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Johan Elmberg

Census data from a eutrophic lake collected in 1987-1999 were used to study nesting and breeding success in mallards *Anas platyrhynchos*. In each year there were 6-19 pair counts and 13-34 brood counts. The maximum combined count of single males and pairs (i.e. on any day in any of three census periods in May) provided the best fit with subsequent estimates of breeding success. Nesting success (average brood:pair ratio = 0.52), brood size of older ducklings (mean = 5.7) as well as fledgling success (2.86 juveniles per nesting pair) were higher than in many previous mallard studies. *Per capita* brood production as well as *per capita* fledgling production was negatively density dependent, but the latter was not statistically independent of the former. There was no correlation between *per capita* fledgling success and duckling mortality on a year-by-year basis, hence the density-dependent pattern in breeding success appears to be mediated through variation in nesting success. The number of paired females at the start of the breeding season correlated positively with the production of fledged juveniles the year before.

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Density-dependent population processes remain a central and controversial issue in ecology, conceptually, statistically as well as for applied purposes (e.g. Nicholson 1933, Shenk, White & Burnham 1998, Berryman & Turchin 2001, White 2001). Duck populations have been part of this debate for decades, but there is as of yet little consensus as to whether numbers of these and many other harvested wildfowl are primarily determined by density-independent factors such as winter cold and summer drought, or by density-dependent feedback on breeding success or mortality (Trost, Dickson & Zavaleta 1993, Newton 1998, Miller 2000).

Being one of the most important game species in the Holarctic, the mallard's *Anas platyrhynchos* population ecology has been studied extensively (Anderson & Burnham 1976, Burnham & Anderson 1984, Hill 1984, Kaminski & Gluesing 1987, Sheaffer 1998), but few general patterns emerge concerning limitation or reg-

ulation. One reason may be that patterns and processes actually vary significantly between years or among populations. For example, between-year variation in population size and in the availability of breeding habitat appear to be much less in Northern Europe than in North America (e.g. Cowardin & Blohm 1992, Bethke 1993, Bethke & Nudds 1993, Pöysä 1998, Väisänen, Lammi & Koskimies 1998).

From 'a European mallard perspective', little is known about natural temporal variation in vital rates, and no population model has been published yet. Breeding success is addressed in several European papers, at least two of which present some evidence for negative density dependence (e.g. Hill 1984, Pehrsson 1991, but see Pöysä 2001). Our own studies of breeding boreal mallards have revealed no sign of competition in the nesting phase (Elmberg, Pöysä, Sjöberg & Nummi 1997, Pöysä, Elmberg, Sjöberg & Nummi 1998), but have also shown that ducklings may experience food limitation on oligotrophic lakes (Nummi, Sjöberg, Pöysä & Elmberg 2000, Sjöberg, Pöysä, Elmberg & Nummi 2000, Pöysä, Sjöberg, Elmberg & Nummi 2001). Breeding success and recruitment patterns thus need to be studied under a wider range of natural settings, and there is a general lack of long-term lake-level population studies.

This paper is based on a 13-year data set from a eutrophic lake in south-central Sweden, and it has three objectives: 1) to document natural variation in the number of pairs, broods, young ducklings and older (prefledgling) ducklings, 2) to describe between-year variation in nesting success and brood mortality, and 3) to test the main prediction of the hypothesis of density-dependent breeding success, i.e. a decrease in *per capita* birth rate with increasing population density.

Material and methods

Study area

Nasen is a shallow (0.3-0.5 m deep in most places) eutrophic lake situated on clay-rich soil 34 m a.s.l. in a mixed agricultural-wooded landscape 14 km east-southeast of Eskilstuna (59°20'N, 16°45'E) in the boreo-nemoral transition zone of south-central Sweden. The area of open water is approximately 22 ha during the breeding season, but the surroundings are quite level, making the actual lake area 10-20% larger in wet and phenologically late springs, i.e. at the beginning of the mallard's nesting period. Extensive stands of reeds *Phragmites australis* surround the lake, and it is also the dominant emergent plant in the lake proper, covering

some 15% of its area. Nasen's shoreline is 2,200 m measured along the mean water level line. As witnessed by aerial photographs the extent of reed beds has not changed much from 1976 to 1993. There are no adjacent wetlands at all, and the nearest lake is some two kilometres to the east. Hence, the mallard population at Nasen can be considered as closed when it comes to broods and pre-fledgling ducklings.

