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RESPONSE OF MALLARD DUCKLINGS TO VARIATION IN HABITAT QUALITY: AN EXPERIMENT OF FOOD LIMITATION

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Abstract. Occurrence of Mallard (*Anas platyrhynchos*) pairs and broods was studied on 86 boreal lakes in two areas in south Finland during 1988–1997 (35 lakes) and 1989–1996 (51 lakes), and field experiments were conducted to determine whether food limitation is an important factor regulating population densities. In general, pairs and broods used and avoided the same lakes, but in both study areas, the proportion of lakes that were unoccupied every year was higher for broods (71% and 69%) than for pairs (26% and 31%). We hypothesized that lakes without breeding Mallards, and especially broods, were too poor to raise young in, and we tested that in field experiments on 22 lakes in boreal Sweden. Based on concentration of total phosphorus in the water, these lakes were divided into two groups: 11 “poor” lakes and 11 “rich” lakes. Mallard ducklings imprinted on humans were used to address brood-stage food limitation by studying mass change. Thirty-one individually marked ducklings were divided into three experimental groups: 12 ducklings were used in poor lakes, 12 ducklings in rich lakes, and 7 ducklings were used as controls receiving no experimental treatment in the field. Each group was studied in 11 daytime trials on 11 different lakes, except the control group which was kept in a pen with free access to food. Ducklings of all groups spent nights together as a big 31-individual group in the same pen and with free access to food. Ducklings foraging on poor lakes gained significantly less body mass than those feeding on rich lakes. At night, when ducklings of both groups had equal and free access to food, ducklings that had been feeding in a poor lake that day gained more mass than those that had been feeding in a rich lake. Overall, ~95% of daily mass gain was accounted for by daytime gain in the control group, the corresponding percentage was 35% in the rich-lake experimental group and 11% in the poor-lake experimental group. Thus, we have observational, as well as experimental, evidence to conclude that many boreal lakes are inferior breeding habitat for Mallards, especially during the brood stage. Our results suggest (1) that it is important to recognize at what stage of the yearly reproductive cycle food limitation may occur, (2) that brood stage may be more important than nesting stage for possible population limitation and regulation in breeding Mallards, and (3) that the reason why so many lakes in the boreal region lack breeding Mallards may be food limitation.

Key words: *Anas platyrhynchos*; Finland; food limitation; habitat saturation; Mallard; mass gain; population limitation; Sweden.

INTRODUCTION

Food limitation may influence individual reproductive success and survival (review in Martin 1987), limit number of breeding individuals and population densities (reviews in Newton 1980, 1998, Boutin 1990), and affect species diversity through interspecific competition (review in Wiens 1989). However, as is evident in all reviews mentioned, it is difficult to demonstrate food limitation directly in the field, though both food addition experiments (Boutin 1990) and density-perturbation experiments (Harrison and Cappuccino 1995)

done on a variety of animal taxa have detected resource-based bottom-up regulation.

Some of our earlier studies of assemblages of breeding dabbling ducks (*Anas* spp.) indicate that food limitation may affect breeding density and species diversity (Elmberg et al. 1993, Pöysä et al. 1994). Introduction experiments showed that a notable proportion of our study lakes lacked ducks in some years, and that lakes remained unoccupied despite the fact that introduced ducks can attract wild birds (see Elmberg et al. 1997, Pöysä et al. 1998).

Those results concern the Mallard (*Anas platyrhynchos*), the most common and widespread species of dabbling duck in the world. One explanation of our findings may be that the boreal forest biome, with its many lakes, is not saturated with Mallards, i.e., that

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number of birds returning from wintering areas is not enough to fill up all suitable breeding lakes (see also Järvinen and Ulfstrand 1980, Elmberg et al. 1997:134). On the other hand, some lakes may produce too little food to meet dietary demands of Mallard ducklings. In other words, food resource limitation may operate in some years or at some stage of the breeding cycle, possibly influencing habitat selection of nesting pairs via their capability to raise young. Further, as indicated by differences in habitat distribution and lake use between pairs and broods of Mallards within a region (Danell and Sjöberg 1978, Pehrsson 1984, Nummi and Pöysä 1993), it may be a common pattern that lakes do have breeding pairs but not broods. In such lakes, food resources may not be abundant enough for raising young.

