

POPULATION LIMITATION IN DABBLING DUCKS AT MÝVATN, ICELAND

GARDARSSON, A.¹, PETERSEN, A.² and EINARSSON, Á.³

¹*University of Iceland, Department of Biology, Askja, Sturlugata 7, IS-101 Reykjavik, Iceland
E-mail: arnthor@hi.is*

²*Icelandic Institute of Natural History, P. O. Box 5320, IS-125 Reykjavik, Iceland*

³*Mývatn Research Station, IS-660 Mývatn, Iceland*

Numbers of five dabbling duck (*Anas*) species were studied during 1975–2002 at Mývatn, Iceland, in relation to reproductive success, abundance of aquatic insects and density. In Eurasian wigeon (*Anas penelope*), spring numbers, proportion of yearlings and numbers of young were studied. In gadwall (*A. strepera*), mallard (*A. platyrhynchos*), pintail (*A. acuta*) and Eurasian teal (*A. crecca*), only spring numbers were estimated annually. Comparisons of spring numbers at Mývatn with numbers wintering in Iceland (mallard) and Britain (the other four species) were made. Change in habitat use and in total spring numbers of all five species tracked chironomid abundance. Change in numbers of mallard, pintail and teal was negatively associated with density in the year before. Production of young wigeon was correlated with chironomid abundance although weather played a role. Reproductive success, which was determined by the availability of protein food (Chironomidae) on the breeding grounds, was the main variable determining dispersion and return rates, and hence annual change in spring densities on the breeding grounds of all five species.

Key words: *Anas*, waterfowl breeding populations, reproductive success, resource limitation, density dependence

INTRODUCTION

Waterbird populations and their reproductive success have been monitored at Lake Mývatn, north Iceland, for three decades, beginning in 1975. At the same time, the population levels of important food species, especially aquatic insects, have been followed. The research questions asked at Mývatn have partly been framed in terms of conservation and management of this internationally important wetland, but at the same time the data invite more general questions, such as: How are the numbers of migratory ducks limited?

On a large, or flyway, scale, local breeding populations could be limited by total resources in the flyway, perhaps mainly on the winter grounds, or by local shortages or bottlenecks somewhere in the migratory system. How such limitation works as a population regulatory mechanism is less clear (SUTHERLAND 1996, NEWTON 2004, 2006, DRENT *et al.* 2006).

If density is to regulate populations on the local scale, whether at breeding, staging or wintering sites, dispersion in relation to the distribution of resources

should come into play; in other words local density at any time is limited by the availability of local resources and density regulation presumably works through dispersion, i.e., the buffer effect (BROWN 1969).

On the local scale of breeding grounds, reproductive output and return rates to particular breeding localities are especially important objects of research, as witnessed by numerous workers (see review in NEWTON 1998). Unless we are dealing with populations that mix little during the non-breeding seasons, it cannot be assumed that events in a breeding region determine population density in the migratory system or flyway as a whole. A clear link occurs where a migratory population occupies a separate spatial unit throughout the annual cycle, as is the case in many goose populations (e.g., OWEN & BLACK 1991, ARZEL *et al.* 2006) and has recently been demonstrated in a shorebird (GUNNARSSON *et al.* 2005). Dabbling ducks may be an example of the other extreme, tending toward much more mixing on the wintering grounds (SOWLS 1955, MCKINNEY 1986, GARDARSSON & EINARSSON 1997).

At Lake Mývatn, diving ducks of several species are numerous and have been the subject of long-term population studies in relation to their food and other living conditions (e.g., GARDARSSON 1979, GARDARSSON & EINARSSON 1994, 2004, EINARSSON *et al.* 2006, GARDARSSON 2006). At the same time, most less-abundant species of waterbirds have been monitored and this paper describes some results obtained from the dabbling ducks (*Anas* spp.). Most of these are fairly scarce and relatively difficult to observe in the open, although the Eurasian wigeon (*Anas penelope*) is an exception (GARDARSSON & EINARSSON 1997). The importance of local feeding conditions in determining reproductive success is by now well established, although much work remains to be done to clarify the details. Studies of several duck species at Mývatn demonstrate that the production of young is limited by food, although weather can at times have considerable influence (GARDARSSON & EINARSSON 1994, 2004, EINARSSON *et al.* 2006). Moreover, production is dependent on a food supply that varies greatly in quantity and is governed by bottom-up processes (EINARSSON *et al.* 2002).

In this paper we explore two questions about population limitation of ducks, both address the return rates and dispersion in relation to environmental conditions at a single breeding locality. The questions that we ask are: (1) Is change in numbers of breeders related to previous reproductive success, or local feeding conditions, or local population density? (2) Is change in numbers of breeders related to population levels in the winter range?

