

Pair formation in relation to climate: Mallard, Eurasian Wigeon and Eurasian Teal wintering in Iceland.

J. E. Jonsson¹ & A. Gardarsson

Institute of Biology, University of Iceland, Grensasvegur 12, 108 Reykjavik, Iceland
Email: arnthor@hi.is

¹Present address: School of Forestry, Wildlife and Fisheries, Louisiana State University,
Baton Rouge, LA 70803, U.S.A. Email: jjonss1@lsu.edu

*The pairing chronologies of Mallard *Anas platyrhynchos*, Eurasian Wigeon *A. penelope* and Eurasian Teal *A. crecca* wintering in Southwest Iceland were studied over the winters of 1997-98 and 1998-99. Mallard paired first of the three species, with over 60% of all females paired by November. Wigeon and Teal had started pairing in early October, and the proportion of paired females increased gradually through winter until spring. In Mallard, the percentage of paired females was 60-70% during midwinter, the last females became paired in March and April. All three species paired later in Iceland than reported in more southern European and North American areas. In all winter months, especially November, December and January, the proportion of paired Mallard females at each location showed a positive relationship with mean monthly temperature. Fewer data are available on other dabbling duck species, but their pairing chronology seems related to climatic conditions.*

Key Words: *Anas platyrhynchos*, *Anas penelope*, *Anas crecca*, *Anatidae*, pairing chronology, winter climate.

Mate defense is energetically costly, because courtship, breeding and repelling rivals cost time and energy (Afton & Sayler 1982; Wishart 1983). At high latitudes, limited food availability and rough weather in winter may cause starvation and poor physiological condition (Hepp 1989). As well as being at risk from starvation, birds face the danger of hypothermia in cold and windy conditions. At air temperatures below the thermoneutral zone, birds need to conserve energy by limiting energetically costly behaviour, such as courtship displays (Newton 1998).

The wintering range of many northern dabbling ducks is between 30°N and 60°N. Individuals of widely distributed species, such as Mallard *Anas platyrhynchos*, may face very variable temperatures during a year. Behavioural decisions of ducks wintering at the edges of the range should differ from those of individuals wintering in central areas. Among species, the ability to tolerate cold weather depends partly on body size, as larger species benefit from a relatively slower metabolic rate, reduced surface-to-volume ratio, and thicker plumage compared to smaller species (Blem 1990; Dawson & O'Connor 1996). Perhaps even more important is the higher ability of larger species to store endogenous reserves (Skutch 1962; Afton 1980; Afton & Paulus 1992).

Ducks, swans and geese form pairs on the wintering grounds and migrate to the breeding grounds in pairs (McKinney 1986; Rohwer & Andersson

1988). The sex ratio of northern hemisphere ducks is usually male-biased (Bellrose 1980; McKinney 1986), which means that some males will be left unpaired every season, even though all the females become paired. This leads to sexual selection among males, and females can probably afford to be selective in their search for a mate (Rohwer & Anderson 1988). The females choose males by age, plumage quality, body mass and the intensity of their courtship displays (Wishart 1983; Bossema & Roemers 1985; Hepp 1986; Holmberg *et al.* 1989; Weidmann 1990; Heitmeyer 1995).

In contrast to the life-long pair bonds of swans and geese, ducks form pair bonds each year (Williams & McKinney 1998). Ducks form pairs on the wintering grounds and a pair will remain together until the female starts to incubate. Then the male deserts the female. In the autumn, the sexes meet again on the wintering grounds, and observations of marked individuals have shown that pairs from the previous season may reunite if both members return to same wintering locality (Savard 1985; Mjelstad & Sørensdal 1990; Robertson *et al.* 1998; Williams & McKinney 1998). The timing of pair formation differs between species and populations (Weller 1965; Hepp & Hair 1983; Rohwer & Anderson 1988). The formation and maintenance of a pair bond is costly to the male, since he must actively defend the female from rival males and predators (Afton & Sayler 1982; Wishart 1983). On

the other hand, pairing is beneficial to the females because paired females are able to forage more efficiently than single females (Paulus 1983).

Mallard *Anas platyrhynchos*, Wigeon *Anas penelope* and Teal *Anas crecca* are common breeding birds in Iceland. The Mallard population apparently does not leave Iceland during winter, but the majority of Wigeon and Teal migrate to western Europe, mostly the British Isles (Gardarsson 1975). However, some Wigeon and Teal overwinter in south Iceland. In Iceland, all three species are at the northern edge of both their breeding and wintering range (Cramp & Simmons 1978).

The aim of this study was to describe and compare the pairing chronology of Mallard, Wigeon and Teal in Iceland. Wintering in Iceland, these species are evidently near the lower limit of their temperature tolerance, pairing chronologies different from those reported at southern locations can be expected. In order to test this prediction, the results were compared with published data from North America and Europe.

