

Breeding success of sympatric dabbling ducks in relation to population density and food resources

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Breeding success in sympatric mallard *Anas platyrhynchos*, teal *A. crecca* and wigeon *A. penelope* in a boreal watershed in Finland was studied for 12 years. Benthic and surface-emerging prey animals were trapped to obtain annual indices of food abundance. Mallard and teal were equally abundant over the years, being roughly twice as numerous as wigeon.

Pair density, brood:pair ratio and duckling:pair ratio were used to test the hypothesis that per capita breeding success decreases in a density-dependent fashion as either pair density or the number of nesting pairs per available food unit increases. In mallard we found no density-dependent patterns at all. In teal per capita brood production decreased as prey animals became relatively scarcer, but this interpretation may not be robust. In wigeon, however, there were two independent significant patterns of direct density-dependence in a temporal succession, i.e. between pair density and per capita brood production in the early part of the breeding season, and then between per capita abundance of surface-emerging insect prey and the number of ducklings per pair. Despite wide dietary overlap and frequent co-occurrence on single lakes among species in the guild, we found no evidence for interspecific density-dependent effects. We hypothesize that there is no or infrequent food limitation for breeding dabblers in this system, and that behavior may be the process behind the pattern of density-dependence in wigeon.

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Nicholson (1933) was one of the first to discuss whether animal populations are regulated by density-dependent feed-back processes on breeding performance and mortality. Almost 70 years later the topic remains controversial and largely unresolved despite extensive research and syntheses (Woiwood and Hanski 1992, Newton 1998). Important reasons for this are a continuous development and change of analytical tools to detect density-dependence as well as recurring disagreement about the conceptual foundation (Vickery and Nudds 1984, Pollard et al. 1987, Dennis and Taper 1994, Reddingius 1996, Shenk et al. 1998, Berryman and

Turchin 2001, White 2001). Moreover, when and where there is actually consensus that density-dependent processes affect populations, they may vary in strength in space and time, or act only intermittently.

Despite these difficulties, interest in density-dependent population processes is likely to remain strong, especially when it comes to wildfowl and other harvested animals. This is because decisions about conservation as well as levels and timing of harvest need to rest on an understanding of how and when populations are limited or regulated (Caughley and Sinclair 1994, Kokko et al. 1998, Boyce et al. 1999), e.g. whether

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harvest mortality is compensatory or additive in relation to natural mortality.

Population ecology of ducks in the Holarctic has been part of the issue of density-dependence for decades, but evidence is still contradictory whether duck numbers are mainly determined by density-independent factors such as winter cold and summer drought, or by density-dependent feedback on breeding success or mortality (Anderson and Burnham 1976, Burnham and Andersson 1984, Kaminski and Gluesing 1987, Bethke 1993, Trost et al. 1993, Krapu et al. 1997, Newton 1998, Sheaffer 1998). One reason for disagreement may be that patterns and processes really do differ significantly between years, sites, species, and even between populations of the same species. As most studies of per capita breeding success in dabbling ducks have been done in their North American range there is a general lack of corresponding European data.

Taking the mallard (*Anas platyrhynchos* L.) as an example, there is no consistent pattern even in the rather few European studies which have addressed resource limitation during the breeding period and density-dependence in breeding success. Based on long-term observational data, Hill (1984) found evidence for direct density-dependence in breeding success, and we have experimental data showing that ducklings may experience food limitation on some oligotrophic boreal lakes (Nummi et al. 2000, Pöysä et al. 2000, Sjöberg et al. 2000). However, in contrast to the latter three studies, descriptive long-term data from similar settings in Finland reveal no pattern of density-dependent breeding success (Pöysä 2001). From a European perspective per capita breeding success and recruitment patterns thus need to be studied under yet a wider range of natural settings, regionally as well as on the continental scale.