MATERIALS AND METHODS

The study area

Lake Mývatn is volcanic, subarctic, shallow, large (37 km²), eutrophic and highly productive. It lies in a shallow basin with many smaller waterbodies and marshlands, bringing the total surface area of permanent water usable for waterbirds to over 50 km². For descriptions of the lake and its ecology see, for instance, JÓNASSON (1979), GARDARSSON and EINARSSON (2000) and EINARSSON *et al.* (2004). The lake and surrounding wetlands support dense populations of aquatic insects, mainly Chironomidae (EINARSSON *et al.* 2002, GARDARSSON *et al.* 2004), and waterbirds (e.g. GARDARSSON 1979, 2006, GARDARSSON & EINARSSON 1994, 2000, 2004), mainly diving ducks but also dabbling ducks (*Anas* spp.) of which five species breed regularly in some numbers.

Methods

A long-term ecological study of Mývatn was started in 1975; standardized methods for waterbirds are described in GARDARSSON (1979) and GARDARSSON & EINARSSON (1994). All waterbirds in the study area were counted each spring, before egg-laying of most ducks. The study area was divided into 8 natural subareas for counting in the spring (GARDARSSON 1979). The subareas were used to explore habitat preferences of adult ducks in spring. Three of the subareas (termed SF, YF and BO) comprised the "open lake" habitat, four (GV, FE, SV, NB) were small lakes and wetlands, classified as "wetlands", and one (LM) was the "river outlet".

Each year, the production of young Eurasian wigeon was estimated. Two estimates were made: (1) Age ratio, i.e. brood size and the number of females with and without broods, was estimated in early July in year (t), when the young were approximately 2 weeks old or older. (2) Yearling ratio, the ratio of yearling males in year (t+1) to the total number of males in year (t).

In the other *Anas* species, production was not estimated on an annual basis and the estimates were much less reliable than for wigeon, but in those years when samples were available, production (as age ratio) was correlated with the age ratio and the yearling ratio of wigeon: Gadwall (*A. strepera*) age ratio $r_p = 0.72$, $P < 0.001$, yearling ratio $r_p = 0.74$, $P < 0.001$ ($n = 18$). Mallard (*A. platyrhynchos*) age ratio $r_p = 0.89$, $P < 0.0001$, yearling ratio $r_p = 0.70$, $P < 0.01$ ($n = 16$). Pintail (*A. acuta*) age ratio $r_p = 0.86$, $P < 0.01$, yearling ratio $r_p = 0.70$, $P < 0.05$ ($n = 11$). Eurasian teal (*A. crecca*) age ratio, $r_p = 0.80$, $P < 0.001$, yearling ratio $r_p = 0.78$, $P < 0.001$ ($n = 17$).

While the duck species in question are mostly herbivores, insect food plays an important role in their reproduction (SEDINGER 1992, GARDARSSON & EINARSSON 2002). Variation in the abundance of aquatic insects was monitored by means of window traps, which catch flying imagines. The traps were set up at the beginning of each field season (May) and run until September each year beginning in 1977 (JÓNSSON *et al.* 1986, GARDARSSON *et al.* 2004).

We explored the data mainly by means of correlation analysis and stepwise multiple regression. The dependent variable of chief interest was change between years in the number of breeders, actually males, as $\log(N_{t+1}/N_t)$. As explanatory variables we used the following: Local food resources, as total Chironomidae trapped in a season (C_t). Reproductive success, using the yearling ratio of wigeon (Y_{t+1}/N_t) as a surrogate for reproductive success of all species. Local or breeding ground density (N_t), obtained from spring censuses at Mývatn. Index of winter numbers (W_t). Indices of winter numbers were obtained from Britain (POLLIT *et al.* 2003) for all species except mallard. At Mývatn, the mallard is a partial resident. Numbers in January 1976–1986 varied between 90 and 270, and appeared to be much affected by ice conditions (GARDARSSON 1991). It is mostly resident in Ice-

land, although a few birds have been recovered abroad in winter (PETERSEN 1998). The winter index for mallard was constructed from Christmas bird counts organized by the Icelandic Institute of Natural History (PETERSEN & HJARTARSON 1989, IINH unpublished data). Since the chironomid food resource is the main determinant of reproductive success, we did not use food and the index of reproductive success as independent variables in the same regression models.

RESULTS

In spring, at the outset of the nesting season, the dispersion of the dabbling ducks varied, both between species and between years (Fig. 1). Eurasian wigeon and gadwall occurred mainly on the open lake, mallard occupied an intermediate position, pintail and Eurasian teal tended toward wetlands; all five species responded to annual change in chironomid abundance by their dispersion in habitat types, the teal showing the strongest response (Table 1).

Spring censuses began in 1975 when numbers of all *Anas* species were at an all-time low level (Fig. 2). On the whole, total numbers in spring were associated with variation in chironomid abundance. The most abundant species was wigeon, mean density of 23 km⁻² water surface (mean total 1223 males), with mallard in the second place and pintail the rarest (Table 2). During the study period, the gadwall showed a highly significant increasing trend of 7% per annum and wigeon increased by an average of 3%. Numbers of the other three species did not show significant trends (Table 2).