Methods

Study area

Observations were made on the southern coastline of Faxaflói, south-west Iceland, from September 1997 to April 1998 and from August to April 1999. Reykjavík (64°09'N, 21°57'W) lies at the centre of the study area. The area

has been described in detail by Egilsson (1985). The climate is subarctic and oceanic. January is the coldest month with a mean monthly temperature of -0.5°C and an average number of 21 frost days. Along the coast there are important estuarine and marine habitats used by waterfowl and shorebirds. Several lakes, ponds and streams are open through the winter.

Observations

Mallard, Wigeon and Teal were counted twice per month from November to February, and in April. During autumn and spring migrations, additional counts were made to ensure adequate sample sizes: four counts were made in September, and three in October and March, respectively. The counts were made in the four hours around low tide.

The birds were identified as pairs and single males and females. Pairing status was assigned after Paulus (1983): Birds were considered paired if they: (1) Mutually avoided or chased other birds. (2) Exhibited consistent synchrony in activity, especially locomotion. (3) Remained within 3 m distance from each other. To reduce risk of error, birds in very dense temporary flocks, such as ducks being fed by the public, were excluded from the analysis. For each set of observations of pairing status of females, 95% confidence limits were estimated from the Standard Error of Proportion, $t\sqrt{pq/n}$, where t is Student's t , P =proportion paired females, q =proportion unpaired

females and n =total number of females examined.

Comparison with other areas

The pairing chronology of Mallard has been described for several locations on both sides of the Atlantic Ocean. Three studies have been carried out in continental Europe: in Munich, Germany (Bezzel 1959); in Middelburg, The Netherlands (Lebret 1961) and in Helsinki, Finland (Raitasuo 1964). In North America, pair formation of Mallard has been studied in Ithaca, New York (Johnsgard 1960b); in the Mingo basin, Missouri (Heitmeyer 1987) and on the Atchafalaya River delta, Louisiana (Johnson & Rohwer 1998).

The relationship between the proportion of paired females and mean monthly temperatures was tested by analysis of covariance (ANCOVA, PROC GLM, SAS Institute 1990). The final model was determined by backward selection. The variables entered into the initial model were: month (October-March), as a class variable; mean monthly temperature for each location; and the month \times temperature interaction. Data residuals were tested for normality by the Shapiro-Wilkes test (SAS Institute 1990).

Results

Observations in Iceland

Pairing chronology of all three species was similar in 1997-98 and 1998-99; the rate of pairing differed, the

Mallard paired mostly in October, Wigeon and Teal at a slower rate through the winter (**Figure 1**). All three species began pairing in the autumn, Mallard by early September, Wigeon in mid-September and Teal at the end of September. By late October, 60-70% of the female Mallard had paired. The percentage of paired female Mallard remained at around 60% until early March. In late April, at the beginning of the nesting season, 75% of all females were paired in 1998 and 90% in 1999. At the end of October, the percentage of paired Wigeon females was 29% in 1997 and 19% in 1998. In March, 70% of all female Wigeon had become paired, and in April well over 80%. Pairing progressed at a similar rate in Teal as in Wigeon; by March about 70% of the females had paired and in April about 90%.

Differences in the progress of pairing between Mallard and the other two species were most pronounced, and highly significant in October and November. For instance, combined observations from 31 October 1997 and 23 October 1998 yield $\chi^2=219.65$ ($P<0.001$) for Mallard vs. Wigeon, $\chi^2=22.63$ ($P<0.001$) for Mallard vs. Teal and $\chi^2=8.03$ ($P<0.01$) for Wigeon vs. Teal; and for 14 November 1997 plus 3 November 1998 $\chi^2=51.92$ ($P<0.001$) for Mallard vs. Wigeon, $\chi^2=20.81$ ($P<0.001$) for Mallard vs. Teal, but $\chi^2=0.002$ (n.s.) for Wigeon vs. Teal.

Mallard used mainly two habitats: intertidal areas, either mudflats or seaweed beds, or urban fresh waters. Pair