Another but general and more fundamental problem to this date is the total lack of studies of density-dependence in waterfowl and in other species in which per capita birth or death rate is related to resource units instead of density (i.e. individuals per area unit; cf. Newton 1998, p. 115). As levels of crucial resources frequently vary between years and among superficially similar patches, this lack may disqualify conclusions in many previous studies, especially if density-dependence is thought to be mediated through resource competition. A connection between abundance of invertebrate prey and breeding success, specifically duckling performance, is well established for waterfowl (Hill et al. 1987, Sediger 1992, Cooper and Anderson 1996, Cox et al. 1998), highlighting the relevance of studies combining density and per capita resource availability.

We here relate variation in per capita breeding success in three sympatric breeding dabbling ducks to population density and food resource abundance over a 12-year period. Specifically, we: a) describe natural variation in the number of pairs, broods, and older

(pre-fledgling) ducklings, b) describe between-year variation in nesting success and brood mortality, c) test the hypothesis of intraspecific density-dependent breeding success (per capita birth rate), and d) test the rarely addressed hypothesis of intraguild heterospecific density-dependence in breeding success.

Materials and methods

Study area

This study was carried out in an oligotrophic mid-boreal 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 (Kaitalammi at the Evo Game Research Station). Total lake area is 290 hectares and their total shoreline 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 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 *Carex* spp.), although a few are more mesotrophic with narrow stands of *Equisetum* spp., *Typha* spp., and *Phragmites australis* (Cav.) Steud.

Located in a continental cool climate, the study lakes are frozen over from November to late April. They are thus “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.

Waterfowl counts

The number of nesting pairs of mallard, teal (*Anas crecca* L.), and wigeon (*Anas penelope* L.) was estimated using data from the earlier of two pair counts in May each year in 1989–2000 (Nummi and Pöysä 1995; see Koskimies and Pöysä 1991 for general method). Breeding success was monitored in five brood counts (combined point and round counts as described in Nummi and Pöysä 1995) in June through July. Duckling age was determined following the classification by Pirkola and Högmänder (1974) i.e. a combination of schemes in Gollop and Marshall (1954) and Linkola (1962). Breeding success is here expressed as: a) the number of broods, and b) the number of ducklings in stage 2a or older per brood (i.e. 19–25 days old; Schemnitz 1980). When there were multiple observations of a brood in stage 2a or older, we used data from the latest sighting until stage 3 if fledglings were ob-

served too. If fledged juveniles but not stage 3 ducklings were seen, the number of juveniles on a lake was used instead. Fledged birds on lakes where there were no previous duckling observations were included, as they were supposed to be of local origin.

Food resources

Our general methods for trapping prey invertebrates in activity and emergence traps are described in Nummi and Pöysä (1993). For the present study we used catch data from eight of the 52 lakes: Iso Vehkajärvi, Iso Ruuhijärvi, Keskinen Mustajärvi, Majajärvi, Pitkänniemenjärvi, Rahtijärvi, Tekumi (Saukonlammi), and Ylinen Rautjärvi. Samples were from one week's trapping in early June each year (exact dates somewhat different between years in order to adjust for phenological differences), assuming that prey abundance at this time best reflects what is available to ducklings of all three species during their early and most vulnerable period in life (Hill et al. 1987). Activity traps were used to catch benthic and free-swimming taxa, of which all invertebrates and small tadpoles were used for the present analyses. Floating emergence traps were used to sample invertebrates leaving their aquatic stage.

Food index 1 (FI 1) is based on activity trap data and was obtained by weighting for differences between lakes in size-abundance distribution of prey and in vegetation luxuriance (as in Nummi and Pöysä 1993, 1995). Food index 2 (FI 2) is based on the same data from the same traps but is simply the mean number of invertebrates caught per trap per day, i.e. there was no weighting for differences in prey size or in vegetation luxuriance. Food index 3 (FI 3) is the mean number of insects per emergence trap per day. As the present analysis is on the watershed level, food indices for each of the eight lakes were pooled and averaged on a year-by-year basis to obtain resource abundance esti-

mates assumed to be representative for the entire watershed that breeding season (cf. pp. 583–585 in Pöysä et al. 2000). There were generally four traps of each type on all lakes, but food indices are expressed as means per 100 trap days to compensate for lost traps and a shorter sampling period in 1989.