From 1977 to 2002 chironomids fluctuated greatly in abundance, with peaks about 1981, 1987, 1993 and 2001 and lows in 1984, 1989 and 1998 (Fig. 3). These fluctuations were tracked broadly by the reproductive success of wigeon, whether estimated as age ratios of young per female in the same season or as yearlings in the following year per male in the previous year. In some years, weather depressed the number of ducklings produced (GARDARSSON & EINARSSON 1997, 2004).

Change in numbers between years was correlated with resources, as expressed by chironomid abundance, and with reproductive success in the previous year (Fig. 4). Significant correlations with chironomid abundance were shown by wigeon ($r_p = 0.60$), gadwall ($r_p = 0.54$) and pintail ($r_p = 0.43$). All species showed significant correlations when change in numbers was correlated with reproductive success; as expected, wigeon had the closest correlation ($r_p = 0.87$) (Fig. 4).

Density dependence, expressed simply as the correlation of change between years (N_{t+1}/N_t) as a function of local numbers in the year before (N_t), appeared to play a role in all species except the gadwall (Fig. 4). Since change in number and number are not independent variables, we carried out a randomization test to investigate how much of the density dependence might be due to this effect, and hence

Table 1. Proportional habitat use of dabbling ducks at Mývatn, shown as mean proportion of duck numbers in spring 1977–2002 (p , $n = 26$) and Spearman rank correlation coefficients of habitat use with annual abundance of Chironomidae (r_s). * = $P < 0.05$, ** = $P < 0.01$

Habitat (% water surface)	Lake (0.67)		Wetland (0.30)		River (0.03)	
	p	r_s	p	r_s	p	r_s
<i>A. penelope</i>	0.73	0.45*	0.21	-0.28	0.06	-0.62**
<i>A. strepera</i>	0.75	0.43*	0.10	-0.13	0.15	-0.44*
<i>A. platyrhynchos</i>	0.54	0.48*	0.28	-0.42*	0.18	-0.33
<i>A. acuta</i>	0.43	0.45*	0.45	-0.25	0.12	-0.40
<i>A. crecca</i>	0.47	0.56**	0.41	-0.49*	0.11	-0.27

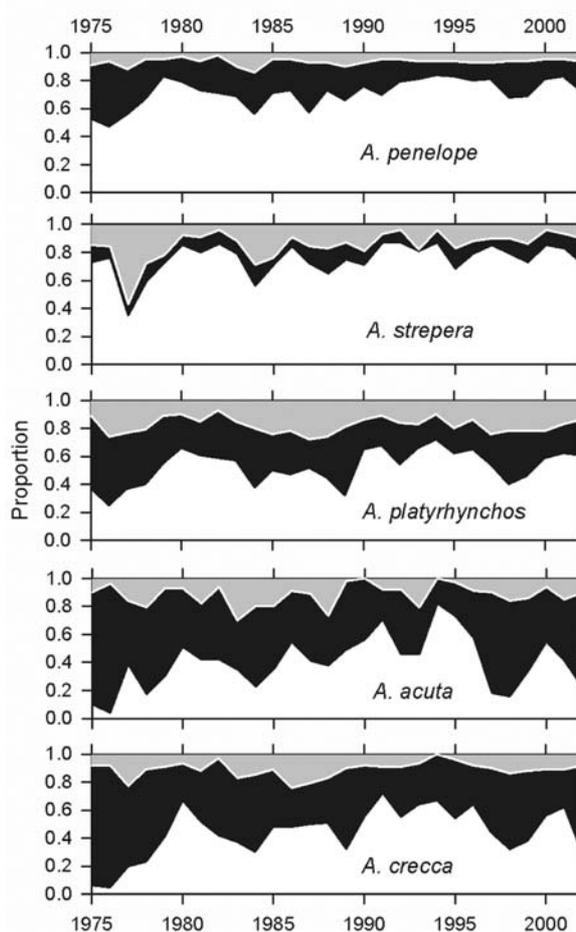


Fig 1. Time series of the proportion of *Anas* species found in the three main habitats at Mývatn in spring: open lake (unfilled area), surrounding wetlands (black) and the river outlet (grey)

Table 2. Densities of dabbling ducks at Mývatn during 28 years (1975–2002): mean number of males km⁻², standard error, coefficient of variation, minimum, maximum, mean per cent change between years and significance level of the trend. * * * = P < 0.001

	mean	SE	CV	min	max	% change p.a.
<i>A. penelope</i>	22.4	1.5	36	9.6	42.2	2.7***
<i>A. strepera</i>	1.7	0.2	71	0.5	5.6	6.9***
<i>A. platyrhynchos</i>	4.3	0.2	22	3.0	6.9	0.1
<i>A. acuta</i>	0.8	0.1	36	0.4	1.4	0.7
<i>A. crecca</i>	2.4	0.2	39	0.9	5.5	0.3