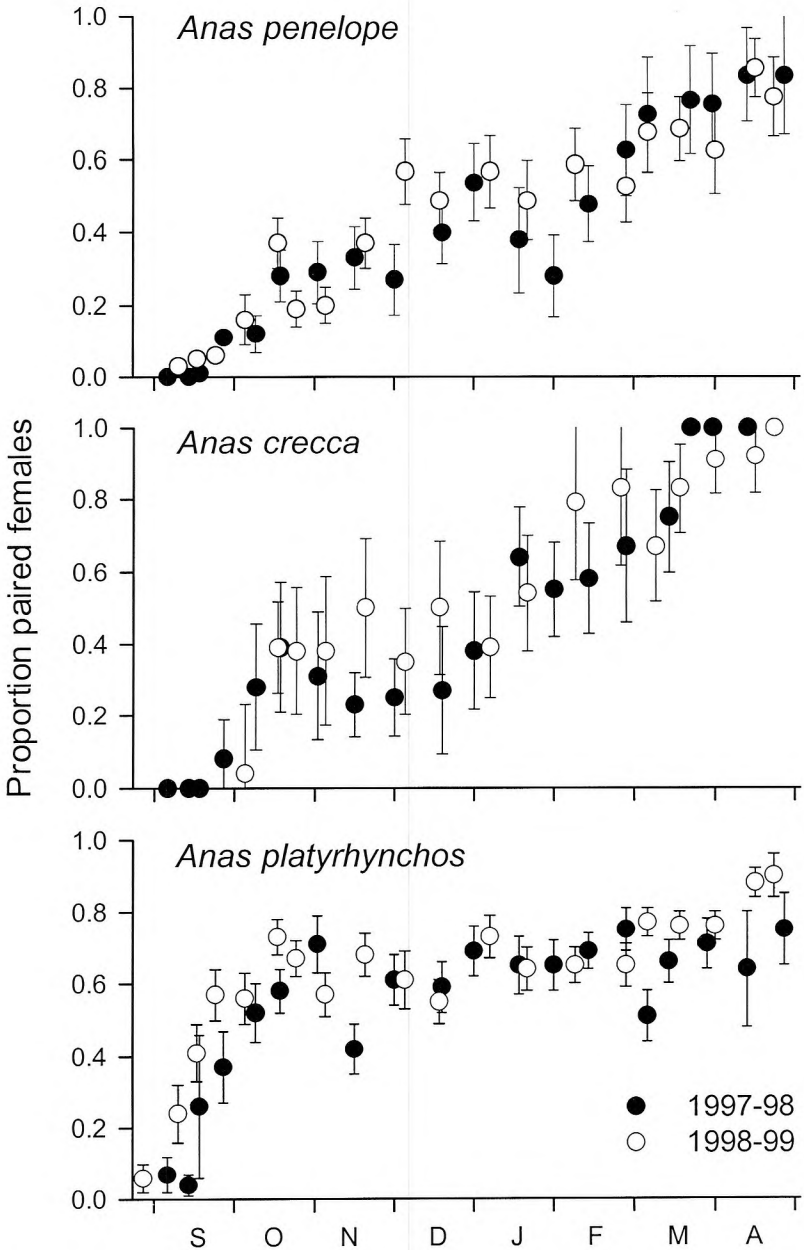


Figure 1. The pairing chronology of Wigeon *Anas penelope*, Teal *A. crecca* and Mallard *A. platyrhynchos* wintering in Iceland in 1997-98 and 1998-99. Error bars show 95% confidence limits, estimated as Standard Error of Proportion $\times t$.

formation began at the same time in both habitats. In the intertidal, the percentage of paired females was higher from November until April, staying well above 70% in both years. In contrast, the percentage of paired females on freshwaters was about 60% for most of the winter. The differences were usually statistically significant as indicated by the lack of overlap of the 95% confidence limits (**Figure 2**).

Comparison with other areas

One objective of this study was to compare the pairing chronologies of Mallard, Eurasian Wigeon and Teal wintering in Iceland at the northern edge of the distribution range, with pairing chronologies reported for the same or closely related species from other, more southern regions. We found little information on Eurasian Wigeon and Teal, but analysed published data for Mallard from seven North American and European localities (**Figure 3**). In the analysis of covariance, the final model included month ($F=4.98$, $P=0.0009$, $df=6$) and mean monthly temperature ($F=5.75$, $P=0.02$, $df=1$), both significantly affecting the percentage of paired females. The residuals were normally distributed (Shapiro-Wilkes test: $W=0.98$, $P=0.84$).

Mallard pair later at the colder locations in Finland, Iceland and New York. In all winter months, especially November, December and January, the proportion of paired females at each location shows a positive relationship

with mean monthly temperature (**Figure 3**). In November, more than half of all females are paired everywhere, except in Finland, Iceland and New York. The relationship between the proportion of paired females and monthly temperature is clearest in December (**Figure 3**). In December, about 40% of all females were paired in Finland and New York, where mean monthly temperatures were below -2°C . The mean monthly temperature in December for Iceland, Germany and Missouri is around 0°C and at that time 60–80% of all females were paired. At locations with December temperatures over 2°C , 80–100% of all females were paired in December. In January and February, the percentage of paired females was higher than 80% everywhere except in Finland and Iceland. By March, Mallards in the southern wintering areas leave for the breeding areas (Bellrose 1980) and have all become paired. At the coldest locations in the north, Finland and Iceland, the remaining females became paired in March and April.

Discussion

Pairing chronology in Iceland

Mallard were the first species to pair, and most Mallard females were already paired by the time the first Wigeon and Teal pairs were observed (**Figure 1**). Wigeon and Teal paired at similar times, unlike the same species in Germany where Wigeon paired earli-