Statistical procedures

All tests were run with SYSTAT 9.01 (SPSS Inc.), and two-tailed probabilities were used unless stated otherwise. Variables that deviated significantly from normality as revealed by the Lilliefors test ($P < 0.05$, $N = 12$ years throughout) were log-transformed before subsequent analyses. Arcsine transformation was not used as no ratio variables deviated significantly from normality. All tests were also run with corresponding non-parametric procedures, producing the same result in 98% of the cases (all tests but one).

Results

Duck numbers

Pair counts revealed that mallard and teal were equally numerous in the Evo watershed over the years and roughly twice as abundant as the wigeon (Table 1). In all three species, pair, brood and duckling numbers varied considerably, being up to four times higher in "peak years" than in "bottom years". Between-year variations were larger in mallard and teal than in wigeon. Teal and wigeon produced more broods per pair than did mallards (ANOVA; $F = 5.76$, $N = 36$, $P < 0.01$). The number of ducklings per pair averaged more similar among the species, but it was significantly higher in teal than in mallard (t-test; $t = -2.24$, $P < 0.05$).

Table 1. Breeding data for dabbling ducks on 52 lakes in a watershed in southern Finland in 1989–2000. All numbers are based on data from 12 breeding seasons. "Density" denotes mean per 1000 m shoreline.

	Pairs	Broods	Ducklings	Broods/pair	Ducklings/pair
Mallard					
Mean	21.3	5.1	20.7	0.24	0.96
Range	9–35	2–11	7–46	0.11–0.41	0.56–1.48
CV	0.39	0.55	0.52	0.41	0.31
Density	0.42	0.10	0.41		
Teal					
Mean	20.2	8.0	28.0	0.40	1.36
Range	12–41	2–16	8–68	0.15–0.58	0.62–2.42
CV	0.39	0.46	0.58	0.34	0.40
Density	0.40	0.16	0.55		
Wigeon					
Mean	8.9	3.33	10.2	0.42	1.23
Range	4–14	2–5	1–17	0.17–0.71	0.11–2.20
CV	0.36	0.32	0.43	0.42	0.47
Density	0.18	0.07	0.20		

Teal and mallard co-varied in the sense that “good mallard years” were also “good teal years”, measured as the correlation between pair number, brood number and duckling number in these species (Pearson correlation coefficients (r): 0.77 ($P < 0.001$), 0.63 ($P < 0.02$), 0.73 ($P < 0.005$), $N = 12$ years throughout). Pair, brood as well as duckling number in wigeon varied independently of the other two species ($P > 0.1$ in all cases; $N = 12$).

Food resources

A general picture of the taxonomic composition of the catch in the activity traps is given by Elmberg et al. (1992) and in Table 1 in Pöysä et al. (1994a, b). Emergence trap catches were totally dominated by *Diptera*, *Trichoptera*, and *Ephemeroptera* in order of decreasing abundance. Overall prey abundance varied considerably between years as revealed by the food indices, but decreasingly so from FI 1 to FI 3 (Table 2). Fluctuations were general on the watershed level, i.e. lakes kept their general rank between years, further justifying the use of pooled indices as measures of food resource levels (Fig. 1; Kendall's coefficient of concordance (W): 0.23 for FI 1, 0.36 for FI 2, and 0.25 for FI 3; $P < 0.006$ in all cases; $M = 12$ years, $N = 8$ lakes). Food indices were not significantly correlated with each other, and r -values in pair-wise tests were not even consistent in sign. Thus, all three indices were used as independent variables in subsequent analyses when looking for patterns in breeding success.