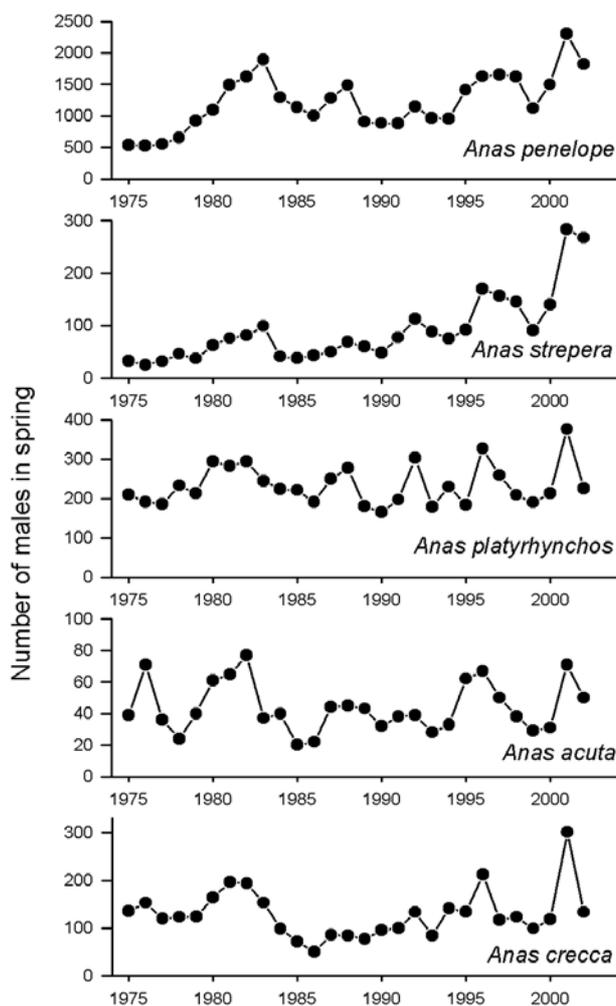


Fig. 2. Time series of total spring numbers (males) of five dabbling duck species at Mývatn

Table 3. Dabbling ducks at Mývatn, Iceland. Results of forward stepwise regressions of change in numbers between years, using apparent reproductive success (as yearling ratio of male wigeon), local density and winter index as explanatory variables

	Reproductive success		Local density		Winter index		F	P
	Beta	R ²	Beta	R ²	Beta	R ²		
<i>Anas penelope</i>	0.85	0.72	–	–	–	–	58.49	< 0.001
<i>A. strepera</i>	0.66	0.39	–0.62	0.17	0.83	0.10	10.47	< 0.001
<i>A. platyrhynchos</i>	0.53	0.26	–0.55	0.47	–	–	33.52	< 0.001
<i>A. acuta</i>	0.39	0.15	–0.55	0.30	–	–	8.95	0.001
<i>A. crecca</i>	0.68	0.20	–0.60	0.28	0.40	0.14	11.56	< 0.001

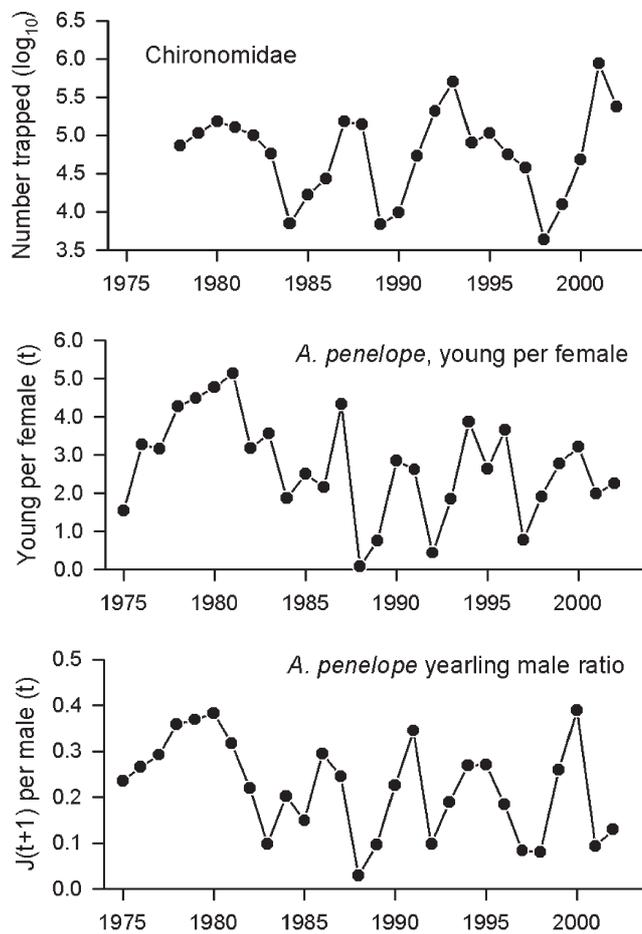
**Fig. 3.** Time series of the protein resource, Chironomidae, and two indices of reproductive success of wigeon at Mývatn