Nasen has a long history of frequent visits by ornithologists. Regularly breeding wetland birds include great crested grebe *Podiceps cristatus*, bittern *Botaurus stellaris*, whooper swan *Cygnus cygnus*, greylag goose *Anser anser*, teal *Anas crecca*, mallard *Anas platyrhynchos*, common goldeneye *Bucephala clangula*, marsh harrier *Circus aeroginosus*, water rail *Rallus aquaticus*, coot *Fulica atra* and common crane *Grus grus* (Anon. 1994, 1999). Other species, notably gadwall *Anas strepera*, garganey *Anas querquedula*, shoveler *Anas clypeata*, common pochard *Aythya ferina*, and tufted duck *Aythya fuligula* nest in some years and can be seen foraging in summer.

Data collecting

In 1986 an observation platform overlooking all open water of the lake was erected on its north shore. Since then the Eskilstuna Ornithological Club has organised annual breeding season bird counts. I first used data from counts covering the mallard's breeding season in south Sweden, i.e. 13 April - 31 July. However, it was obvious that the April counts included many transient individuals, so I based the subsequent analysis on data covering the period 1 May - 31 July. The reduced data set contained 13 years of data collected on 23-53 days each year (Table 1). Census procedures were strictly standardised as a large number of observers (>40) were involved. Each census consisted of a 2-hour repeated-scan point count by two or three people standing on the

Table 1. Number of census days per month and year at lake Nasen during 1 May - 31 July.

Year	May	June	July	Total
1987	12	11	9	32
1988	19	20	8	47
1989	8	8	12	28
1990	13	11	9	33
1991	18	8	5	31
1992	19	17	17	53
1993	14	11	12	37
1994	14	15	14	43
1995	12	8	13	33
1996	7	11	9	27
1997	6	11	8	25
1998	11	9	4	24
1999	10	6	7	23
Mean	12.5	11.2	9.8	33.5
Range	6-19	6-20	4-17	23-53

observation platform (Koskimies & Väisänen 1991, Bibby, Burgess & Hill 1992). Most counts were done in the morning, when waterfowl activity peaks.

Interpretation of data

In order to reduce interpretation bias, all compilation and all estimates of adult number, brood number, brood history, and the number of juveniles for all years were made jointly in one batch by the author and the local ornithologists Brita and Gösta Nilsson in 2000. Data from three periods in May (i.e. 'early counts': 1-8 May; 'median counts': 12-18 May; and 'late counts': 19-24 May) were used to estimate the number of nesting pairs. The highest number of single males and heterosexually paired males counted on a single day in each period are given in Table 2. These two categories were also combined into 'a nesting estimate' for each period under the conventional assumption that each male in both categories represents a breeding pair (*cf.* Koskimies & Väisänen 1991). Hypothetically, single females would also qualify as 'breeding pairs', but all females seen on Nasen at this time of year were paired. A tenth pair count variable, 'maximum nesting estimate', is simply the highest of the three nesting estimates, and it was used in subsequent analyses (no separate column in Table 2).

Breeding success was measured in three ways: 1) the number of broods, 2) the number of young ducklings (newly hatched; i.e. stage 1a-1c in Gollop & Marshall 1954), and 3) the number of older, almost fledged or fledged ducklings (i.e. stage 2c-3 in Gollop & Marshall 1954). Detailed age classification of ducklings (e.g. Fjeldså 1977: 30) was not part of the original census protocol and could not be reliably reconstructed. As broods were not the same age and because some broods were surely missed on some visits, there is inevitably a degree of subjectivity in the estimates of the number of broods, young ducklings and older ducklings (*cf.* note about bias reduction above).