Although nesting and brooding generally preceded prey sampling, the number of broods observed was

Table 2. Food indices (FI 1–3) obtained from eight lakes in the Evo watershed. Annual numbers are mean and standard deviation ($N = 8$ lakes). All indices are expressed per 100 trap days. FI 1 and FI 2 were obtained from activity traps catching mainly benthic and free-swimming taxa, whereas FI 3 was based on floating emergence traps catching insects leaving their aquatic stage.

Year	Food index 1	Food index 2	Food index 3
1989	69.4 (45.9)	138 (85.4)	72.6 (48.5)
1990	184 (110)	156 (172)	40.2 (19.8)
1991	202 (272)	217 (351)	71.4 (35.3)
1992	426 (338)	264 (212)	46.2 (18.1)
1993	177 (74.7)	60.7 (32.0)	26.8 (21.8)
1994	196 (142)	311 (274)	55.4 (24.1)
1995	118 (36.0)	126 (49.6)	30.4 (19.5)
1996	103 (67.1)	156 (123)	43.3 (21.6)
1997	382 (381)	118 (89.6)	24.1 (17.0)
1998	447 (326)	146 (58.2)	58.9 (23.5)
1999	475 (296)	134 (45.0)	33.0 (17.8)
2000	318 (273)	109 (88.9)	44.2 (39.9)
12 year mean	257.8	161.4	45.6
12 year range	69.4–475	60.7–311	24.1–72.6
CV	0.56	0.43	0.36

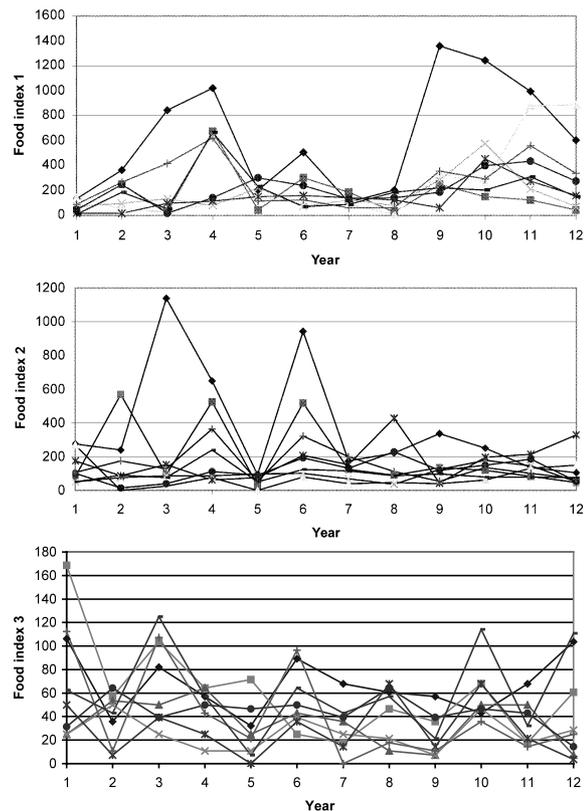


Fig. 1. Lake-level between-year variation in food resources on eight lakes. Food index 1 and 2 concern benthic invertebrates, food index 3 surface-emerging insects (see methods for calculation and units). Year 1–12 is 1989–2000.

positively correlated with FI 3 in teal ($r = 0.74$, $P < 0.005$, $N = 12$) and with FI 1 in wigeon ($r = 0.56$, $P < 0.05$, $N = 12$). Mallard brood number did not correlate with any food index ($P > 0.2$). Based on the well-established positive association between invertebrate abundance and duckling performance (Hill et al. 1987, Sediger 1992, Cooper and Anderson 1996, Cox et al. 1998) we next considered an explicitly one-sided assumption of positive correlation between food indices and duckling number. There was none in mallard and wigeon, but in teal duckling number was significantly correlated with FI 3, i.e. surface-emerging insects ($r = 0.51$, $P < 0.05$, $N = 12$ years).