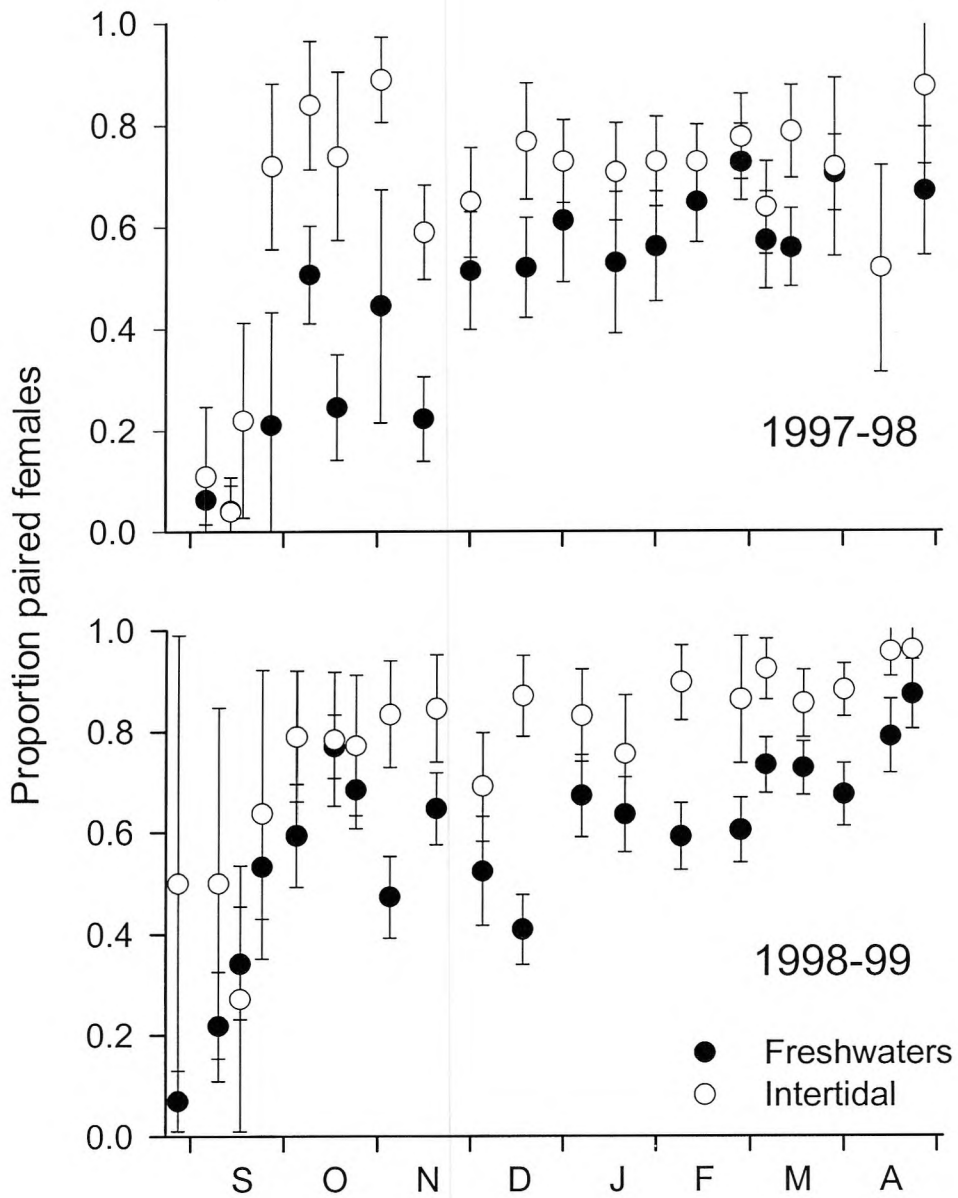


Figure 2. The proportion of paired female Mallards in intertidal and fresh water habitats in Iceland in winters 1997-98 and 1998-99. Error bars show 95% confidence limits (Standard Error of Proportion $\times t$).