Here we address the question of food resource limitation in breeding Mallard populations focusing on the brood stage. First, we use long-term data on lake occupancy by breeding pairs and broods from two study areas to show that, indeed, a notable proportion of lakes are unoccupied year after year and that this pattern is more pronounced for broods than for pairs. Second, we report on an experiment testing the hypothesis that lakes without breeding Mallards, and especially broods, are too poor in invertebrate food to raise young. By using Mallard ducklings imprinted on humans in controlled field experiments, we examined daily changes in body mass in relation to lake quality.

METHODS

Observational study of lake occupancy

We collected data on lake occupancy of Mallard pairs and broods in Häme (61°10' N, 25°05' E) and Karjala (61°30' N, 29°30' E) in south Finland (study regions number 3 and 4, respectively, in Fig. 1 in Elmberg et al. 1993). Every year from 1989 to 1996 in Häme, and from 1988 to 1997 in Karjala, number of breeding pairs and broods was recorded on 51 (Häme; mean size 5.8 ha, range 0.1–49.5 ha) and 35 lakes (Karjala; mean size 3.7 ha, range 0.2–24.0 ha), respectively. Pairs were censused with a standard waterfowl point-count method (Koskimies and Väisänen 1991) and, according to recommendations about optimal census times in Pöysä (1996), presence-absence in each year on a given lake was determined from a census conducted in the middle of May. Five (Häme) or three (Karjala) brood surveys were made each year between mid-June and early August using the point-count method. If a brood was observed on a given lake on any survey, the lake scored as hosting Mallard broods in that particular year; if no broods were seen in any census, the lake was considered to be unoccupied by broods.

Duckling experiments

We selected 22 lakes in the Umeå region in north-central Sweden (63°40' N, 20° E), an area situated in

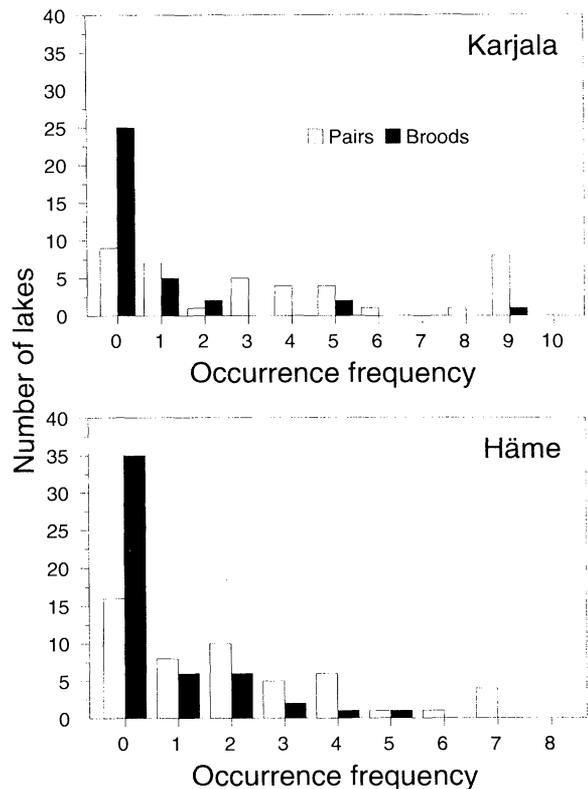


FIG. 1. Distribution of occurrence frequencies of breeding Mallard pairs and broods on 35 lakes in Karjala, Finland, 1988–1997, and on 51 lakes in Häme, Finland, 1989–1996. Frequency 0 means that a given lake was unoccupied every year in the 10-year (Karjala) or 8-year (Häme) study period; frequency 10 (Karjala) or 8 (Häme) means that a given lake was occupied every year.

