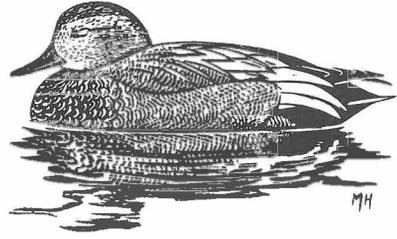


Wintering strategies and breeding success: hypothesis for a trade-off in some waterfowl species



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The dependence of the breeding performance of Anatidae on the body condition of birds (stored fat and protein) at the end of the winter season often has been reported. Several behavioural and ecological mechanisms observed on three species of waterfowl at different periods of the winter season in the Camargue, south France, are interactive. They are integrated in a model of wintering strategy where birds optimise daily allocation of time and energy at all stages during the wintering period in order to be in "pole position" throughout the season for access to food. Thus, body condition of birds at the beginning of the winter season can control body condition at the end of the season. We hypothesise the existence of a trade-off between wintering strategies and breeding success in that allocation of time and energy during winter can be adapted for better fitness. We predict that, at a specific level, the heaviest and/or the first birds to arrive at the winter quarter are the first to pair and have the best reproductive success during the following breeding season. Other cross-seasonal interactions are also suggested between breeding success and body condition during the following winter season.

Key-words: *Nutrient Reserves, Winter Strategies, Trade-off, Breeding Success, Cross-seasonal Interactions, Waterfowl.*

Theoretical studies of life history traits suggest trade-offs between reproductive success and survival on future reproductive success (Williams 1966, Stearns 1976). Since one individual cannot maximise all life history traits related to fitness, an improvement in one trait is associated with a decrease in some other trait related to fitness (Reznick 1985). Ryder (1970) proposed that mean clutch size had evolved in relation to events occurring before the breeding season in arctic-nesting geese. Since this early study, it has become more and more obvious that spatial and temporal isolation between a winter season and the following summer does not reflect a biological discontinuity (Weller 1982, Weller & Batt 1985). Many papers on Anatidae and Coot *Fulica* spp. have shown a link between individual female's nutrient reserves and breeding performance measured as egg production or survival of young (Ankney & McInnes 1978, Drent *et al.* 1978/79, Heitmeyer & Fredrickson 1981,

Krapu 1981, Teunissen *et al.* 1985, Heitmeyer 1988, Ankney & Alisauskas 1991). These reserves are most often stored during the last days or weeks on wintering grounds and/or on stop-over areas during spring migration; they are mostly lipids, although protein reserves are supposed to play an important role also, especially for larger species (Lindström & Piersma 1993). For instance, protein reserves are known to be used in species like Northern Pintail *Anas acuta* (Mann & Sedinger 1993) and American Coot *Fulica americana* (Alisauskas & Ankney 1985). This result gives rise to some controversy (Eisler & Grand 1994); for a review, see Ankney *et al.* (1991).

If body condition of ducks at the end of the winter is associated with breeding success, it is important to know which variables control this body condition. Some previously published data dealing with surface-feeding duck species wintering in the Camargue, France, can provide some answers. Time budget

analysis and seasonal trends of body-mass revealed several interspecific similarities and convergent patterns (Tamisier 1974, Campredon 1982, Allouche 1988). Therefore the question can be addressed in new terms: (1) Through which mechanisms can the body condition of birds at the end of the winter season be associated with biological features of birds at the beginning of the same winter season? (2) Can the Camargue results be extended to other species and winter areas, and to what extent? (3) Is there a trade-off between these winter features and breeding success?

Site description, material and methods

Climatic conditions in the Camargue include heavy rains in autumn and winter, mild temperatures until November and coldest temperatures between December and February (Heurteaux 1976) (Figure 1). Cold periods are associated with strong northwesterly winds when most or all wetlands freeze for periods lasting usually three to eight days, up to a maximum of three weeks. Such frosts occurred 11 times during the last 30 years, mostly in January. Most marshes are managed for hunting and water level is controlled by landowners. We measured water level monthly for the last 12 years on every marsh according to an index (from 0=dry to 5=overflooded); mean water-level index increases regularly from August (beginning of the hunting season) to February (end of the hunting season) and decreases thereafter (Figure 1).