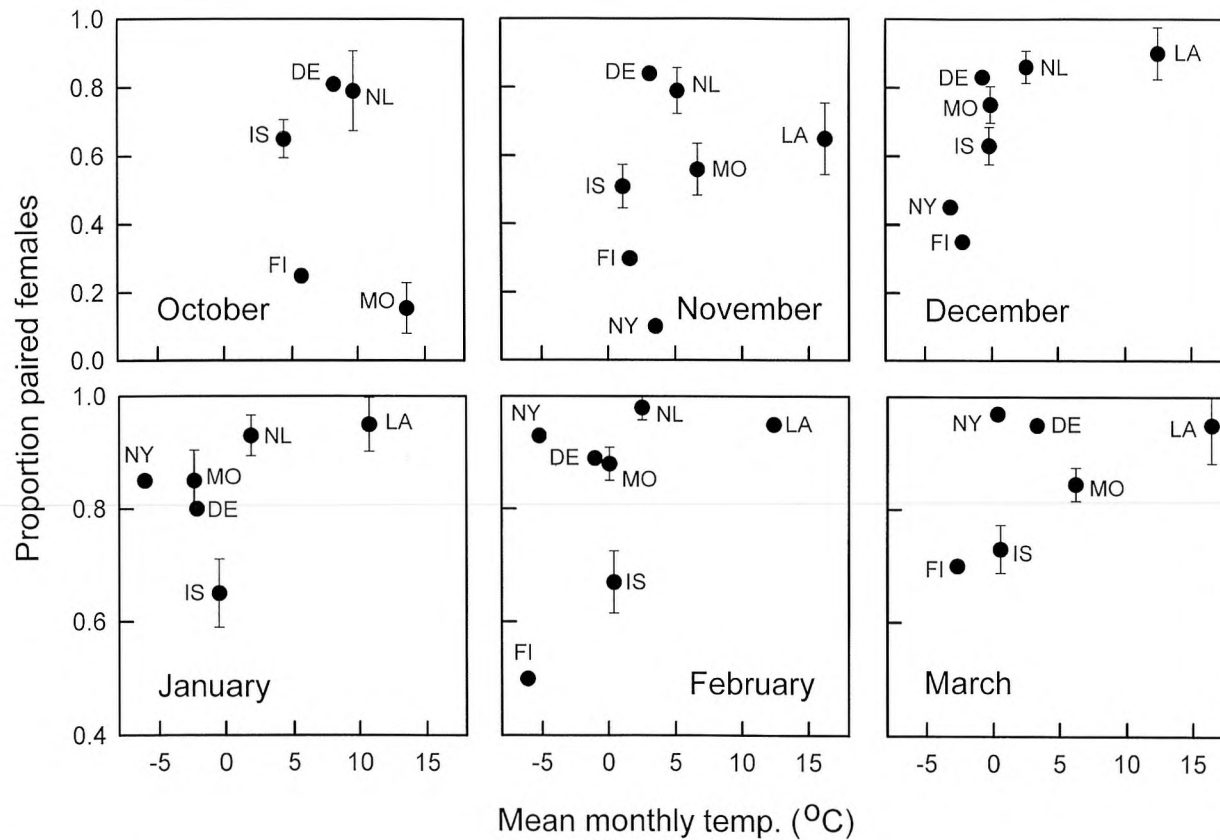


Figure 3. The relationship between the proportion of paired female Mallards and mean monthly temperatures in several European and North American localities. Error bars show 95% confidence limits [Standard Error of Proportion $\times t$]. Localities are shown with standard abbreviations: DE = Germany, FI = Finland, IS = Iceland, LA = Louisiana, MO = Missouri, NL = Netherlands, NY = New York State. Note: different scales in upper and lower row of graphs.

er than Teal (Bezzel 1959). The difference between Wigeon pairing chronology in Germany and Iceland can possibly be attributed to local differences in sex ratio, the sex ratio of wintering Wigeon in Germany was 55-58% males (Bezzel 1959), whereas that in Iceland was 45-51% (Jonsson 2000). In 1975-1995 the sex ratio of Wigeon breeding at Lake Myvatn, North Iceland, varied between 50% and 51% males in all years, except 1975 when 54% were recorded (Gardarsson & Einarsson 1997). The higher number of surplus males in Germany might increase the pressure on males to form pair bonds at an earlier date, or else face the risk of being left unpaired when all females have become paired.

Mallards on urban ponds had a lower proportion of paired females than the intertidal Mallards. One possible explanation for this may be that assigning pair status is more difficult at the crowded urban fresh waters in winter. However, Mallards in temporary dense flocks, at times being fed by the public, were eliminated from the sample to reduce that risk (see Methods). The numbers and densities of Mallard and the area of ice-free water available in mid-winter differed between the two urban ponds studied. At Lake Tjörnin, the mean number of Mallard was 276 on 0.4 ha of ice-free water and at Laekurinn Mallard averaged 189 on 1.2 ha. Hence, the average density of Mallard (690 ha^{-1}) at Tjörnin was about four times that at Laekurinn (157 ha^{-1}) and consequently, the risk of missing

out pairs was considerably less at Laekurinn. The proportion of females paired was very similar for the two lakes (**Figure 2**), so the proportion of paired females in the urban fresh waters was probably not underestimated. Movements of radio-tagged Mallards (Jonsson 2000) and recognized individuals (Nielsen 1992) show that the same individuals use urban freshwaters and intertidal areas on the same days. For instance on the urban lake Tjörnin, ducks are regularly fed by the public and are seen to make frequent flights between several freshwater and intertidal locations (Nielsen 1992). Paired ducks tend to avoid crowded places and feed away from single individuals to avoid disturbance from them (Johnsgard 1960a). Many Mallard pairs were recorded on the urban ponds, but the proportion of single males and females was higher there than in the intertidal, it seems that unpaired individuals prefer urban ponds over the intertidal habitats.

In Mallard and Wigeon, the percentage of paired females did not reach 100% in spring as it did with Teal, hence some Mallard and Wigeon females did not pair. In late March, the number of ducks in the study area decreased as the wintering birds left for the breeding areas in other parts of Iceland (Nielsen 1992; Jonsson 2000). By that time, only 40-60 Wigeon were left in the study area and among them were few unpaired females. In spring 1999 the sex ratio was about 45% males, and the unpaired females were surplus. In

Iceland, no marked differences between the winters 1997-98 and 1998-99 were observed in the pairing chronology of Mallard, Wigeon and Teal, but neither winter can be considered 'extreme' (Icelandic Meteorological Office). Elsewhere, effects of weather on pairing chronology have been reported. In a particularly cold winter in Finland, most Mallard delayed pair formation until spring (Raitasuo 1963) and Mallard in Missouri paired earlier in a wet winter (Heitmeyer 1987).