the mid-boreal zone, and rich in lakes and wetlands. Experimental lakes are typical for the region, i.e., they are surrounded by mixed coniferous forest or wetlands, and they freeze over in winter. In total, 33 potential experimental lakes were selected. Primarily we looked for lakes ~10 ha in size and on which Mallard pairs had been observed during previous breeding seasons, but the following selection criteria were added: (1) no cabins or other buildings or frequent human activities around the lakes that could influence breeding results, (2) within convenient distance from where the experimental birds were kept, and short distance to carry ducklings from a road to the lake, (3) tall vegetation should be sparse to minimize risk of losing experimental ducklings (thus excluding lakes at the eutrophic end of the local productivity gradient), and (4) having a well-defined shoreline. In the region Mallard broods can be found in lakes down to 0.05–0.10 ha in size (Danell and Sjöberg 1978).

To get an objective value of the productivity level of each lake, we measured the concentration of total P in the water, a good indicator of trophic status of lakes (e.g., Kerekes et al. 1990, Staicer et al. 1994). In a

closely related species, the Black Duck (*Anas rubripes*), total phosphorus has been found to be a good predictor of lake utilization by broods (Staicer et al. 1994). Water samples were taken in winter when lakes were frozen over and ice effectively reduced turbulence. Based on phosphorus values we selected two groups of lakes as experimental lakes, (1) the 11 "richest" (mean size 5.3 ha, median 4.1 ha, range 1.7–12.6 ha), and (2) the 11 "poorest" (mean size 4.3 ha, median 3.0 ha, range 1.5–13.4 ha) among the 33 lakes ("rich" lakes, 19–30 $\mu\text{g/L}$ total-P; "poor" lakes, 8–18 $\mu\text{g/L}$ total-P; note that the term rich is used here only in a relative sense and not to refer to the locally most productive lakes, see above). This classification corresponds well to results from counts of wild broods in the same lakes in 1995 and 1996 (two brood censuses each year per lake): one brood was observed in the poor lakes and 14 in the rich, the number of lakes without broods was 10 (out of 11) among the poor and 5 (out of 11) among the rich lakes (Fisher's exact test, $P = 0.032$). Each day experiments were run (see below) we used one lake from each of these groups, the within-group order of usage being random.

Thirty-one Mallard ducklings from a hatchery in Södermanland (central Sweden), hatched on 11 June 1996, were delivered to the experimental area the same day. An outdoor pen supplied with a heating bulb served as a "nest." Initially ducklings had free and direct daytime access to a fenced area along the shore of Umeälven river, permitting them to search for food in water in a natural manner. They were also fed ad libitum with a diet consisting of 5% animal protein and 95% barley. To obtain effective imprinting one person spent several hours per day with the ducklings. The day before experiments started, a short test was made by releasing some ducklings along the shoreline. They reacted as expected by responding to the activities of the person following them. For example, they left the water when the person walked away from the shore at the same time calling to them by whistling.

Experiments started when ducklings were 4 d old. We randomly picked birds and put them in two baskets until there were 12 in each, i.e., about the number in a large wild-Mallard brood. One group of ducklings was assigned to always forage on rich lakes, the other on poor. The seven remaining ducklings were used as a reference group not subjected to daytime experimental treatment. All ducklings (including the reference group) were individually color-marked so that we could tell them apart from a distance even when they were swimming. This made it possible to identify individual birds in the field experiment. During the experimental period, food was taken away from the pen at 0800 each morning, and the two groups of experimental ducklings were collected. After that, reference ducklings got access to food again. When experimental birds were brought back to the pen in the afternoon (normally around 1700), they too had free access to food. In other

words, all 31 ducklings spent roughly two-thirds of each day as one big "super brood," and 2×12 ducklings were taken out on experiments and were absent for 8–9 h each day. Experiments were run between 15 and 27 June with two interruptions (one rain day and one holiday; all ducklings kept in the pen the whole day).

Upon arrival to an experimental lake, each duckling was weighed (nearest milligram) on a battery-driven balance. Thereafter they were released as a group on the shoreline, and the experimental trial started. Our aim was to start trials at 1000, but some variation due to different travel time to lakes was unavoidable. Each experimental trial lasted 6 h, after which ducklings were collected as quickly as possible and then again weighed individually, transported to the pen and the super brood was restored.