According to complete censuses in the Camargue conducted monthly from 1964-65 to 1992-93, the first ducks arrive in July-August and become numerous from September. Peak numbers occur in December and fluctuate around 110,000 ducks and 30,000 coots, most birds have gone by March (Figure 2).

Feeding is a key parameter influencing nutrient reserves. In winter, many ducks feed essentially at night (Tamisier 1985, Jorde & Owen 1988, Owen 1991) and this pattern is not linked directly to hunting pressure (Tamisier 1989). We used data from three well studied species in the Camargue: a granivorous species, Common Teal *Anas c. crecca*, and two herbivorous ones, Gadwall *A. strepera* and European Wigeon *A. penelope*. We used seasonal variation in feeding duration per 24 hours to reflect the variation in energy intake, assuming that food availability and quality do not affect feeding duration (Tamisier 1974). Body mass of birds shot by hunters was recorded during the winters of 1964-65, 65-66, 79-80 and 80-81. They are known to be biased as regards to live bird mass (Dufour *et al.* 1993) but the pattern of monthly variation for birds shot in the Camargue (maximum values in mid-winter) is similar for trapped birds (Cramp & Simmons 1977, 1980). Specific mass was standardised (Sokal & Rohlf 1981) so that direct comparisons could be made between species by ANOVA where month, age, sex and species are considered as independent variables. When no interaction occurred between species and month, data were pooled (Teal and Gadwall). European Wigeon were kept apart because maximum weight

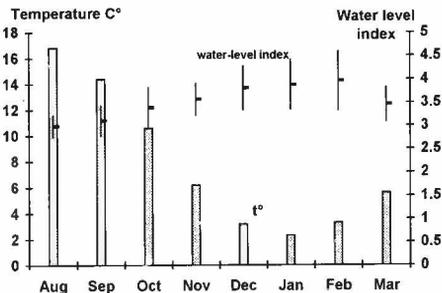


Figure 1. Mean monthly minimum temperatures (°C, 1944-1990) and water-level index (√ sd) of marshes in the Camargue (0=dry, 5= overflooded, 1980-1992).

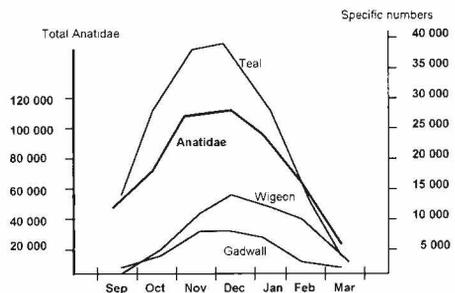


Figure 2. Mean numbers of ducks wintering in the Camargue (aerial censuses from 1964-65 to 1992-93).

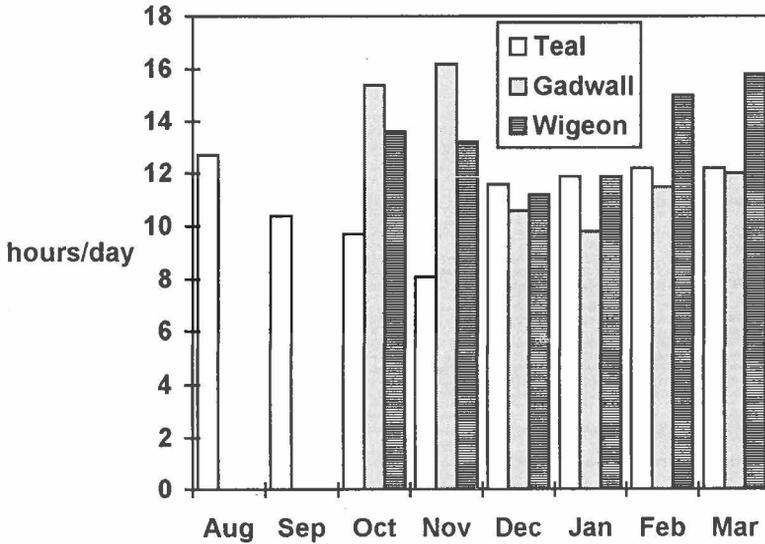


Figure 3. Mean daily duration of feeding (in hours) according to three *Anas* species in the Camargue (Tamisier 1974, Campredon 1982 and Allouche 1988).

occured one month later. A non-parametric analysis of variance (Global test of Friedman, Sokal & Rohlf 1981) was used to test feeding duration differences among species and months.