Per capita breeding success vs density

As lake area and shoreline length did not vary between years, the number of nesting pairs in a given year became a density measure in itself. We thus used pair number as “the classical density measure”, and broods/nesting pair as well as ducklings/nesting pair as measures of per capita breeding success. In pair-wise correlations there is no pattern of density-dependent decrease in productivity in either mallard or teal (den-

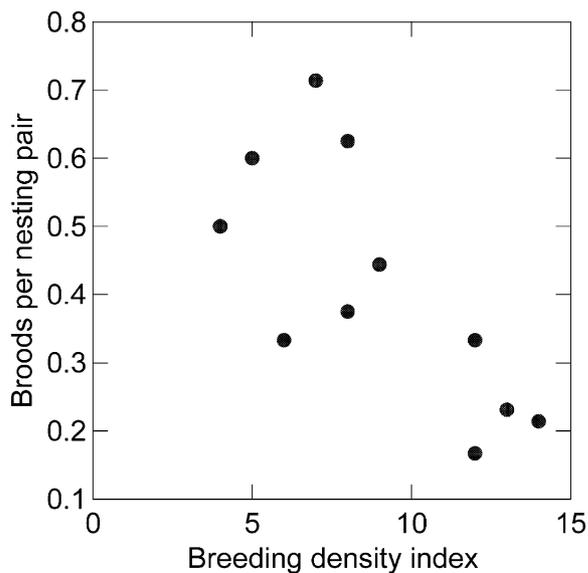


Fig. 2. Intraspecific direct density-dependence in per capita brood production in wigeon in an oligotrophic watershed in southern Finland. Pearson correlation coefficient = -0.72 , $P < 0.005$, $N = 12$ years. "Breeding density index" is the number of pairs in the watershed. To obtain pairs per km^2 lake area divide the index by 2.9, and to obtain pairs per 1000 m shoreline divide by 50.8. Two data points have the same value at $X = 9$, $Y = 0.44$.

sity vs broods per pair and density vs ducklings per pair: $P > 0.5$, and $N = 12$ in all four cases). In wigeon, however, brood:pair ratio decreases significantly as pair density increases (Fig. 2). Tested similarly, there is no significant density-dependence in wigeon duckling productivity, although the trend was clearly negative also in this case ($r = -0.43$, $P > 0.10$).

Years of high or low per capita productivity were not the same in the three species; i.e. there was no correlation in pair-wise comparisons (mallard vs teal, teal vs wigeon, mallard vs wigeon), neither for per capita brood number nor for per capita duckling number (r with no consistency in sign within species-pair comparisons; $P > 0.1$ and $N = 12$ in all six cases).

As a consequence of the wide dietary overlap between ducklings of dabbling ducks (Sugden 1973, Sedinger 1992) it is fair to hypothesize that density-dependent processes may also occur within the guild, i.e. as a result of interspecific interactions. We thus tested for correlation between breeding performance in a certain species and its corresponding heterospecific pair density, i.e. the combined pair number (density) of the two other species in a given year. Neither brood:pair ratio nor duckling:pair ratio correlated with the combined heterospecific pair density in any of the three species ($P > 0.5$ in mallard and teal, $P > 0.05$ in wigeon; $N = 12$). Finally, assuming combined intra- and interspecific competition produced the same result for all species, i.e. no correlation between combined

density on the one hand, and per capita brood or duckling productivity on the other (test results as in previous sentence).

Per capita breeding success vs food resources

When it comes to food and the general hypothesis of resource-mediated density-dependence in breeding success we have an explicitly directional prediction; brood and duckling production per pair should both increase as the number of food units per pair and brood increases. This is often considered 'the true test' of density-dependence, though so far only rarely performed (Newton 1998).

For each species each food index was divided by pair number on an annual basis to obtain an intraspecific estimate of "food units per pair", which in turn was tested for correlation with the per capita breeding success variables for this species (Table 3, "conspecific rows"). For mallard there was neither any significant correlation nor any consistency in sign. However, the correlation coefficient was positive throughout for teal and wigeon, and four pair-wise tests were significant, meeting the prediction of increased per capita breeding success with increased per capita food abundance in both species. Per capita production of ducklings in wigeon was the most significant association and FI 3 is here in practice abundance of *Diptera*, mainly *Chironomidae* (Fig. 3).