Two persons accompanied ducklings, but remained on the shore, while the latter searched for food along the shoreline and in aquatic vegetation (observers followed ducklings during the experiment, ducklings did not follow them). During each experimental period, all broods traveled around the lake at least once, so that all sections of shoreline were used for food searching. After ~1 h of foraging, ducklings normally selected a place along the shore to rest together. Roughly half an hour later they usually started looking for food again. This behavior was surprisingly independent of weather and not induced in any way by the observer.

Statistical analyses

Our experiment had a repeated-measures design with 11 trials for each of the three (body mass) groups of ducklings. Repeated measures were obtained for changes in body mass for each duckling from each experimental trial ("day-time change" is the mass after a trial minus the mass before) from (1) 11 poor lakes (12 ducklings in each), 11 rich lakes (12 ducklings in each), and 11 controls (7 ducklings kept in the pen; timing and weighing procedure as in experimental ducklings), and (2) the night following each of eleven trials ("night-time change" is the body mass before the trial in a given day minus mass after the trial the day before). We used absolute mass change in the analyses because: (1) duckling body mass did not differ among the three groups when the experiments started (ANOVA, $F = 1.096$, $df = 2, 28$, $P = 0.348$), (2) all ducklings were the same age, and (3) parallel trials were run on the same days in all three groups. Since individuals within each treatment group did not belong to the same natal brood, but were randomly selected from a large group of ducklings, and because they showed reasonable between-individual variation in terms of foraging place and body-mass change in each trial, we consider individuals within treatment groups as independent observations. Repeated-measures analysis of variance had one grouping factor (three levels: control, poor lakes, rich lakes) and one 11-level, with-

TABLE 1. Repeated-measures analysis of variance of daytime mass change of Mallard ducklings in poor-lake and rich-lake experimental groups.

Source	SS	df	MS	F	P
Between subjects					
Group	3.713	1	3.713	29.984	<0.001
Error	2.725	22	0.124		
Within subjects†					
Trial	11.470	10	1.147	22.622	<0.001
Trial × group	5.516	10	0.552	10.879	<0.001
Error	11.155	220	0.051		

Notes: The analysis is based on data presented in Fig. 2, excluding the control group, using $\log(y + 1)$ transformed data (see Methods). The repeated factor was trial.

† Multivariate tests based on Wilks' lambda also showed that all effects were highly significant.

in-subject factor (trial). This was done separately for daytime and nighttime changes in body mass. After a linear transformation of the mass changes (i.e., because some values were negative, the origin was translated; see Zar 1996:27), data were $\log(y + 1)$ transformed to improve normality and homoscedasticity. As mass changes in the control group appeared to differ drastically from those of the experimental groups (see Results), we first tested differences between the latter excluding the control group. We then ran analyses with all groups, and the only difference was that results were even more significant. Adopting a conservative approach we thus give results only with the experimental groups included.

All statistical analyses were run with SYSTAT procedures (Wilkinson 1992). When interpreting the output of repeated analysis of variance we followed instructions given in Wilkinson (1992:307–308, 336–339). All probability values are two-tailed, according to SYSTAT procedures or Zar (1996), as appropriate.

RESULTS

Observational study of lake occupancy

In both study areas, frequency of unoccupied lakes was high for pairs as well as for broods (Fig. 1). In general, pairs and broods used and avoided the same lakes; their lake-specific occurrence frequencies were correlated (Spearman rank correlations, Karjala region, $r_s = 0.707$, $N = 35$, $P < 0.001$; Häme region, $r_s = 0.429$, $N = 51$, $P < 0.01$). However, there was a clear difference between pairs and broods in distribution of occurrence frequency, especially in number of unoccupied lakes. In Karjala, proportion of empty lakes was 26% in pairs and 71% in broods (Kolmogorov-Smirnov two-sample test, $D = 0.486$, $P < 0.001$). The corresponding proportions were 31% and 69%, respectively, in Häme (Kolmogorov-Smirnov two-sample test, $D = 0.373$, $P < 0.01$).

