DOI: 10.17242/MVvK_3.16

# AUTUMN DUCK PAIRING AND WINTERING STRATEGIES: AN ADAPTIVE RESPONSE TO ENVIRONMENTAL WINTER CONDITIONS

**Alain Tamisier and Olivier Dehorter**

Centre d'Ecologie Fonctionnelle et Evolutive, CNRS, F 34033 Montpellier Cedex, France

## ABSTRACT

Recent papers demonstrated a strong correlation between body conditions of ducks at the end of the winter season and breeding success. From data (feeding duration per day and body mass) collected in the Camargue, south France, on three duck species, we already suggested that birds adopt a sets of behavioural and ecological mechanisms, so called a wintering strategy, from which body conditions at the beginning of the winter season predict body conditions at the end of the season (Tamisier *et al.* 1996). Within this strategy which has an adaptive value, autumn pairing seems to have a key position since paired birds are hierarchically dominant for food access at the end of the winter when food shortage occurs. Hence early pairing would be an advantage, not only for females, as most often thought, but also for males. The cost of early pairing would be recuperated later on in terms of breeding success.

## INTRODUCTION

Until the beginning of the 80's, breeding performance was supposed to be controlled by variables associated to breeding environment, and no functional link was supposed to exist between winter season and breeding season (Anderson and Batt, 1982). Following the Puxico Symposium in Missouri (Anderson and Batt, 1982) and the Conference at Galveston, Texas (Weller, 1988), an increasing number of papers revealed the existence of strong correlations between body condition of birds (mostly waterfowl and more recently waders) at the end of the winter season, and breeding performance (see Ankney *et al.*, 1991 for a review). Birds which

are able to store enough energetic reserves (mostly lipids, but also proteins in some circumstances) while they still are on their winter quarters, are those which have the highest breeding success several months later, at several thousands km further north. Conversely birds which fail storing reserves at the end of the winter or at intermediate stopping areas will produce less or no juveniles. Thus two points occurring in winter are of prime importance in the breeding success of waterbirds: 1) food resources that exist at the wintering grounds and/or at the stopping areas and 2) the capability of birds to have access to these resources.

In the Camargue, one of the major wintering grounds for western paleartic duck species in the Mediterranean basin, we developed the model of wintering strategies (Tamisier *et al., in press*), first proposed by Heitmeyer (1985) and Allouche (1988), for 3 duck species according to observed changes in energy demand and body mass. Autumn pairing is part of the wintering strategy. The aim of this paper is to propose that pairing in autumn, so far considered as an advantage only for females who benefit of their mate's attention to store reserves more easily (Rohwer and Anderson, 1988), has a decisive function for both partners in terms of breeding success. And if it can be associated to the availability of food resources once ducks arrive at the Camargue, then the environmental conditions that prevail during the fall months in these south-western winter quarters would actively participate in controlling breeding performance of the following season in reproductive areas.

## STUDY AREA AND METHODS

The Camargue, delta of the Rhône river in the Mediterranean sea, is a wide area of 145,000 ha where wetlands cover less than 40 % of the surface. Out of them, 19,000 ha are included in strictly protected areas (Reserves, mostly state owned). Other parts are affected to agricultural, industrial and urban use. In spite of several prestigious conservation policies, the trend is a decrease of wetlands because of the extension of human activities; after a rapid decrease between 1942 and 1984 (40,000 ha of wetland loss) the present trend is less but still at a rate of 0.5 % per year (Tamisier, 1990; ARPE, 1992; Tamisier, 1994). Furthermore, qualitative modification occurs on non protected wetlands; in effect those wetlands, privately owned, are used mostly for hunting (and more recently for tourism for some of them) which

leads to a mean kill of 150,000 ducks per year, to a high shooting disturbance during the 7.5 month hunting season. Hunting also implies water management; natural summer drying up of the marshes is replaced by permanent or semi-permanent flooding, salt or brackish water are replaced by fresh water pumped from the Rhône river. As a consequence, losses of heterogeneity and biological diversity of Mediterranean-type marshes are observed while monospecific continental-type communities become the most frequent on these private wetlands. They also are more predictable and more productive in terms of aquatic plant biomass than natural wetlands. Nevertheless they could not favour any increase of the size of the waterfowl populations since these populations are likely to be limited by hunting (Tamisier and Grillas, 1994). For a more detailed description of the Camargue wetlands, see Dehorter and Tamisier in this volume).