Similarly, annual food indices were divided by the combined number of pairs of two species at a time to obtain a heterospecific "food units per pair" estimate for the third species (e.g. FI 1 for a given year was divided by the combined number of mallard and teal pairs that year to address food-mediated heterospecific density-dependence in breeding success in wigeon). Again, per capita breeding success in a species was predicted to increase as the food abundance per putative competitor increased, but there were no significant correlations and no consistency in sign for any species (Table 3, lower three rows). With respect to food resources our data thus refute the hypothesis of intraguild heterospecific density dependence in breeding success.

Models for density-dependence

Multiple stepwise regression was applied to analyze the three cases in which breeding success showed density-dependent patterns in pair-wise tests, i.e. brood:pair ratio in teal and both breeding success measures in wigeon. Independent variables were pair density for each of the three species and the intraspecific food unit abundance for FI 1 through FI 3. Combining variables of plain pair density and food units per pair in this way, did not, however shed any new light. When the original

Table 3. Per capita breeding success in relation to per capita prey abundance in dabbling ducks. Given are Pearson correlation coefficients, and one-tailed probabilities because a positive association is assumed. N = 12 years in all cases. Food indices (FI 1, FI 2, and FI 3) are explained briefly in Table 2 and fully in the methods section.

Food resource measure	Mallard breeding success			Teal breeding success			Wigeon breeding success		
	Broods/pair	Ducklings/pair	Ducklings/pair	Broods/pair	Ducklings/pair	Ducklings/pair	Broods/pair	Ducklings/pair	Ducklings/pair
FI 1/breeding conspecific pairs	0.44, P > 0.05	-0.13, P > 0.25	0.36, P > 0.10	0.42, P > 0.05	0.14, P > 0.25	0.29, P > 0.10	0.42, P > 0.05	0.29, P > 0.10	0.29, P > 0.10
FI 2/breeding conspecific pairs	-0.10, P > 0.25	0.27, P > 0.10	0.49, P < 0.05	0.42, P > 0.05	0.40, P > 0.05	0.25, P > 0.10	0.42, P > 0.05	0.25, P > 0.10	0.25, P > 0.10
FI 3/breeding conspecific pairs	-0.14, P > 0.25	-0.10, P > 0.25	0.49, P < 0.05	0.49, P < 0.05	0.14, P > 0.25	0.65, P < 0.01	0.49, P < 0.05	0.65, P < 0.01	0.65, P < 0.01
FI 1/breeding heterospecific pairs	0.32, P > 0.10	-0.05, P > 0.25	0.29, P > 0.10	0.28, P > 0.10	0.19, P > 0.25	0.07, P > 0.25	0.28, P > 0.10	0.07, P > 0.25	0.07, P > 0.25
FI 2/breeding heterospecific pairs	-0.25, P > 0.10	0.22, P > 0.10	-0.01, P > 0.25	-0.24, P > 0.10	0.18, P > 0.25	-0.43, P > 0.05	-0.24, P > 0.10	-0.43, P > 0.05	-0.43, P > 0.05
FI 3/breeding heterospecific pairs	-0.25, P > 0.10	-0.12, P > 0.25	0.31, P > 0.10	-0.18, P > 0.25	0.06, P > 0.25	0.10, P > 0.25	-0.18, P > 0.25	0.10, P > 0.25	0.10, P > 0.25

