, range 2.2–4.3 ha) to be experimental, at which duck food was provided. The remaining five lakes (mean size 3.5 ha, range 1.9–4.5 ha) served as controls (i.e., no food was added).

Mallard ducklings usually start including plant matter in their diet when they are about 2 weeks old (e.g., Chura 1961; Sugden 1973; Pehrsson 1979; Reinecke 1979;

Sedinger 1992). We took this into consideration by making the food that was added to the experimental lakes a mixture of barley grain and fodder pellets intended for young poultry. Thus, for the first 12 days, a fodder containing 27% protein was added every day. After day 12, we provided a fodder containing 23% protein every 3rd day until 24 days after introduction.

The added food was presented on five wooden plates (80 cm × 80 cm) at each experimental lake. Plates were placed on the shore at the water edge at approximate 30-m intervals. Mallard broods forage by swimming along the shore or by walking in the vegetation close to the water (Pehrsson 1979); thus, plates were placed so that foraging ducklings could easily detect them. Visual observations confirmed that ducklings as well as hens consumed the supplied food. On each occasion the volume of added pellets was 400 cm³/plate and that of barley grain 100 cm³/plate. The total volume of 500 cm³ was enough to cover the entire fodder plate, and it was effectively an ad libitum treatment. At least one plate had always fodder left from the previous visit, and old fodder was removed from those plates before adding fresh fodder.

Pehrsson (1979) showed that even ducklings led by a domestic duck had very similar foraging behaviour to that of wild ducklings (which is described in Chura 1961). In earlier field experiments we have shown that ducklings hatched in captivity and fed with fodder forage in a natural way when released onto a lake (Nummi et al. 2000; Sjöberg et al. 2000). In the present study, introduced ducklings were also seen eating insects from the water surface and from vegetation in addition to the added fodder. We argue that ducklings hatched in captivity are an effective way to study food limitation under the present conditions. In addition, foraging behaviour and body-mass change of human-imprinted ducklings well reflect habitat differences (Hunter et al. 1986, 1987; Nummi et al. 2000; Sjöberg et al. 2000). This was confirmed by the present study, as ducklings in broods on experimental lakes stayed more closely together compared with those on control lakes. Broods on experimental lakes were also seen resting in the vegetation more often than were those on control lakes, implying a behavioural change caused by food abundance.

Survival of ducklings was recorded every day for the first 12 days after release and then every 3rd day until day 24. Birds no longer present on the lake were assumed to be dead. Observations were made with a standard waterfowl point-count method (Koskimies and Väisänen 1991). Because introduced and wild ducks were vigilant, observations were made from a concealed position in the forest edge. Fodder pellets and barley grain were always added after the point count of waterfowl.

Data modelling

We constructed the encounter histories of ducklings based on 16 sampling occasions (day 0–12, 15, 18, and 21), followed by 2 group codes (experimental lakes and control lakes). Data from the last study day (i.e., day 24) was thus entered as encounter history for the post interval of day 21. Program MARK (White and Burnham 1999) can normally estimate daily survival rates, but we lacked sufficient data to get such estimates because models were over-parameterized.

However, effects of age can also be included by entering such data in design matrices using logit-link functions. Because we assumed missing birds to be dead we used “known fate models” in the program MARK.

According to a priori biological hypotheses we ran the following general and predefined contrasting MARK models, respectively, on our duckling survival data: (i) $S_{(t)}$ (single estimate of survival) and (ii) S_{treat} (effect of experimental treatment). Additional models included effects of duckling age as well as a weather index (see below). The different effects of age explored in the models were (i) linear, (ii) quadratic, and (iii) nonlinear, defined by the arbitrarily chosen equation $y = a(1 - b^x)$, where a is the maximum age (i.e., 21 days), x is the actual day, and b is a value between 0 and 1 describing the slope (the b value with the best fit in the models was used).

We constructed a weather index by summing the z standardized values of three weather variables (data obtained from the official weather stations “Vindeln-Sunnansjönäs” and “Umeå airport”, and both situated in the study region). In this calculation we used the pre-interval (last visit to present visit) values of (i) mean temperature, defined as the absolute difference between the maximum mean value for the entire study period and the actual 24-h mean value, (ii) mean wind speed, and (iii) total rainfall. High weather index values thus constitute harsher conditions for ducklings.

Survival of ducklings could not be assumed to be independent within a brood. By calculating overdispersion, problems with such dependence can be controlled for by using an adjusted variance inflation factor (\hat{c}) (Pelayo and Clark 2003 and references therein). Adjusted \hat{c} was calculated by dividing the observed mean \hat{c} of the most general predefined model (S_{treat}) by the mean \hat{c} from simulating the same model (bootstrap simulations with 1000 iterations).