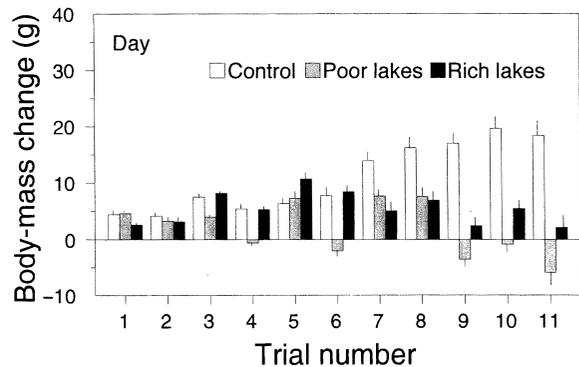


FIG. 2. Average (+1 SE) change in body mass of Mallard ducklings in control ($N = 7$ ducklings), poor-lake experiment ($N = 12$), and rich-lake experiment ($N = 12$) groups in 11 daytime trials. Control-group ducklings were kept in a pen with free access to fodder, and each bar corresponds to separate and consecutive days. In experimental groups, each trial corresponds to a different lake and a separate consecutive day (access to natural food only). Duckling age increases similarly with trial number in all groups.

Experiments on duckling body-mass change

There were clear differences in daytime and nighttime mass change among the three groups of ducklings. In daytime experimental trials, ducklings feeding on poor lakes gained less mass than those feeding on rich lakes (Table 1), and highest mass gain was recorded in the control group (Fig. 2; means (± 1 SE) of the eleven trial means: control, 11.0 ± 1.8 g; poor lakes, 1.9 ± 1.4 g; rich lakes, 5.5 ± 0.8 g). By contrast, at night, when ducklings of all three groups had equal and free access to food, the reverse was the case: ducklings that had been feeding on a poor lake that day gained more mass than those that had been feeding on a rich lake (Table 2), and the control group gained the least (Fig. 3; means (± 1 SE) of the eleven trial means: control, 0.6 ± 0.8 g; poor lakes, 15.2 ± 2.7 g; rich lakes, 10.3 ± 2.1 g). Duckling age (increasing with trial number, see Figs. 2 and 3) also had a significant effect on mass change, the interaction between age (trial number) and

TABLE 2. Repeated-measures analysis of variance of nighttime mass change of Mallard ducklings in poor-lake and rich-lake experimental groups.

Source	SS	df	MS	F	P
Between subjects					
Group	1.338	1	1.338	11.600	0.003
Error	2.538	22	0.115		
Within subjects†					
Trial	10.913	10	1.091	85.461	<0.001
Trial × group	0.806	10	0.081	6.314	<0.001
Error	2.809	220	0.013		

Notes: The analysis is based on data presented in Fig. 2, excluding the control group, using $\log(y + 1)$ transformed data (see Methods). The repeated factor was trial.

† Multivariate tests based on Wilks' lambda also showed that all effects were highly significant.

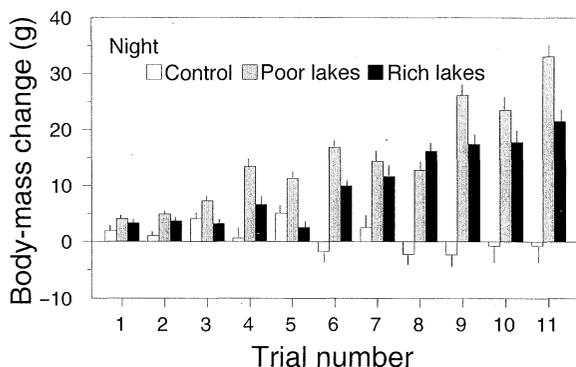


FIG. 3. Average (+1 SE) nighttime change in body mass of Mallard ducklings in control ($N = 7$ ducklings), poor-lake experiment ($N = 12$), and rich-lake experiment ($N = 12$) groups after 11 daytime trials (see Fig. 2). Ducklings of all groups were kept together overnight in a pen with free access to fodder. Duckling age increases similarly with trial number in all groups.

treatment type being significant. Based on overall daytime and nighttime mass changes averaged over the 11 trials (see above), ~95% of daily mass gain was accounted for by daytime gain in the control group, the corresponding percentages being 35% in the rich-lake experimental group and 11% in the poor-lake experimental group.