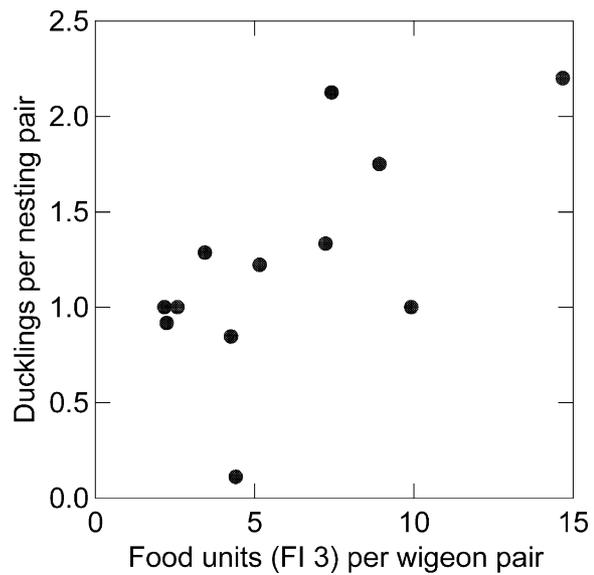


Fig. 3. Intraspecific prey resource-related direct density-dependence in breeding success in wigeon, i.e. the number of ducklings per pair decreases as the number of emerging insects per wigeon pair decreases. Pearson correlation coefficient = 0.65, $P < 0.01$, $N = 12$ years. Food index 3 is described in materials and methods.

strongest pair-wise correlation had entered each model, coefficients of partial correlations for the remaining variables were too low to let them enter, and all models thus remained univariate.

Discussion

Abundance of ducks

Species composition and relative abundance of the species in this study are representative for waterfowl communities of the boreal forest biome in the Western Palearctic (Haapanen and Nilsson 1979, Elmberg et al. 1994, Hagemeyer and Blair 1997, Väisänen et al. 1998). In all three species pair density corresponds well with Finnish national means (Väisänen et al. 1998). Together this indicates that we have been studying rather typical duck communities in rather typical years.

Mallard brood:pair ratios are somewhat higher than those observed in boreal Canada by Nudds and Cole (1991), but they fall in the middle of the general range reported for this widespread species (Johnson et al. 1992). Brood:pair ratios fell in the order wigeon–teal–mallard, a pattern corresponding well to previous Finnish findings (Nummi and Pöysä 1995, 1997). The proximate cause behind this trend is unclear, but it may reflect differences between species in nesting phenology and a concurrent decrease in predation from early to late nesters. Support for this hypothesis is provided from Latvia, where Opermanis et al. (2001) found that

large corvids were the main predators on early nests, i.e. chiefly mallard.

Food resources

Plain brood number was correlated with prey abundance in two out of nine pair-wise tests (3 species \times 3 indices). In general this watershed level study thus shows surprisingly weak links between annual invertebrate abundance and overall breeding output (Hill et al. 1987, Sediger 1992, Cooper and Anderson 1996, Cox et al. 1998). However, none of the latter studies concerns an oligotrophic boreal scenario, where density-independent factors such as cool weather and late frosts may be more important on the population level in most years than is food limitation.

Per capita breeding success vs density

Our present findings agree with those of Pöysä (2001) in refuting direct density-dependence in breeding success in mallard. Both studies thus appear to disagree clearly with Hill (1984), who found that mallard duckling mortality was density-dependent. It should be noted, though, that the main regulatory mechanism in Hill's case was not duckling mortality but rather the subsequent density-dependent winter mortality. The latter factor remains to be studied in boreal populations of dabbling ducks in the Western Palearctic (Pöysä 2001), hence the disagreement with Hill's overall conclusion may be less than it seems. Kaminski and Gluesing (1987) gave some support for direct density-dependence in recruitment in hemi-boreal Canadian mallards, but we still regard the evidence for density-dependent breeding output in mallard as contradictory.

It is premature to offer an explanation why wigeon was different from mallard and teal in its density-dependent decrease in brood and duckling production. We may have to step down from the watershed to the lake level in order to understand the processes behind this pattern, and that was not the object of the present study. However, census data show that wigeon does not breed in lakes different from those of the other two species, and also that it does not tend to crowd into more lakes than the other species do. Being a breeder of boreal forest lakes the wigeon simply remains inadequately studied and little is known of its population biology.