Table 4. Results of forward stepwise regressions of change between years in numbers of dabbling ducks at Mývatn, using chironomid food, local density and winter index as explanatory variables

	Total Chironomidae		Local density		Winter index		F	P
	Beta	R ²	Beta	R ²	Beta	R ²		
<i>Anas penelope</i>	0.62	0.39	–	–	–	–	13.31	0.002
<i>A. strepera</i>	0.51	0.26	–	–	–	–	7.45	0.013
<i>A. platyrhynchos</i>	0.38	0.14	–0.75	0.51	–	–	20.53	< 0.001
<i>A. acuta</i>	–	–	–0.51	0.26	–	–	7.47	0.012
<i>A. crecca</i>	–	–	–0.44	0.2	–	–	5.16	0.034

not ecologically significant. The test was performed by randomizing the time series for rate of change and calculating a new series of spring numbers based on these values, using one of the spring numbers, picked at random, as a seed for the calculations. The new time series were then correlated. This procedure was repeated 500 times for each species, allowing the calculation of mean regression coefficients (*b*). The test was significant for mallard ($P < 0.001$), pintail ($P < 0.01$) and teal ($P < 0.05$) which thus showed indication of density dependence.

When explored in forward stepwise regression, change in numbers (return rates) of all five species showed significant relationships with at least some of the explanatory variables. The surrogate (wigeon) reproductive success produced models with more explained variation (Table 3). In the wigeon itself, reproductive success was the only significant variable ($R^2 = 0.72$, $P < 0.001$). In the other four species, local density in the previous year was also significant (but see above). In two species, gadwall and teal, the winter index, based on total estimates in Britain had a significant but weak influence.

Using the chironomid food resource, instead of surrogate reproductive success, in general produced models with less explained variation (Table 4). In wigeon and gadwall, only chironomid abundance was admitted into the model. In mallard, local density and chironomids were in. Local density was the only variable in pintail and teal. Winter indices were not significant and could not be admitted into the models.

DISCUSSION

To reiterate, previous work has shown that the high density of duck populations at Mývatn is based on a rich food supply (GARDARSSON 1979, GARDARSSON & EINARSSON 1994, 2000, 2004). Reproductive success of the ducks is to a large extent dependent on invertebrate food that is rich in protein. In dabbling ducks, this