The less mass ducklings gained in experimental trials or in the pen (control group) during the day, the more they seemed to gain during the following night, but, interestingly, the correlation was significant only for ducklings feeding in poor lakes (Table 3). In all groups, the correlation between daytime mass gain and mass gain during the previous night was also negative but not significant (Table 3). These results, together with those in the paragraph above, indicate that food resources in poor lakes did not meet energy demands of ducklings as well as did food resources in rich lakes. Hence, ducklings feeding on the former compensated by feeding more the night after.

DISCUSSION

Considering lake occupancy, proportion of unoccupied lakes was high for pairs as well as broods, but considerably higher for the latter on both Finnish study areas. Because those patterns were derived from long-term data gathered in intensive brood-survey programs, we can exclude chance effects, and we thus consider absence of broods in those lakes a genuine pattern. Furthermore, among lakes used for duckling experiments in Sweden, the proportion without wild broods in the 1995 and 1996 censuses was 68% (see *Methods: Duckling experiments*), which is remarkably close to figures from our Finnish study areas (69% and 71%).

What might explain the difference in lake occupancy between pairs and broods? Some of it may be due to nesting failure owing to predation on nests and adults. However, because the pattern was so consistent among

years within study areas, between different study areas differing in terms of nest predation pressure, at least for hole-nesting ducks (Karjala vs. Häme, see Pöysä et al. 1997, study areas Evo and Intsilä corresponding with Karjala and Häme, respectively), and between different studies (citations in *Introduction*), we suggest that predation explains only a minor part of this difference.

In ducks, breeding period can be divided into at least two parts, pair phase and brood phase, and those may be rather different with respect to food limitation (e.g., Pehrsson 1984, Nummi and Pöysä 1993; see also Rohwer 1992). Breeding females carry fat reserves to breeding grounds, reserves which they may use while searching for protein- and calcium-rich invertebrates needed for egg production (Krapu 1981, Krapu and Reinecke 1992). Adult Mallards are further capable of foraging both on and under the water surface (to a depth of 40 cm; Pöysä 1983), giving access to a wide range of food resources. On the other hand, newly hatched ducklings are very dependent on emerging insects encountered on the water surface or on emergent plants (Chura 1961, Pehrsson 1979), availability of which may be weather dependent (Sjöberg and Danell 1982). As found in studies with radio-marked females in North America, movements between ponds are frequent in Mallard broods during the first weeks after hatching (Talent et al. 1982, Rotella and Ratti 1992, Mauser et al. 1994, Dzus and Clark 1997). Those movements may be important in locating habitats rich in food and cover (Talent et al. 1982, Rotella and Ratti 1992; but see Dzus and Clark 1997). Furthermore, broods that move frequently may suffer greater mortality (Rotella and Ratti 1992; but see Talent et al. 1983, Dzus and Clark 1997) and fledging success may be lower in nonpreferred than in preferred habitats (Mauser et al. 1994). Hence, observations from two continents together suggest a general pattern that some ponds or lakes are inferior brood habitats, but the reason why remains unclear.

Our experimental results of changes in duckling

TABLE 3. Pearson correlations between daytime mass change and mass change the following night, and between daytime mass change and mass change the previous night in three groups (control, poor-lake experiment, and rich-lake experiment).

Experimental group	N	r	P
Daytime mass change vs. mass change the next night			
Control	11	-0.555	>0.05
Poor-lake experiment	11	-0.745	<0.02
Rich-lake experiment	11	-0.378	>0.20
Daytime mass change vs. mass change the previous night			
Control	8	-0.736	>0.05
Poor-lake experiment	8	-0.461	>0.20
Rich-lake experiment	8	-0.535	>0.10

Notes: Analyses are based on trial-specific averages given in Figs. 2 and 3. Sample sizes for the second set of correlations are smaller because the experimental series were interrupted two times.

mass give further evidence that many boreal lakes are indeed inferior duckling habitats. Ducklings foraging on poor lakes gained less mass than ducklings foraging on rich lakes despite the fact that our contrast was conservative (i.e., excluding eutrophic lakes). Furthermore, at night when ducklings from both lake types had equal and free access to food, those from poor lakes gained more body mass than those from rich lakes, indicating that ducklings feeding on poor lakes during the day compensated for inferior habitat quality by feeding more the following night. This dynamic response was clearest in ducklings foraging on the poor lakes.