Statistical analyses

All tests were run with SYSTAT 9.01 (SPSS Inc.), and probabilities are two-tailed unless otherwise stated. Non-parametric statistics were used throughout because: a) the sample size was limited, b) density-dependent patterns cannot *a priori* be assumed to be linear, and c) almost half of the variables deviated significantly from normality as revealed by the Lilliefors test at $P = 0.05$. If anything, this tends to give conservative interpretations due to Type II statistical errors.

Table 2. Number of mallards on lake Nasen during 1987-1999. Early, median and late nesting estimates each comprise the sum of the next two columns on their left, respectively. 'Number of broods' refers to young ducklings. 'Young' and 'older' ducklings are defined in the text.

1. Year	2. Pairs 1-8 May	3. Single males 1-8 May	4. Early nesting estimate	5. Pairs 12-18 May	6. Single males 12-18 may	7. Median nesting estimate	8. Pairs 19-24 May	9. Single males 19-24 May	10. Late nesting estimate	11. Number of broods	12. Young ducklings	13. Older ducklings	14. Older ducklings per brood	15. Brood/pair ratio (highest nesting estimate)	16. Juvenile/pair ratio (highest nesting estimate)
1987	10	5	15	0	10	10	1	9	10	12	48	37	3.1	0.80	2.47
1988	0	10	10	2	24	26	5	28	33	12	106	100	8.3	0.37	2.03
1989	3	20	23	6	26	32	6	27	33	10	57	52	5.2	0.30	1.58
1990	4	10	14	6	15	21	16	36	52	13	88	75	5.8	0.25	1.44
1991	4	11	15	1	23	24	2	21	23	7	52	50	7.1	0.29	2.08
1992	1	3	4	3	11	14	2	22	24	14	135	115	8.2	0.58	4.79
1993	3	17	20	5	12	17	12	28	40	7	38	24	3.4	0.18	0.60
1994	0	10	10	2	7	9	2	12	14	11	44	41	3.7	0.79	2.93
1995	1	4	5	1	3	4	1	11	12	6	51	33	5.5	0.50	2.75
1996	1	2	3	0	1	1	0	7	7	6	39	35	5.8	0.86	5.00
1997	0	3	3	0	3	3	0	6	6	3	28	20	6.7	0.50	3.33
1998	1	7	8	1	11	12	0	15	15	9	51	56	6.2	0.60	3.73
1999	1	6	7	2	7	9	2	10	12	8	45	42	5.2	0.67	3.50
Mean	2.2	8.3	10.5	2.2	11.8	14	3.8	17.8	21.7	9.1	60.1	52.3	5.7	0.52	2.86
Range	0-10	2-20	3-23	0-6	1-26	1-32	0-16	6-36	6-52	3-14	28-135	20-115	3.1-8.3	0.18-0.86	0.6-5.0
C.V.	1.23	0.66	0.61	0.97	0.70	0.68	1.31	0.54	0.66	0.36	0.51	0.54	0.29	0.44	0.44

Results

Translated to the conventional pair-brood count concept (e.g. Koskimies & Väisänen 1991) there were data from 6-19 pair counts and 13-34 brood counts per year. I used 31 May as the dividing date between these two categories (see Table 1), although the earliest broods were generally seen in the last week of May. The number of pair counts did not correlate with their respective result variables in any of the three census periods (N = 13 years; Spearman rank correlation with r_s ranging from 0.06 to 0.33 for the six early measures (columns 2-7 in Table 2; P > 0.20), and r_s 0.39-0.54 for the three late measures (columns 8-10; P > 0.05)). The correlation coefficient was positive in all 10 tests. The number of brood counts did not correlate with the number of observed broods, young ducklings or old ducklings (N = 13; P > 0.10 in all cases; r_s ranged from 0.14 to 0.43 and was positive throughout).

Because females begin incubating in May, the number of single males can be expected to increase from the first through the third pair count period. This is also what happened on Nasen (see columns 3, 6, and 9 in Table 2; P < 0.05, Kruskal-Wallis test statistic: 7.659). Pair number too seemed to increase with time, but this trend was not significant (Kruskal-Wallis test: P > 0.5). This raises the question of which nesting estimate and period provide the best prediction of subsequent breeding success.