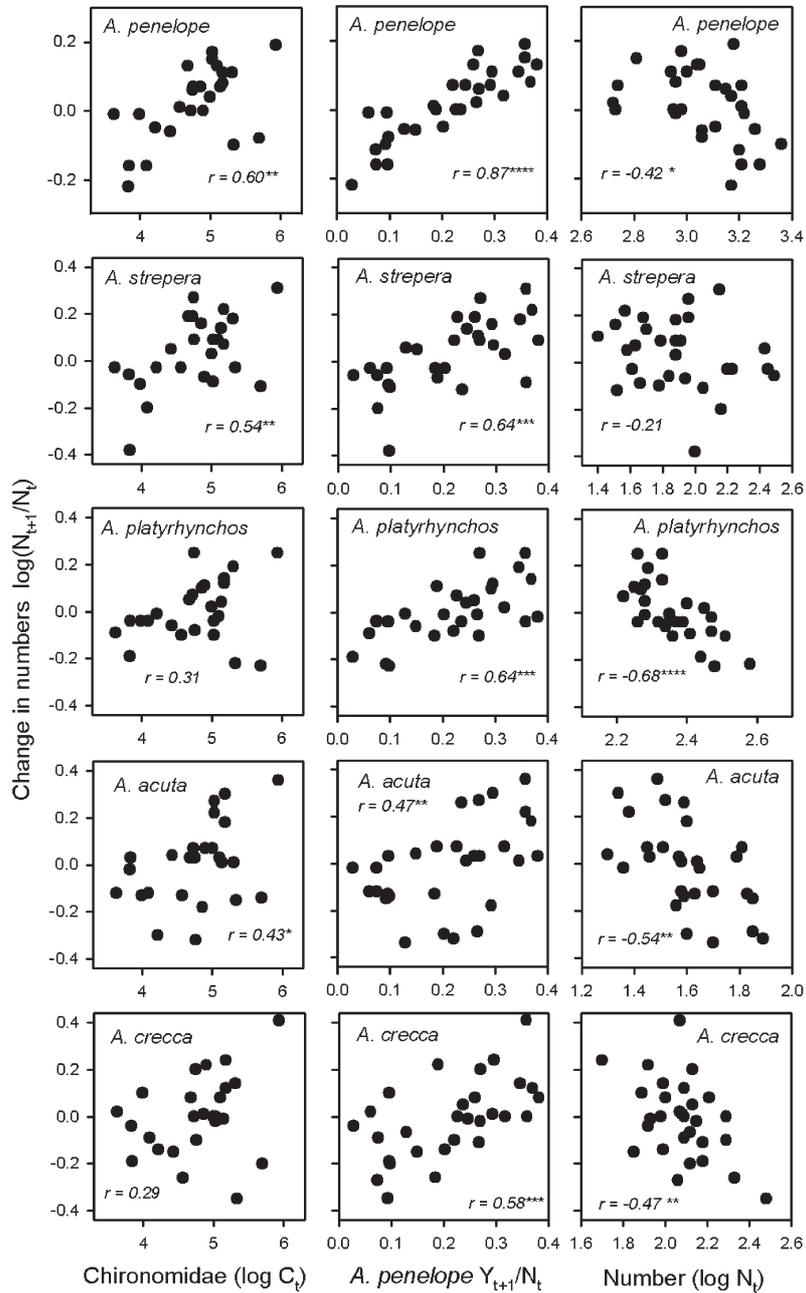


Fig. 4. Scatter diagrams showing annual change in breeding numbers of five species of dabbling ducks plotted against chironomid abundance in 25 years, 1977–2001 (first column), reproductive success in 29 years, 1975–2003 (second column), and local density in 29 years (third column). Also shown are Pearson correlation coefficients for each scattergram

food supply is largely chironomids that are caught during emergence, on the water surface or when made available by disturbance of the benthos whether by wave action or by other waterbirds. Very occasionally, cold windy weather was shown to reduce breeding success either by causing mass desertion of nests (as found in several diving ducks in 1992) or perhaps by killing large numbers of the young (GARDARSSON & EINARSSON 1994, 1997).

This paper adds little new information on the relationship between a nutritious diet and reproductive success, as we consider this well established. Rather, what is at issue here, is how food conditions in the breeding area affect change in numbers (return rates), whether by change in survival or dispersion during the spring return migration, and how variation in food conditions affects dispersion within each breeding area. Such dispersion on a local scale is shown by the dabbling ducks at Mývatn. Elsewhere, several duck species have been shown to move between breeding areas, depending on wetland conditions (HESTBECK 1995, ROSHIER 2001, AUSTIN 2002).

Our results from the dabbling ducks tend to confirm those obtained from the diving ducks at Mývatn, however, randomization tests on density dependence have yet to be carried out on the diving duck populations. Change in the spring density of diving ducks of five species was inversely associated with local density in the year before, including harlequin duck (*Histrionicus histrionicus*) where no other explanatory variable was significant; three species, tufted duck (*Aythya fuligula*), greater scaup (*A. marila*) and common scoter (*Melanitta nigra*) also showed positive correlation with prior reproductive success; and Barrow's goldeneye (*Bucephala islandica*) with insect food (GARDARSSON & EINARSSON 2004).

Reproductive success and local breeding ground density in the previous year seem to be the most important variables influencing density regulation in four of the five dabbling duck species studied at Mývatn. In turn, reproductive success is dependent on a nutritious food supply. Wigeon seem to have well-developed dispersion mechanisms whereby they can rapidly recruit to lakes that intermittently support high densities of aquatic insects. At Mývatn these aquatic insects, especially the chironomid *Tanytarsus gracilentus*, fluctuate in a cyclic manner with a difference of four orders of magnitude between troughs and highs (EINARSSON *et al.* 2002, GARDARSSON *et al.* 2004). Should dominant aquatic insect populations in other lakes turn out to fluctuate so violently, the apparent lack of density dependence in the wigeon is most likely part of its repertoire of adaptations for maximizing its use of food for reproduction. If this is the case, single breeding localities are not likely to show density dependence.

Gadwall show many life history similarities to the wigeon, including the preference for open water and lack of local density dependence. The gadwall which

in north-western Europe has a very restricted distribution, both in summer and winter (CRAMP & SIMMONS 1977), showed a density dependent relationship with the British winter index, which was significant in a multiple regression model, although rather weak, but so also did the widely distributed teal. Conversely, in the mallard, with its highly localized population restricted to Iceland, we found no relationship with winter numbers (or their residuals). However, local density dependence was most pronounced in the mallard. This is interesting, and one might speculate that it is somehow linked to the mallard being the only dabbling duck in the Mývatn area that is partly a year-round resident and thus dependent on local resources throughout the year. Such an explanation leaves local density dependence in the strongly migratory pintail unaccounted for. In the resident mallard, the food resources in winter and summer are likely to overlap broadly and individuals have relatively good opportunities to monitor local resources through the seasons. Such opportunities are hardly open to long-distance migrants which must use information storage and transfer of some sort to return successfully in spring to a distant breeding location. The form of such “memory” aiding migratory birds in returning to a breeding area may be simply their body condition in the previous autumn or the prior success of breeders at producing offspring. Whether density dependence in relation to winter numbers has any role in such a system is open to question, and indeed may be particularly difficult to establish in duck populations that occupy extensive wintering areas and may move between adjacent flyways (GARDARSSON & EINARSSON 1997).