The quasi-likelihood Akaike's Information Criterion (QAIC_c) was used to evaluate model fit (Akaike 1973; Burnham and Anderson 1998). Besides QAIC_c values, we also provide values of ΔQAIC_c (difference between the minimum QAIC_c and the actual QAIC_c), w_i (i.e., how well the model approximates data; higher values approximate data better), K (number of parameters), deviance (defined as the difference in $-2\log(\text{likelihood})$ of the current model and $-2\log(\text{likelihood})$ of the saturated model), and β for main effects and covariates. Only models with $\Delta\text{QAIC}_c < 4.0$ and other models needed for interpretation are presented. Models including interactions were run only if they made biological sense.

Results

Bootstrap simulations revealed overdispersion in duckling survival and \hat{c} was thus adjusted to 2.00 (~1.61/0.80). “Treatment” was an important factor in all models and it had a high fit with the data (QAIC_c < 4.0; Table 1). Food addition thus increased survival on the experimental lakes ($\beta = 2.40$, SE = 0.43; Fig. 1). Adding linear or quadratic effects of duckling age to the model S_{treat} did not improve it, but so did adding a nonlinear effect ($b = 0.1$) ($\beta = 0.05$, SE = 0.02; Table 1).

The weather index added as a covariate to the model $S_{\text{treat+N.L.age}}$ did neither increase nor decrease the fit with the

Table 1. Fit of MARK models to survival data for mallard (*Anas platyrhynchos*) ducklings ranked by quasi-likelihood Akaike's Information Criterion (QAIC_c) values.

Model	QAIC _c	ΔQAIC _c [*]	w _i [†]	K [‡]	Deviance [§]
S _{treat+N.L.age}	206.23	0.00	0.43	3	105.31
S _{treat+N.L.age+weather}	208.08	1.85	0.17	4	105.14
S _{treat}	208.26	2.03	0.16	2	109.34
S _{treat+N.L.age+weather+treat×weather}	208.97	2.74	0.11	5	104.01
S _{treat+L.age}	209.62	3.39	0.08	3	108.69
S _{treat+Q.age}	210.53	4.30	0.05	4	107.59
S _(.)	248.97	42.74	0.00	1	152.06

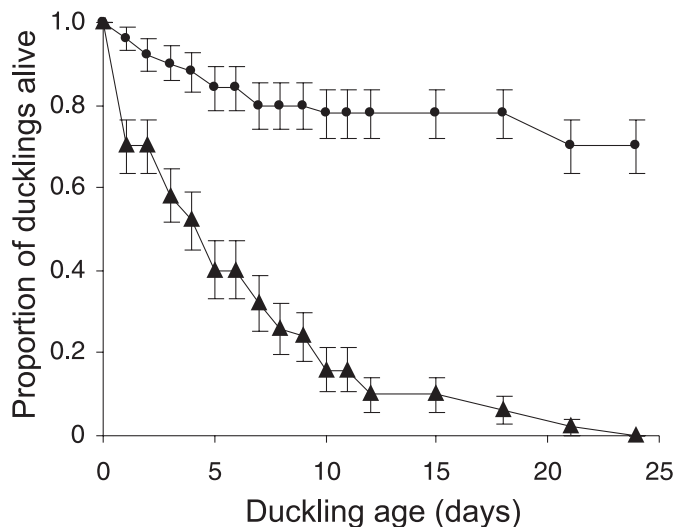
Note: Factors in the models are treat (i.e., treatment, which is either food addition or control), age (either linear (L), quadratic (Q), or nonlinear (N.L.)), and weather (an index defined in the Materials and methods). Model S_(.) only includes the intercept.

^{*}Difference between QAIC_c of the current model and the minimum QAIC_c value.

[†]Model weight.

[‡]Number of parameters.

[§]Difference in $-2\log(\text{likelihood})$ of the current model and $-2\log(\text{likelihood})$ of the saturated model.

Fig. 1. Mean (\pm SE) survival in relation to age of mallard (*Anas platyrhynchos*) ducklings ($n = 2 \times 50$) on experimental (●, food added) and control lakes (▲, no food added).

data (Table 1), implying a negative influence ($\beta = -0.04$, $SE = 0.09$). Adding the interaction term treatment \times weather did not reduce the fit with the data significantly when compared with the model excluding this interaction ($\beta = 0.21$, $SE = 0.20$; Table 1).

To investigate the relative importance of each variable in the best models we summed the model weights for models where these effects occurred alone or in combinations. We thereby calculated the likelihood that a parameter truly belonged in the final models. Thus, treatment was the single most important variable (weight sum 1.00), followed by the nonlinear effect of age (weight sum 0.62). The model weight of the weather index was only slightly higher than its interaction with treatment (0.34 vs. 0.31).

The difference in survival between treatments is evident also when looking at the median day of mortality, being 5 ($SE = 1.04$) on control lakes and 24 ($SE = 1.47$) on experimental lakes (maximum value is 24, i.e., when the study ended). None of the ducklings on control lakes was alive at

the end of the study. In contrast, 70% of the ducklings on lakes with added food was still alive when the study was concluded (Fig. 1).