For each of the three measures of breeding success there are 10 pair count estimates (three periods times three measures (i.e. see columns 2-10 in Table 2), and finally the maximum nesting estimate (the highest of either column 4, 7 or 10)). The number of broods produced on Nasen was best predicted by the maximum nesting estimate ($r_s = 0.613$, P < 0.025; the probability being one-sided because a positive association was assumed). However, all variables representing the median and late pair count periods correlated significantly with brood number, implicating a robust pattern. This was true also for the number of young ducklings, which correlated significantly with five pair count variables. The best correspondence was obtained with the median nesting estimate, but note that in four years the latter provided a pair estimate smaller than the number of broods subsequently observed. Using the maximum nesting estimate is the only way to avoid such unrealistic combinations, and the correlation between the maximum nesting estimate and the number of young ducklings was significant ($r_s = 0.594$, P < 0.05). Fledgling success, here approximated by the number of older ducklings, correlated significantly with the number of

single males and with estimates from the median as well as from the late period. The best predictor was the median nesting estimate ($r_s = 0.65$), but this was due to the outlier year 1996 in which fewer pairs were estimated to nest than the number of broods later seen. Again the maximum nesting estimate was used, and a significant correlation was obtained ($r_s = 0.56$, P = 0.05). Thus, combining pair number and the number of single males produced a significant correspondence between 'pair count' data and subsequent measures of breeding success. The maximum nesting estimate did not always give the best fit, but it was used below in order not to conflict with reality.

Using the maximum nesting estimate (mean of 13 years = 22 pairs) to calculate mean pair density of nesting mallards on Nasen, values were 1 pair/ha and 10 pairs/1,000 m shoreline. Brood density was 0.41/ha and 4.1/1,000 m shoreline. Measured and derived variables of nesting success are listed in Table 2 (see columns 11-16). Note that 'maximum nesting estimate' was used to calculate the brood:pair as well as the juvenile:pair ratios.

As lake area was practically the same in all years from mid-May onwards, the number of nesting pairs becomes a density measure in itself, and it can be used to test the hypothesis of density dependence. There was indeed a strong such pattern in *per capita* brood production (Fig. 1), as well as in *per capita* fledgling production. However, the latter is strongly correlated with the former ($r_s = 0.72$, P < 0.01), and hence it does not provide
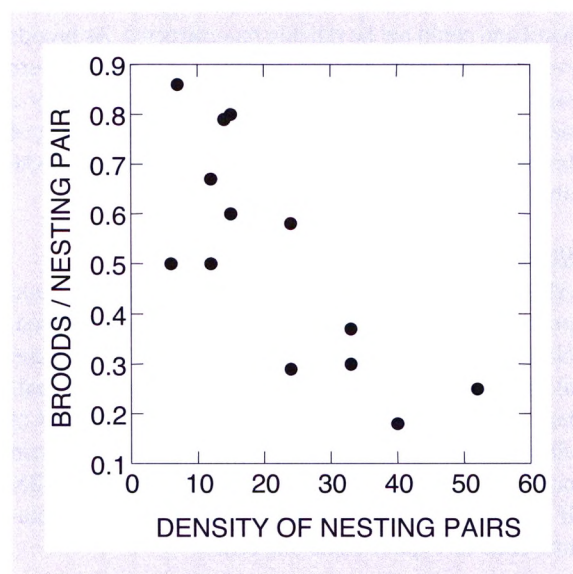

Figure 1. Mallard brood production on Nasen was negatively correlated with density of nesting pairs: $r_s = -0.72$, P < 0.005, one-tailed probability because of a directional prediction; N = 13 years.

Table 3. Mortality in mallard ducklings was not correlated to five density measures from different phases of the breeding season. Mortality was measured as the ratio between 'older ducklings' and 'young ducklings' in Table 2; N = 13 years in all cases.