Comparison with other areas

The effects of cold weather on bird behaviour and physiology are well documented (Blem 1990; Dawson & O'Connor 1996; Newton 1998). During severe winters, ducks experience higher levels of stress, indicated by increased blood concentrations of urea and uric acid (Bennet & Bolen 1978). In particularly cold winters in Finland, Mallards delayed pair formation until spring (Raitasuo 1963) and in Sweden the proportion of paired Mallards declined during the coldest period of midwinter (Hansson 1966). With mean monthly temperature lower than 2°C in December, it appears that proportionally more Mallards delay pair formation for a certain amount of time. In colder areas, a lower percentage of individuals are able to build up reserves while performing courtship behaviour and/or mate defence at the same time. It is also possible that dabbling ducks wintering in colder areas have to be

choosier in mate selection to obtain a mate that is likely to enhance their future breeding success. Individuals which are fit enough to form pairs do so, and gain an advantage in competition for food due to their improved social status (Paulus 1983; Hepp 1986). Individuals vulnerable to cold and starvation delay pairing and hence reduce their energy expenditure and increase their probability of survival.

Although fewer data are available on other dabbling duck species, these indicate a similar relationship between pairing chronology and climate. Consistent with the results of this paper, American Wigeon at Cape Hatteras, North Carolina (Hepp & Hair 1983) paired before American Wigeon in Texas and British Columbia (Soutiere *et al.* 1972; Wishart 1983); the mean temperature in the winter months is higher at Cape Hatteras than in both Lubbock and British Columbia (NOAA). Bezzel (1959) described the pairing chronology of Eurasian Wigeon and Teal near Munich, Germany. Wigeon paired earlier than in Iceland, and there were 20% more paired females in Germany throughout winter. However, the pairing chronologies of Teal in Germany and Iceland are quite similar.

The pairing of Eurasian Teal and Green-winged Teal *A. carolinensis* differ strikingly in timing: Eurasian Teal begin pair formation in October and 40% of all females are paired by January, whereas Green-winged Teal do not begin pair formation until December or January (Hepp & Hair 1983; Johnson & Rohwer

1998). This difference is interesting in view of recent molecular findings that genetic divergence between Eurasian and Green-winged Teal is extremely high (Johnson and Sorenson 1999).

Rohwer & Anderson (1988) reported a significant relationship between body size and timing of pair formation among dabbling ducks. The potential energy conservation by delayed pair formation is greater for the smaller Wigeon and Teal than for Mallard. The pairing of Mallard and Wigeon in Iceland differs from the pairing of these species at southern wintering areas, but the pairing of Teal does not markedly do so. Perhaps Wigeon and Teal in Iceland pair as late as possible for dabbling ducks in relation to the timing of breeding activities. In late March, dabbling ducks start to migrate to the breeding areas (Nielsen 1992; Jonsson 2000), so pairing any later than March brings the risk of remaining unpaired into spring migration, and perhaps failing to obtain a mate. The social gain of pair formation is necessary for breeding success (Hepp 1984) and that limits the time a given individual can remain unpaired. As day length increases in spring, sexual activity increases due to increased concentrations of gonadotropins (Bluhm 1988), driving the last unpaired birds to pair in March.

Acknowledgements

This study was supported by a grant from the Icelandic Hunters' Licence Fund. A great debt is owed to Arni Einarsson, Tomas G. Gunnarsson, Pall Hersteinsson and Thorkell L. Thorarinsson for assistance and support in the fieldwork. Olafur K. Nielsen and Hrefna Sigurjonsdottir provided constructive criticism of previous drafts of this manuscript.

References

- Afton, A. D. 1980. Factors affecting incubation rhythms in Northern Shovelers. *Condor* 82:132-137.
- Afton, A. D. & Sayler, R. D. 1982. Social courtship and pairbonding of Common Goldeneyes *Bucephala clangula* wintering in Minnesota. *Canadian Field Naturalist* 98:295-300.
- Afton, A. D. & Paulus, S.L. 1992. Incubation and brood care. In: *Ecology and management of breeding waterfowl*. Bruce D. J. Batt *et al.* (ed). University of Minnesota Press. pp 62-108.
- Bellrose, F. C. 1980. *Ducks, Geese and Swans of North America*. Stackpole Books, Harrisburg. 540pp.
- Bennet, J. W. & Bolen, E. G. 1978. Stress response in wintering Green-winged Teal. *Journal of Wildlife Management* 42:81-86.
- Bezzel, E. 1959. Beiträge zur Biologie der Geschlechter bei Entenvögeln. *Anzeige der Ornithologischen Gesellschaft in Bayern* 5: 269-355.