Because we were able to exclude all other factors potentially affecting mass changes, except trophic status of lakes, we conclude that poorer performance of ducklings on poor lakes was because of food limitation. This conclusion is consistent with earlier studies addressing possible food competition between ducklings and fish. Mallard and American Black Duck ducklings feeding on ponds with fish-reduced abundance of invertebrates obtained less food and gained less body mass than ducklings feeding on ponds with a high invertebrate abundance (Hunter et al. 1984, 1986, Pehrsson 1984, Hill et al. 1987).

Our experimental results, together with earlier findings show that mass change of Mallard ducklings in response to food limitation is a general phenomenon. How does this relate to population limitation and regulation? Because the proportion of lakes lacking wild Mallard broods was higher among poor lakes than among rich ones, and because proportion of unoccupied lakes in general was higher for broods than for pairs, we suggest that, if present, food limitation at the population level is likely to operate at the brood stage, rather than during the preceding phases of lake selection and nesting. As proportion of lakes lacking wild Mallard broods was similar and quite high in all three study areas (see above), food limitation operating at the brood stage may be a frequent and general phenomenon on boreal lakes. In another experiment we (Pöysä et al. 1998) manipulated occupation of lakes by introducing extra Mallard pairs to study habitat selection rules used by later arriving, wild, Mallard pairs. Many (29%) lakes lacked wild Mallard pairs following manipulation, even though, based on the conspecific attraction hypothesis (Stamps 1988), we expected that introduced birds should attract wild conspecifics (see Pöysä et al. 1998 for details). However, the reason why lakes lacked wild pairs in that experiment remains unclear. The present results suggest that many unoccupied boreal lakes are inferior Mallard habitats and that food-based limitation of population density may occur during the brood stage. Thus, the fact that many boreal lakes are unoccupied does not necessarily support the hypothesis that boreal bird communities are unsaturated (cf. Järvinen and Ulfstrand 1980).

However, the connection between food limitation

found here, at the brood stage, and the actual limitation and regulation of breeding Mallard populations remains open for further studies. We have indeed shown that ducklings on poor lakes gain less mass, but we do not know whether this reduction is great enough to actually affect survival of individuals and broods, let alone to limit or regulate populations. There is evidence that slow growth rate, due to late hatching, affects survival and recruitment of goslings in Lesser Snow Geese (*Anser c. caerulescens*) (Cooke et al. 1984, Cooch et al. 1991) and Black Brant (*Branta bernicla*) (Sedinger and Flint 1991, Sedinger et al. 1995). In a review of the effects of intraspecific variation in egg size in birds, Williams (1994) stressed that slower growth of smaller chicks (hatched from smaller eggs) immediately after hatching could determine high levels of early chick mortality observed in many species. In addition, lower survival of young that fledge at lower masses has been demonstrated in many species with altricial young (Martin 1987). Finally, even though Mallard females can take their broods to lakes with ample food, movements between poor and rich lakes may increase duckling mortality (see above), thus directly influencing fitness and population regulation.

Studying mechanisms of population dynamics and regulation with controlled field experiments remains a challenging task for the future even in the most well-known and frequently studied taxonomic groups (Boutin 1990, Harrison and Cappuccino 1995, Myers and Rothman 1995). With respect to Mallards, the body of evidence accumulated so far suggests that (1) it is important to recognize at what stage of the yearly reproductive cycle food limitation may occur, (2) brood stage may be more important than nesting stage for possible population limitation and regulation, and (3) absence of Mallards from a high proportion of lakes in the boreal region of Fennoscandia may be a result of low production of ducklings due to food limitation, rather than a result of unsaturated populations.

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