Time budgets and organization during the winter season

Teal spend as much as 12.7 hours per

day feeding in August (maximum), 8.1 hours in November (minimum) and 12.2 hours in February and March (Tamisier 1974) (Figure 3). Similar monthly changes in daily feeding duration (maximum variation from the lowest value is 40 to 60%) are observed for Gadwall (Allouche 1988, Allouche & Tamisier 1989) and Wigeon (Campredon 1982). Although herbivorous species consistently fed for longer each day

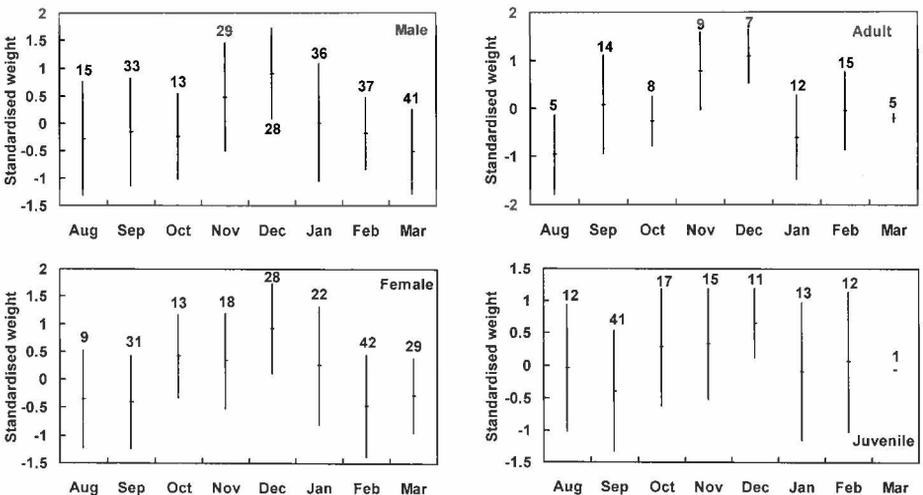


Figure 4. Monthly variation of body mass of juveniles and adults. Data from Teal and Gadwall, being similar, are pooled. Wigeon are kept apart because maximum weight occurs one month later. Numbers refer to sample size.

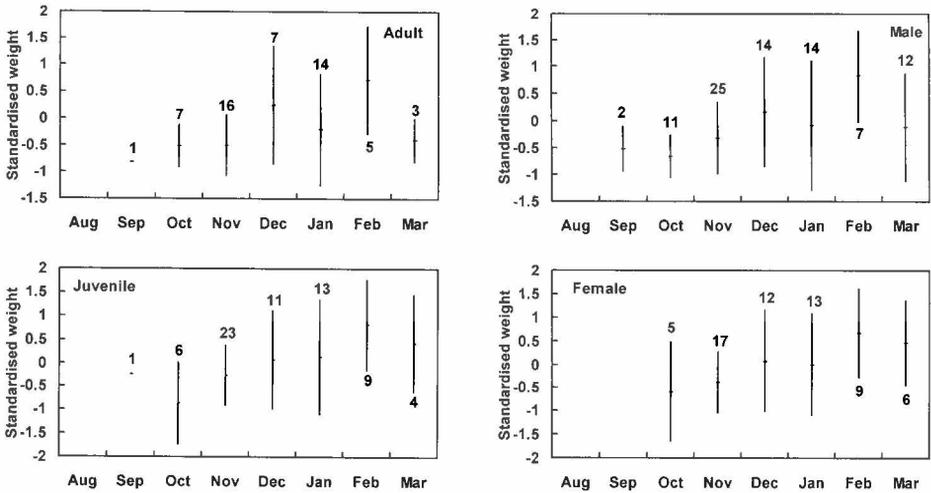


Figure 5. Monthly variation in body mass of Wigeon. Data from Teal and Gadwall, being similar, are pooled. Wigeon are kept apart because maximum weight occurs one month later. Numbers refer to sample size.