- Blem, C. R. 1990. Avian energy storage. *Current Ornithology* 7:59-113.
- Bluhm, C. K. 1988. Temporal patterns of pair formation and reproduction in annual cycles and associated endocrinology in waterfowl. *Current Ornithology* 5:123-185
- Bossema, I. & Roemers, E. 1985. Mating strategy, including mate choice, in Mallards. *Ardea* 73:147-157.
- Cramp, S. & Simmons, K. E. L. (eds). 1978. *The Birds of the Western Palearctic. Vol. 1.* Oxford University Press, Oxford.
- Dawson, W. R. & O'Connor, T. P. 1996. Energetic features of avian thermoregulatory responses. In: *Avian Energetics and Nutritional Ecology*. C. Carey (ed). Chapman and Hall, pp 85-124
- Egilsson, K. (ed.) 1985. *Innnes. Natturufar, minjar og landnyting*. [Innnes. Nature, antiquities and land use]. Museum of Natural History, Reykjavik. 82 pp.
- Gardarsson, A. 1975. Islenskir votlendisfuglar. [The birds of Icelandic Wetlands]. In: *Rit Landverndar 4: Votlendi*. Arnthor Gardarsson (ed). Landvernd, Reykjavik, pp. 100-134.
- Gardarsson, A. & Einarsson, A. 1997. Numbers and production of Eurasian Wigeon in relation to conditions in a breeding area, Lake Myvatn, Iceland. *Journal of Animal Ecology* 66:439-541.
- Hansson, L. 1966. Studies on the adaption of the Mallard *Anas platyrhynchos* to urban environments. *Vår Fågelvärld*, Suppl. 4:95-140.
- Heitmeyer, M. E. 1987. Body composition of female Mallards in winter in relation to annual cycle events. *Condor* 90:669-680.
- Heitmeyer, M. E. 1995. Influences of age, body condition, and structural size on mate selection by dabbling ducks. *Canadian Journal of Zoology* 73:2251-2258.
- Hepp, G. R. & Hair, J. D. 1983. Reproductive behaviour and pairing chronology in wintering dabbling ducks. *Wilson Bulletin* 94: 675-682.
- Hepp, G. R. 1984. Dominance in wintering Anatinae: potential effects on clutch size and time of nesting. *Wildfowl* 35:132-134.
- Hepp, G. R. 1986. Effects of body weight and age on the time of pairing of American Black Ducks. *Auk* 103:477-484.
- Hepp, G. R. 1989. Benefits, costs and determinants of dominance in American Black Ducks. *Behaviour* 109:224-234.
- Holmberg, K., Edsman, L. & Klint, T. 1989. Female mate preferences and male attributes in Mallard Ducks *Anas platyrhynchos*. *Animal Behaviour* 38:1-7.
- Icelandic Meteorological Office. *Vedrattan [Annual Icelandic Weather Report]*. Website: <http://www.vedur.is>.
- Johnsgard, P. A. 1960a. Pair-formation mechanisms in *Anas* (Anatidae) and related genera. *Ibis* 102:616-618.
- Johnsgard, P. A. 1960b. A quantitative study of sexual behaviour of Mallards and Black Ducks. *Wilson Bulletin* 72:133-155.
- Johnson, K. P. & Sorenson, M. D. 1999. Phylogeny and biogeography of dabbling ducks (Genus: *Anas*): a comparison of molecular and morphological evidence. *Auk* 116:792-805.
- Johnson, W. P. & Rohwer, F. C. 1998. Pairing chronology and agonistic behaviours of wintering Green-winged Teal and Mallards. *Wilson Bulletin* 110:311-315.