Climate is mediterranean-type in Camargue, with heavy rains in autumn and winter, mild temperatures till November and coldest temperatures from December to February (Heurteaux, 1976). Cold spells cause freezing of most or all marshes and lakes for periods which last usually 3-8 days, up to 3 weeks. For the last 30 years, freezing occurred 11 times, mostly in January. Water level increases regularly from September (usually low waterlevel in most marshes, many being even dry in Reserves) to February-March (all wetlands usually are inundated).

Camargue is the most important wintering area for ducks and Coots (*Fulica atra*) in France with a mean maximum population of about 125,000 ducks and 30,000 coots for the last 30 years. These numbers are those that can be counted at a given time, they do not take into account the number of birds which transit over the Camargue (probably around 500,000 birds). We selected three species which represent ca. 40% of the total wintering duck population: European Teal *Anas c. crecca*, European Wigeon *A. penelope* and Gadwall *A. strepera*. We used two sets of data, time budgets and body mass. Time budgets provided feeding durations per 24 hour cycle (Tamisier, 1974; Campredon, 1982; Allouche, 1988). Body mass were those of hunted ducks in the Camargue. Specific mass were standardised in order to allow interspecific comparisons through ANOVA. Details are provided in Tamisier *et al.* (1995).

## DISCUSSION AND CONCLUSIONS

### The wintering strategy

From these Camargue data, the winter season can be divided in three successive periods, each period lasting 2-3 months according to species:

1) *Restoring period.* Birds arrive in the Camargue, they must gain energy to recuperate the energy lost during the migration flight. Furthermore juveniles must gain some more energy to reach adult weight. As a consequence, all birds feed actively, feeding duration per 24 hour cycle is very long (12 to 16 hours according to species), and the 24 hours of the day are fully occupied by feeding (which brings energy) and sleeping (which limits at a minimum the energetic losses). Only a few hours in Teal are devoted to preening, a necessary activity related to moult of body-feathers.
2) *Pairing period.* Bird weights are maximum, climatic conditions are still comfortable. This is the only period in the winter season when ducks have extra time and they take advantage of that situation for swimming, courtship and pair formation.
3) *Fattening period.* From January onwards, environmental conditions become worst, food is scarcer and birds must store energy for spring migration and breeding. Sleeping is long again and feeding durations become longer than ever. Interspecific competition is probably at its highest and paired birds are hierarchically dominant for food access.

These three phases of the winter season are not only successive phases, they interact effectively in that only paired birds have a sure access to food at the end of the season (when food is less abundant); and paired birds are those which could perform courtship at mid-winter, that is to say those which had previously stored enough energy during the first period of the winter season. The three phases have functional links and support the model of a wintering strategy; we can hypothesise that body conditions of birds when they arrive in the Camargue have a predictive value for the conditions of birds 6 months later, when they leave to the breeding grounds (Tamisier *et al.*, 1995). In this context, pairing is a full component of the wintering strategy (**Figure 1**).