Studies of the waterfowl of the Mývatn region have produced much information that we believe points the way to explain the mechanisms of how bird populations in a large-scale seasonal environment may be regulated. Clearly an array of explanations is called for. Not only do we find differences that suggest species-specific adaptations, but site-specific differences that are outside the scope of the present paper are emerging when comparison is made with other studies (e.g. VICKERY & NUDDS 1984, ELMBERG *et al.* 2003, VILJUGREIN *et al.* 2005). An extension of the geographic scale of the Mývatn studies seems likely to produce vast improvement on the current knowledge of how migratory bird populations manage to succeed in a risky and ever-changing environment.

*

Acknowledgements – This paper is a product of a long-term monitoring study on the Mývatn ecosystem and its waterfowl. Thanks especially to THÓRA HRAFNSDÓTTIR, HARALDUR R. INGVASON, the late ERLENDUR JÓNSSON and JÓN S. ÓLAFSSON for expert work on the chironomids and to THORKELL L. THÓRARINSSON and YANN KOLBEINSSON for their contributions to censusing in recent years. Numerous students and colleagues assisted in the field and laboratory and provided data and insights from their studies. The Iceland Science Fund and the University of Iceland Research Fund supported these studies with grants.

REFERENCES

- ARZEL, C., ELMBERG, J. and GUILLEMAIN, M. (2006) Ecology of spring-migrating Anatidae: a review. *Journal of Ornithology* **147**: 167–184.
- AUSTIN, J. E. (2002) Responses of dabbling ducks to wetland conditions in the Prairie Pothole region. *Waterbirds* **25**: 465–473.
- BROWN, J. L. (1969) The buffer effect and productivity in tit populations. *American Naturalist* **103**: 347–354.
- CRAMP, S. & SIMMONS, K. E. L. (eds) (1977) *The Birds of the Western Palearctic*, Vol. 1. Oxford University Press, Oxford. 722 pp.
- DRENT, R. H., FOX, A. D. & STAHL, J. (2006) Travelling to breed. *Journal of Ornithology* **147**: 122–134.
- EINARSSON, Á., GARDARSSON, A., GÍSLASON, G. M. & IVES, A. R. (2002) Consumer-resource interactions and cyclic population dynamics of *Tanytarsus gracilentus* (Diptera: Chironomidae). *Journal of Animal Ecology* **71**: 832–845.
- EINARSSON, Á., STEFÁNSDÓTTIR, G., JÓHANNESSEN, H., ÓLAFSSON, J. S., GÍSLASON, G. M., WAKANA, I., GUDBERGSSON, G. & GARDARSSON, A. (2004) The ecology of Lake Mývatn and the River Laxá: variation in space and time. *Aquatic Ecology* **38**: 317–348.
- EINARSSON, Á., GARDARSSON, A., GÍSLASON, G. M. & GUDBERGSSON, G. (2006) Populations of ducks and trout of the River Laxá, Iceland, in relation to variation in food resources. *Hydrobiologia* **567**: 183–194.
- ELMBERG, J., NUMMI, P., PÖYSÄ, H. & SJÖBERG, K. (2003) Breeding success of sympatric dabbling ducks in relation to population density and food resources. *Oikos* **100**: 333–341.
- GARDARSSON, A. (1979) Waterfowl populations of Lake Mývatn and recent changes in numbers and food habits. *Oikos* **32**: 250–270.
- GARDARSSON, A. (1991) Fuglalíf við Mývatn og Laxá. [Bird-life of Mývatn and Laxá]. Pp 278–319. In: GARDARSSON, A & Á, EINARSSON (eds) *Náttúra Mývatns*. Hid íslenska náttúrufræðifélag, Reykjavík [In Icelandic]
- GARDARSSON, A. (2006) Temporal processes and duck populations: examples from Mývatn. *Hydrobiologia* **567**: 89–100.
- GARDARSSON, A. & EINARSSON, Á. (1994) Responses of breeding duck populations to changes in food supply. *Hydrobiologia* **279–280**: 15–27.
- GARDARSSON, A. & EINARSSON, Á. (1997) Numbers and production of Eurasian wigeon in relations to conditions in a breeding area, Lake Mývatn, Iceland. *Journal of Animal Ecology* **66**: 439–451.
- GARDARSSON, A. & EINARSSON, Á. (2000) Monitoring waterfowl at Mývatn, Iceland. Pp. 3–20. In: COMÍN, F. A., J. A. HERRERA-SILVEIRA, J. A. & J. RAMÍREZ-RAMÍREZ (eds) *Limnology and Aquatic Birds Monitoring. Modelling and Management*. Universidad Autónoma del Yucatán, Mérida (Mexico).
- GARDARSSON, A. & EINARSSON, Á. (2002) The food relations of the waterbirds of Lake Mývatn, Iceland. *Verhandlungen der internationalen Vereinigung für Limnologie* **28**: 754–763.
- GARDARSSON, A. & EINARSSON, Á. (2004) Resource limitation of diving ducks at Myvatn: food limits production. *Aquatic Ecology* **38**: 285–295.
- GARDARSSON, A., EINARSSON, Á., GÍSLASON, G. M., HRAFNSDÓTTIR, Th., INGVASON, H. R., JÓNSSON, E. & ÓLAFSSON, J. S. (2004) Population fluctuations of chironomid and simuliid Diptera at Myvatn in 1977–1996. *Aquatic Ecology* **38**: 209–217.