We see no support for the idea that pair density of other dabbling ducks affects per capita breeding success in any of the three species. Although it is reasonable to look for intraguild heterospecific effects, negative or positive (Toft et al. 1982, Elmberg et al. 1997; for statistical modelling of interspecific effects in

population dynamics of small mammals see Hansen et al. 1999, Merritt et al. 2001), our results may not be all that surprising. Population densities were low in absolute terms and there is sometimes temporal segregation between the brood stage of the three, which would tend to counteract food limitation and competition.

Per capita breeding success vs food resources

Following Newton (1998), p. 115 we performed a more stringent test for density-dependence by also relating breeding success to a specific and measurable crucial resource, i.e. pair-specific prey abundance (Nummi and Pöysä 1993, Cooper and Anderson 1996). From Table 3 it appears that our data support the notion that food resources is a more relevant measure than plain pair density, but note that three of the four significant correlations ($r=0.49$) would not have emerged had not the prediction been explicitly directional. Interestingly, wigeon once more stands out as being different by showing a highly significant pattern of direct density-dependence in breeding success, especially when considering the abundance of emerging insects. This agrees with Gardarsson and Einarsson (1997), who found that variations in per capita breeding success in this species corresponded well to current abundance of *Chironomidae*.

With respect to mallard and teal this study rather provides a case against food-limitation on the watershed level. At first this seems to contradict our experimental results from similar oligotrophic lakes in near-by Sweden (Nummi et al. 2000, Sjöberg et al. 2000). However, the latter studies are lake-level approaches implying that some lakes are simply too poor for successful brood-rearing, and we may moreover have a situation where lake-level patterns do not translate to the watershed or population level. Similarly, Pöysä (2001) found that habitat distribution of breeding mallards indicated habitat-specific limitation but this did not translate to limitation at the population level. In other words, our migratory duck females return to their natal sites, but may change lakes within the watershed in response to current lake-specific food conditions or to some other cue.

We did not study diet choice in ducklings in detail, but as far as we could tell all three species foraged in the same microhabitats at the same time of the day, and they should thus encounter similar prey. We thus believe that dietary overlap is very large. Still, we find no support for density-dependent effects of food resource abundance on breeding success when related to the number of heterospecific congeners. This suggests that the density-dependent patterns in wigeon do indeed arise from intraspecific interactions, possibly aggressive and territorial behavior.

Conclusions

For this boreal setting we find no support for the hypothesis of direct density-dependence in breeding success in mallard. In teal there is a pattern of decreasing per capita brood production with decreasing number of food units per teal pair, but this interpretation may be fragile. In wigeon, however, there is a consistent and highly significant pattern of density-dependence in temporal sequence, i.e. between plain pair density and per capita brood production in the early part of the breeding season, and later between per capita prey abundance and the number of ducklings per pair.

We are well aware of the problems with time series data and type II statistical errors, especially when it comes to analysing patterns of density-dependence in fluctuating population (Woiwood and Hanski 1992). There is also a potential problem of statistical mass significance in our analyses (Rice 1989). However, even though we have the longest time series published for this type of study in a multi-species assemblage of dabbling ducks the power of our tests is low. In addition, we have tested and rejected or accepted the hypothesis of density-dependent breeding success individually in each species. Therefore we do not consider it necessary to correct the type-I error rate (see also Rice 1989, p. 225). Moreover, the patterns observed appear robust because results as well as interpretations were identical when we re-ran all tests with non-parametric methods.

In order to understand population and community processes of these species we need: 1) more data from breeding grounds farther south in Europe, or where the overall breeding density is higher; and 2) to look at mortality patterns on staging and wintering grounds. After all, Hill (1984) found the strongest density-dependent effects in winter, and similar patterns may prevail in some shorebirds (Durell et al. 2001). To truly disentangle causal links behind undiscovered as well as documented patterns of birth and death rate in waterfowl we strongly advocate a more experimental approach (Sheaffer 1998, Shenk et al. 1998).

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