Median day for the disappearance of females from lakes was 21 ($SE = 5.15$) on control lakes and 24 ($SE = 0.75$) on experimental lakes. When the study was concluded on day 24, 20% of the females was still left on control lakes compared with 80% on the lakes with added food.

Discussion

As the lakes selected for this study are typical for the region and for the boreal biome in general, we argue that our experimental evidence for the importance of food to duckling survival may explain why many lakes have low breeding output or are not at all occupied by breeding dabbling ducks. The temporal pattern (Fig. 1) of duckling mortality on control lakes corresponds well to that of wild mallard ducklings on unmanipulated lakes (Talent et al. 1983; Hill et al. 1987; Orthmeyer and Ball 1990; Rotella and Ratti 1992). We therefore argue that our results are applicable to wild mallards in a wide range of natural settings.

In a one-season study like this, exceptional weather may bias results and interpretations. However, nationwide data from neighbouring Finland, collected largely from lakes of the same type as our study lakes, show that 2002 was the best year in 1989–2002 in terms of mallard production (Pöysä et al. 2002). Indeed, mallard ducklings are sensitive to harsh weather, especially as newly hatched (Koskimies and Lahti 1964). Hence, we were not surprised to find the weather index in the top-ranking survival models. Note, though, that the significance of the interaction term treatment \times weather reveals that weather impact was not similar in the two treatments. A closer look shows that the negative impact of weather was valid for the control treatment only ($\beta = -0.21$, $SE = 0.20$) and not when food was added ($\beta = 0.21$, $SE = 0.20$). This latter difference was expected, as ducklings not limited by food should be less vulnerable to adverse weather than ducklings in inferior condition because of low food abundance.

This study demonstrates a very clear effect of food abundance on duckling survival, and that it is, in this context,

more important than duckling age and weather conditions. However, we do not know what is the process behind the pattern. The experimental design does not let us distinguish between different causes of mortality, or whether they are direct (i.e., death by starvation) or indirect (e.g., death by predation); starving ducklings do not spend as much time being alert or in safe sites as do well-fed birds (cf., Jansson et al. 1981; Swennen 1989). Starvation is probably a rather frequent direct cause of death in ducklings (cf., Solman 1945; Talent et al. 1983; Cox et al. 1998), but we believe that it alone does not explain all mortality. Duckling mortality in our study occurred earlier than in Marström's (1966) study, where mortality of experimentally starved mallard ducklings was studied in the absence of predators.

We have two good reasons to consider missing birds as dead. One is that we designed the study (isolated lakes surrounded by forest, nonlocal wing-clipped adult birds) to minimize the probability of ducks changing lakes and of females abandoning their brood (cf. data on other duck species like the common goldeneye; Pöysä et al. 1997). Deserted broods were never seen and consequently we do not consider brood abandonment to be important in our study. However, when the last duckling in a brood died and the female afterwards was not seen on a lake, we do not know whether the female died or simply left the lake. Because of the small sample size, female survival was not modelled, but instead it was represented by the median day for "not longer present on a lake". For hens we regard "apparent survival" as being more appropriate than "survival". The second reason for treating missing birds as dead concerns ducklings and the gradual decrease in brood size rather than a sudden disappearance of entire broods. The sudden disappearance of entire broods was never observed, and it is also very unlikely that individual ducklings would leave their mother and siblings.

A factor that could seriously compromise our results is the presence of breeding wild mallards, as intraspecific competition for food may have consequences for the survival of released birds. However, no wild mallard broods were seen on the study lakes in 2002. Other birds (i.e., jay (*Garrulus glandarius* L., 1758) and common raven (*Corvus corax* L., 1758)) were observed occasionally eating from the fodder plates. However, some fodder was always left on at least one plate, and interspecific competition for food is not considered to have affected the results.

Elmberg et al. (2003) did not find any relationship between food abundance and breeding success of mallards on oligotrophic lakes in southern Finland (i.e., in the same type of habitat and landscape as in the present study). Their conclusion that breeding dabblers are not limited by food may thus appear to contradict the present findings. However, the spatial scale differs between the studies (i.e., lake in the present and watershed (52 lakes) in Elmberg et al. 2003), implying that food limitation may be more important on a finer scale such as the lake level.

The present study supports the hypothesis that food can limit survival in breeding mallards, and it is the first direct demonstration of food limitation in breeding precocial birds in a natural setting (Newton 1998, p. 150; but see Swennen 1989). This may have important effects on recruitment and population growth in dabbling ducks, where females are

considered highly philopatric (e.g., Anderson et al. 1992) and their breeding success potentially dependent on food abundance on breeding sites. The present study may also explain some previous findings from boreal lakes, i.e., a correlation between population density (breeding pairs) and food abundance (Elmberg et al. 1993; Gardarsson and Einarsson 1994; Nummi et al. 1994, 1995), and that duckling mass gain depends on lake nutrient status (Nummi et al. 2000; Sjöberg et al. 2000). One reason that many boreal lakes lack breeding dabblers may thus be that ducks avoid sites not fulfilling dietary demands for raising a brood; a hypothesis that merits further testing.

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