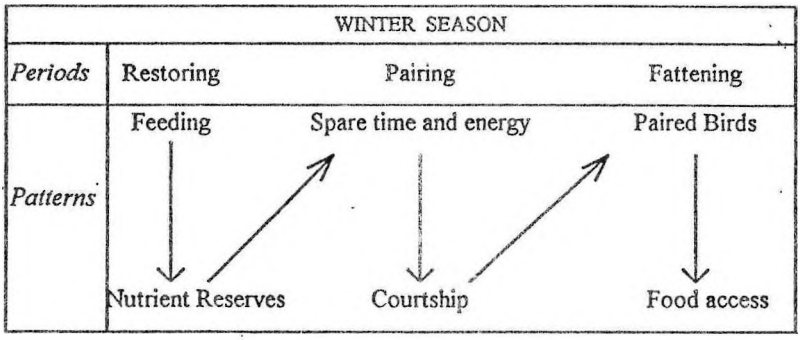


**Figure 1:** The Camargue model of wintering strategies (after Tamisier et al., 1995).

**Autumn pairing**

According to this strategy, it is a selective advantage for an individual to be paired before the end of the winter, so that it can store sufficient reserves, from a qualitative (lipids and proteins) and quantitative point of view, for spring migration and breeding. Hence it can have a better fitness in terms of breeding success. Pairing in autumn probably is the key point of the wintering strategy. As a matter of fact, those birds which failed to pair at that period will have no time to do it after, since they can hardly both store energy and pair at the end of the winter; and they won't have a good breeding success. As a consequence, autumn pairing and wintering strategy are fully integrated into the annual cycle. The cost of pairing so early is recuperated several month later at the breeding grounds. So a trade-off can be suggested between early pairing and breeding success (**Figure 2**).

Pairing in autumn is a very unusual timing characteristic for most waterfowl species as compared to other bird species and families in the northern hemisphere (Anderson *et al.* 1988). So far, pairing early in winter was considered as the result of a strong male competition because of a shortage of females (Spurr and Milne, 1976). Pairing early can be an advantage since, later on, no more females were available. However this advantage for males is counterbalanced by a risk for the paired male not to have enough reserves either for

maintaining pair bond (and be replaced by a male in a better condition) or even for its own energy consumption during spring migration (Afton and Sayler, 1982). Finally most authors considered that pairing early in the winter season was mostly an advantage for females to store nutrients during the last period of the winter while being defended by their mate against courting males (Ashcroft, 1976; Rohwer and Anderson, 1988). Social dominance at feeding sites is also at the advantage of paired females (Paulus, 1980). From our observations, we can add that it is also an advantage for males, since as paired birds, they have a priority access to food at a time when feeding is the most problematic (food shortage).

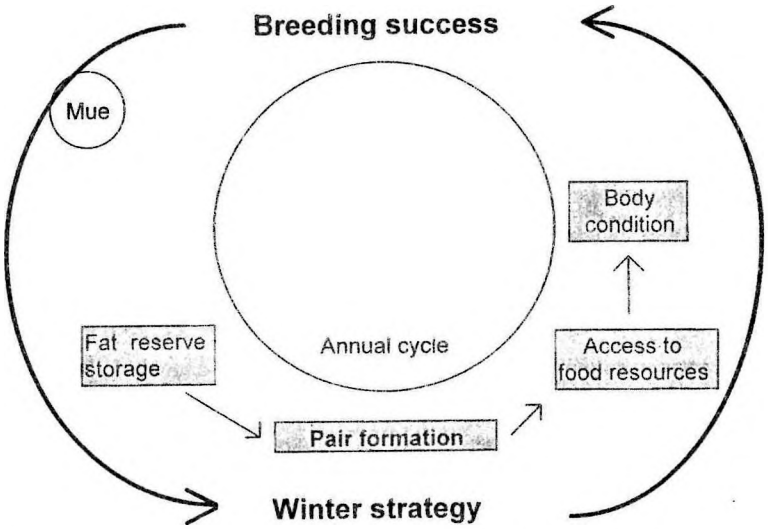


**Figure 2**: Pair formation, a key point in the wintering strategies, and a suggested trade-off with breeding success

Are this wintering strategy and the key position of pairing in the strategy characteristic of a single wintering area (the Camargue from where field data come), or do they have a more general significance ? In spite of detailed analysis from this point of view, we can suspect that ducks which winter in more northern wetlands like Sweden (cf. Nilsson, 1972) or Alaska (Conant *et al.*, 1988), as well as those wintering in tropical areas like Senegal (Roux *et al.*, 1978), behave differently and hence, have different wintering strategies. But we wish to

emphasise that, since birds must have good body conditions at the end of the winter season for a good breeding success, specific mechanisms should allow them to reach that point wherever they winter. The wintering strategy is supposed to be this adaptive set of mechanisms and we can suggest that it has a regional specificity. Now since autumn pairing is a very general life-history trait for most ducks of the northern hemisphere, and considering the cost of pairing, we can suspect that it keeps a central position whatever the wintering strategy. Wintering in tropical zones is probably an exception since palearctic ducks are not known to pair there (Roux *et al.*, 1978). More studies should be done in similar zones, especially in tropical winter quarters of central and south America.