Density measure	Correlation with mortality (r_s)
Median nesting estimate	-0.32, NS
Late nesting estimate	-0.11, NS
Maximum nesting estimate	-0.055, NS
Number of broods	-0.22, NS
Number of young ducklings	-0.35, NS

statistically independent evidence of density-dependent breeding success. Moreover, there is no significant correlation between any density measure and duckling mortality on a year-by-year basis (Table 3). In other words, the density-dependent breeding success observed appears to be mediated through nest number or nesting success rather than duckling mortality.

Discussion

Although not statistically significant, there was a tendency for years with many late pair counts to produce a higher nesting estimate. It can be argued that if a eutrophic and presumably attractive lake is censused almost every day in the early part of the breeding season transient non-nesting birds are more likely to be observed, which will boost the estimate. Indeed, the very high number of pairs in the late May period in 1990 and 1993 (see column 10 in Table 2) may be due to such birds, as these years were phenologically late with very late hatching in locally breeding mallards, too. My interpretation is that the between-year variation in census activity in this study does not bias the breeding success data.

When compared with published densities for meso- and oligotrophic Fennoscandian lakes, Nasen's pair density is 10-20 times higher and the brood density 6-20 times higher (Danell & Sjöberg 1979, Nummi & Pöysä 1995, Pöysä 2001). Moreover, its mallard population is very dense for a eutrophic lake anywhere (*cf*. McLandress, Yarris, Perkins, Connelly & Raveling 1996). Hence, Nasen serves as an example of a population close to the upper limit of the natural variation in breeding density in temperate European mallards. Here, if anywhere, we have reasons to expect density-dependent effects on breeding performance.

The ratio between the estimate of nesting pairs and successfully hatched broods (see Table 2) is a standard measure of nesting success in studies of breeding waterfowl (brood:pair ratio; e.g. Johnson, Nichols & Schwartz 1992). In this ratio Nasen ranks fairly high too, i.e.

there were more broods per nesting pair than in most previous mallard studies, both North American and European (e.g. Johnson et al. 1992, Rotella & Ratti 1992, Nummi & Pöysä 1995, but see Mauser & Jarvis 1994). It may be that Nasen offers unusually safe nesting areas in the brushy bottomlands surrounding the lake. However, I assume that predation still was the most important reason for nest failure (*cf*. Opermanis, Mednis & Bauga 2001).

Duckling survival, expressed either as late brood size ('older ducklings per brood' in Table 2) or as the juvenile:pair ratio, was also high in comparison with previous mallard studies (Hill, Wright & Street 1987, Orthmeyer & Ball 1990, Rotella & Ratti 1992, Mauser & Jarvis 1994, Nummi & Pöysä 1995, McLandress et al. 1996, Longcore, Clugston & McCauley 1998, Krapu, Pietz, Brandt & Cox 2000). This can either be seen as a sign of low predation pressure at Nasen, or as being due to broods being observed the first time rather late in life, i.e. after the mortality peak occurring during the first 10-12 days.

My study demonstrates density-dependent breeding success and also suggests that the underlying processes act during the nesting phase rather than during the duckling phase. This does not exclude density-dependent processes on the staging and/or the wintering grounds. In this context, and considering the pattern of female philopatry in dabbling ducks, it is worth noting that more female mallards arrived to breed on Nasen in springs following a productive summer, i.e. pair number in the early May period correlated significantly with the number of fledged ducklings the year before ($r_s = 0.71$, $P < 0.01$, N = 12). This pattern appears robust, as the other nine nesting number estimates also had a positive and high correlation coefficient, five of them being significantly correlated with last year's fledgling number. However, this is only circumstantial evidence for a carry-over effect between breeding seasons. No birds were marked and I do not know for sure that nesting birds were actually last year's offspring. Finally, there was no correlation between brood or juvenile production in a given year and the number of juveniles fledged the year before, again indicating that processes during the breeding season limit or assist in regulating population size.

In conclusion, this study of mallards on a eutrophic lake demonstrates negative density-dependent breeding success and suggests a positive correlation between juvenile production in one year and the number of returning females the next. Hence, there is a potential in this population for density-dependent regulation to occur.

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