- Jonsson, J. E. 2000. *Felagskerfi graanda ad vetrarlagi* [The social system of Wigeon, Teal and Mallard in winter]. MS thesis, University of Iceland, Reykjavik. 99pp.
- Lebret, T. 1961. The pair formation in the annual cycle of the Mallard, *Anas platyrhynchos*. *Ardea* 49:7-138.
- McKinney, F. 1986. Ecological factors influencing the social systems of migratory dabbling ducks. In: *Ecological Aspects of Social Evolution*. D.I. Rubenstein & R.W. Wrangham (eds). Princeton University Press, Princeton. pp 73-82
- Mjelstad, H. & Sætersdal, M. 1990. Reforming of resident Mallard pairs *Anas platyrhynchos*, rule rather than exception? *Wildfowl* 41:150-151.
- Nielsen, O. K. (ed.) 1992. *Tjörnin, saga og lifriki*. [Lake Tjörnin, history and biota]. Reykjavíkurborg, Reykjavik. 197 pp.
- Newton, I. 1998. *Population Limitation in Birds*. Academic Press. 598 pp.
- NOAA. Website: <http://www.ncdc.noaa.gov/>
- Paulus, S. L. 1983. Dominance relations, resource use, and pairing chronology of Gadwalls in winter. *Auk* 100:947-952.
- Raitasuo, K. 1963. Social behaviour of the Mallard *Anas platyrhynchos*, in the course of the annual cycle. *Finnish Game Research* 24:1-71.
- Robertson, G. J. Cooke, F., Goudie, R. I. & Boyd, W. S. 1998. The timing of pair formation in Harlequin Ducks. *Condor* 100:551-555.
- Rohwer, F. C. & Anderson, M. G. 1988. Female-biased philopatry, monogamy, and the timing of pair formation in migratory waterfowl. *Current Ornithology* 5:187-221.
- SAS Institute. 1990. *SAS/STAT User's Guide. Version 6*. Fourth edition. Volume 2. SAS Institute, Cary, North Carolina, USA.
- Savard, J-P. L. 1985. Evidence of long-term pair bonds in Barrow's Goldeneye *Bucephala islandica*. *Auk* 102:389-391.
- Skutch, A. F. 1962. The constancy of incubation. *Wilson Bulletin* 74:115-152.
- Soutiere, E. C., Myrick, H. S. & Bolen, E. G. 1972. Chronology and behaviour of American Wigeon wintering in Texas. *Journal of Wildlife Management* 36:752-758.
- Weidmann, U. 1990. Plumage quality and mate choice in Mallards *Anas platyrhynchos*. *Behaviour* 115:127-141.
- Weller, M. W. 1965. Chronology of pair formation in some nearctic *Aythya* (Anatidae). *Auk* 82:227-235.
- Williams, M. & McKinney, F. 1998. Long term monogamy in the Blue Duck. In: *Partnerships in Birds. The Study of Monogamy*. J.M. Black (ed). Oxford University Press, Oxford. pp 72- 90
- Wishart, R.A. 1983. Pairing chronology and mate selection in the American Wigeon *Anas americana*. *Canadian Journal of Zoology* 61:1733-1743.

Appendix 1. Sample sizes of Wigeon, Teal and Mallard in Iceland 1997-98 and 1998 -99.
Note: the sexes of Wigeon and Teal were not determined in September.

	Wigeon				Mallard				Teal			
	Females	Females	Males	Total	Females	Females	Males	Total	Females	Females	Males	Total
	Paired	Total	Total		Paired	Total	Total		Paired	Total	Total	
1997-98:												
5 Sept	0	-	-	133	8	115	187	302	0	-	-	21
13 Sept	0	-	-	45	5	113	333	446	0	-	-	17
17 Sept	1	-	-	198	5	19	68	87	0	-	-	14
26 Sept	6	-	-	142	31	84	112	196	13	-	-	34
8 Oct	18	150	107	257	74	143	292	435	7	25	22	47
17 Oct	45	162	114	276	134	231	388	619	11	28	19	47
31 Oct	32	110	88	198	94	133	224	357	8	26	24	50
14 Nov	38	115	98	213	84	200	357	557	19	83	92	175
29 Nov	22	83	108	191	102	168	328	496	15	61	74	135
17 Dec	51	127	128	255	106	179	338	517	6	24	30	54
29 Dec	46	85	119	204	121	176	290	466	13	34	62	96
15 Jan	16	42	41	83	86	133	239	372	30	47	45	92
28 Jan	17	61	51	112	114	176	271	447	30	55	72	127
10 Feb	41	86	81	167	192	278	421	699	23	40	58	98
24 Feb	35	56	60	116	174	232	359	591	13	19	37	56
4 Mar	22	30	30	60	100	196	341	537	23	31	43	74
20 Mar	23	30	39	69	169	256	378	634	2	2	4	6
28 Mar	28	37	36	73	116	163	252	415	18	18	23	41
10 Apr	26	31	33	64	23	36	54	90	7	7	14	21
24 Apr	16	19	22	41	56	75	134	209	-	0	1	1
1998-99												
6 Sept	0	-	-	128	8	133	302	435	0	-	-	23
9 Sept	3	-	-	212	30	123	307	430	0	-	-	10
16 Sept	4	-	-	300	59	143	243	386	0	-	-	96
23 Sept	5	-	-	294	117	205	396	601	0	-	-	84
4 Oct	20	122	68	190	123	219	338	557	1	4	17	21
16 Oct	61	166	151	317	215	295	402	697	22	57	45	102
23 Oct	41	214	124	338	190	283	383	666	11	29	15	44
3 Nov	41	207	131	338	142	249	317	566	8	21	12	33
18 Nov	61	166	145	311	161	237	334	571	13	26	21	47
3 Dec	35	112	75	187	98	160	217	377	14	40	38	78
16 Dec	61	138	112	250	165	300	425	725	14	28	29	57
4 Jan	49	86	75	161	141	193	298	491	18	46	53	99
18 Jan	41	84	64	148	154	240	297	537	20	37	38	75
5 Feb	47	91	73	164	214	329	436	765	11	14	18	32
24 Feb	52	98	71	169	182	280	352	632	10	12	20	32
4 Mar	51	75	75	150	285	370	489	859	24	36	39	75
16 Mar	68	99	94	193	319	420	520	940	30	36	42	78
29 Mar	40	63	47	110	319	420	508	928	31	34	45	79
13 Apr	57	66	61	127	219	249	312	561	24	26	36	62
20 Apr	40	51	41	92	167	185	242	427	27	27	31	58