## REFERENCES

Afton, A. D., R. D. Sayler (1982). Social courtship and pairbonding of Common Goldeneyes Bucephala clangula L. wintering in Minnesota. Can. Field Naturalist, 96: 295-300.

Allouche, L. (1988). Stratégies d'hivernage comparées du canard Chipeau et de la Foulque macroule pour un partage spatio-temporel des milieux humides de Camargue. Thèse, Montpellier, France. 180 pp.

Anderson, M. G., B. D. J. Batt (1982). Workshop on the ecology of wintering waterfowl. Introduction. 14-16 April 1982. Puxico, Missouri. Delta waterfowl Research Station.

Anderson, M. G., G. R. Hepp, F. McKinney and M. Owen (1988). Workshop summary: Courtship and pairing in winter. *In*: M. W. Weller (ed.), Waterfowl in Winter. Univ. of Minnesota Press, Minneapolis, pp: 123-131.

Ankney, R. C., A. D. Afton and R. T. Alisauskas (1991). The role of nutrient reserves in limiting waterfowl reproduction. Condor 93: 1029-1032.

A.R.P.E. (1992). Parc Naturel Régional de Camargue. Occupation du sol en 1991 et évolution depuis 1970. Hémisud Edit. Le Revest. 32 pp.

Ashcroft, R. E. (1976). A function of the pairbond in the Common Eider. Wildfowl 27: 101-105.

Campredon, P. (1982). Démographie et écologie du canard Siffleur *Anas penelope L.* pendant son hivernage en France. Thèse, Montpellier, France.

Conant, B., J. G. King, J. L. Trapp and J. I. Hodges (1988). Estimating populations of ducks wintering in Southeast Alaska. *In*: M. W Weller (*ed.*), Waterfowl in Winter. Univ. of Minnesota Press, Minneapolis, 541-552.

Dehorter, O., A. Tamisier (this volume). Typology of wetlands of the Camargue: a necessary framework for waterfowl studies.

Heitmeyer, M. E. (1985). Wintering strategies of female mallards related to dynamics of lowland hardwood wetlands in the Upper Mississippi Delta. PhD. Diss. Univ. Missouri, Columbia. 448 pp.

Heurteaux, P. (1976). Climatologie des années 1974 et 1975 en moyenne Camargue. Rev. Ecol. (Terre et Vie) 30: 619-627.

Nilsson, L. (1972). Habitat selection, food choice and feeding habits of diving ducks in coastal waters of south Sweden during the non-breeding season. Ornis Scandinavica 3: 55-78.

Paulus, S. E. (1980). The winter ecology of the Gadwall in Louisiana. Ms. Thesis, Univ. North Dakota, Grand Forks. 357 pp.

Rohwer, F. C. and M. G. Anderson. (1988). Female-biased philopatry, monogamy and the timing of pair formation in migratory waterfowl. Cur. Ornith. 5: 187-221.

Roux, F., R. Mahéo, A. Tamisier. (1978). L'exploitation de la basse-vallée du Sénégal (quartier d'hiver tropical) par 3 espèces de canards paléarctiques et éthiopien. Rev. Ecol. (Terre et Vie) 32: 387-416.

Spurr, E. B., H. Milne. (1976). Adaptive significance of autumn pair formation in the Common Eider Somateria mollissima (L.). Ornis Scandinavica 7: 58-59.

Tamisier, A. (1974). Etho-ecological studies of Teal wintering in the Camargue (Rhône delta, France). Wildfowl 25: 122-133.

Tamisier, A. (1990). Camargue, milieux et paysages. Evolution de 1942 à 1984. ARCANE, Arles. 36 pp.

Tamisier, A. (1994). La protection des zones humides. La Camargue. Cour. Environnement INRA, 22: 19-24.

Tamisier, A., P. Grillas. (1994). Habitat changes in the Camargue, France. An assessment of the effects of the loss of biological diversity on the wintering waterfowl community. Biol. Conserv. 70: 39-47.

Tamisier A., L. Allouche, F. Aubry. and O. Dehorter (1996). Wintering strategies and breeding success: hypothesis for a trade-off in some waterfowl species. Wildfowl 46 (in press).

Weller, M. W. (1988). Waterfowl in Winter. Univ. of Minnesota Press, Minneapolis. 625 pp.