- GUNNARSSON, T. G., GILL, J. A., NEWTON, J., POTTS, P. M. & SUTHERLAND, W. J. (2005) Seasonal matching of habitat quality and fitness in a migratory bird. *Proceedings of the Royal Society of London B* **272**: 2319–2323.
- HESTBECK, J. B. (1995) Response of northern pintail breeding populations to drought, 1961–92. *Journal of Wildlife Management* **59**: 9–15.
- JÓNASSON, P. M. (1979) The Lake Mývatn ecosystem, Iceland. *Oikos* **32**: 289–305.
- JÓNSSON, E., GARDARSSON, A. & GÍSLASON, G. M. (1986) A new window trap used in the assessment of the flight periods of Chironomidae and Simuliidae (Diptera). *Freshwater Biology* **16**: 711–719.
- MCKINNEY, F. (1986) Ecological factors influencing the social systems of migratory dabbling ducks. Pp. 73–82. In: RUBINSTEIN, D. J. & R. W. WRANGHAM (eds) *Ecological Aspects of Social Evolution*. Princeton University Press, Princeton.
- NEWTON, I. (1998) *Population limitation in birds*. Academic Press, London, 597 pp.
- NEWTON, I. (2004) Population limitation in migrants. *Ibis* **146**: 107–226.
- NEWTON, I. (2006) Can conditions experienced during migration limit the population levels of birds? *Journal of Ornithology* **147**: 146–166.
- OWEN, M. & BLACK J. M. (1991). The importance of migration mortality in non-passerine birds. Pp. 360–372. In: PERRINS, M. C., LEBRETON, J. D. & G. J. M. HIRONS (eds) *Bird Population Studies. Relevance to Conservation and Management*. Oxford University Press, Oxford.
- PETERSEN, A. (1998) *Íslenskir fuglar [Icelandic Birds]*. Vaka – Helgafell, Reykjavík. 312 pp. [In Icelandic]
- PETERSEN, A. & HJARTARSON, G. (1989) Vetrarfuglatalningar: skipulag og árangur 1987. 42 pp. (English summary: The Icelandic Christmas Bird Counts: Some general points, and results for 1987). *Fjölrit Náttúrufræðistofnunar* **11**. Reykjavík
- POLLIT, M. S., HALL, C., HOLLOWAY, S. J., HEARN, R. D., MARSHALL, P. E., MUSGROVE, A. J., ROBINSON, J. A. & CRANSWICK, P. A. (2003) *The Wetland Bird Survey 2000–01: Wildfowl and Wader Counts*. BTO/WWT/RSPB/JNCC, Slimbridge.
- ROSHIER, D. A., ROBERTSON, A. I., KINGSFORD, R. T. & GREEN, D. G. (2001) Continental-scale interactions with temporary resources may explain the paradox of large populations of desert waterbirds in Australia. *Landscape Ecology* **16**: 547–556.
- SEDINGER J. S. (1992) Ecology of pre fledging waterfowl. Pp. 109–127. In: BATT, B. D. J., AFTON, A. D., ANDERSON, M. G., ANKNEY, C. D., JOHNSON, D. H., KADLEC, J. A. & KRAPU, G. L. (eds) *Ecology and Management of Breeding Waterfowl*. University of Minnesota Press, Minneapolis.
- SOWLS, L. K. (1955) *Prairie Ducks. A study of their behavior, ecology and management*. Wildlife Management Institute and Stackpole Co., Harrisburg. 193 pp.
- SUTHERLAND, W. J. (1996) Predicting the consequences of habitat loss for migratory populations. *Proceedings of the Royal Society London B* **263**: 1325–1327.
- VICKERY, W. L. & NUDDS, T. D. (1984) Detection of density-dependent effects in annual duck censuses. *Ecology* **65**: 96–104.
- VILJUGREIN, H., STENSETH, N. C., SMITH, G. W. & STEINBAKK, G. H. (2005) Density dependence in North American ducks. *Ecology* **88**: 245–254.

Revised version received November 30, 2006, accepted May 25, 2007, published December 30, 2008