than granivorous, the pattern of monthly variation of feeding duration per day ($P < 0.05$, Global test of Friedman) was similar for Teal and Gadwall. Original data for Wigeon were lost and so could not be tested. All species fed least from November to December-January. We treated the winter season as three distinct periods (Tamisier 1974, Campredon 1982, Allouche 1988):

1) The restoring period with long daily feeding times lasts two months after birds reach their winter quarters. Males and females, juveniles and adults, have the lowest weights of the winter (Figures 4 & 5, Table 1). They feed intensively to restore body reserves lost during fall migration whilst juveniles, still lighter than adults (Table 1), must also gain weight. At this time, birds take advantage of abundant food resources (Tamisier 1974, Dervieux & Tamisier 1987, Allouche 1988) made available by low water levels (Pirot *et al.* 1984).

2) The pair formation period, with the shortest feeding times, lasts about two months during which all birds except Wigeon are at their maximum weights (Figures 4 & 5, Table 1). Climatic conditions are still favourable (no ice which prevents access to underwater food), so that daily energy balance can be reached with relatively short feeding and sleeping times. Several hours per

day are available for other activities. Courtship behaviour in ducks usually starts and reaches its peak at this time. In Wigeon 70 to 90% of pairs are formed before the end of January, often as early as December (Campredon 1982).

3) The fattening period with very long feeding times. During the last two to three months of the winter season (January-March), birds face new constraints with required storage of nutrient reserves for spring migration (Lindstrom 1991, Moore 1991) and also to achieve high breeding success. Yet, at this time of year, climatic conditions are usually the worst, food resources are restricted (Campredon 1982, Allouche 1988) and high water levels reduce food availability. As a response to these constraints, birds increase their daily feeding time, sometimes to the highest values of the entire winter season, whilst mean weights decrease (for Wigeon after February only).

Within this common three period scheme, species differ in the precise duration and timing of each phase, because of differences in arrival dates and in energetic needs. For instance, European Teal arrive first and have almost recuperated before Wigeon arrive to start this period. Overlap in timing of different periods probably occurs at the individual level also, although this is not fully documented. We suspect that the first Teal to arrive in

Table 1. Upper part: Mean weights (in g ± sd) according to month, species and sex-classes; sample size in brackets. Lower part: Standardised data at the specific level for monthly comparisons within sex and age-classes of three species (Teal, Gadwall and Coot); sample size in parentheses. Right column: Test F on month effect and levels of significance, *P<0.05, **P<0.01,***P<0.001.

		Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	F
Gadwall	M	650.0 ± 50.0 (2)	824.3 ± 29.1 (15)	837.1 ± 31.7 (7)	910.0 ± 26.5 (12)	935.9 ± 14.4 (11)	840.0 ± 20.9 (15)	823.6 ± 24.9 (7)	812.9 ± 40.4 (7)	4.263(7/68) ***
	F	733.8 ± 33.3 (4)	721.5 ± 19.6 (17)	806.1 ± 18.9 (9)	760.7 ± 36.7 (7)	814.5 ± 18.7 (10)	761.7 ± 36.1 (6)	742.5 ± 28.0 (10)	778.3 ± 42.1 (3)	1.890(7/58) NS
Wigeon	M		710.0 ± 20.0 (2)	711.8 ± 21.3 (11)	718.4 ± 16.9 (25)	785.7 ± 35.7 (14)	769.3 ± 31.0 (14)	837.9 ± 15.6 (7)	768.3 ± 28.0 (12)	2.178(6/78) NS
	F			647.0 ± 37.2 (5)	665.0 ± 11.6 (17)	692.9 ± 24.9 (12)	683.8 ± 22.8 (13)	736.1 ± 28.0 (9)	753.3 ± 30.7 (6)	2.287(5/56) NS
Teal	M	349.2 ± 9.6 (13)	341.4 ± 8.3 (18)	330.0 ± 10.4 (6)	363.0 ± 15.6 (15)	404.7 ± 10.0 (19)	364.8 ± 13.1 (21)	352.2 ± 4.7 (30)	338.0 ± 5.6 (35)	5.717(7/149) ***
	F	318.0 ± 12.4 (5)	298.9 ± 10.6 (14)	323.8 ± 13.4 (4)	348.2 ± 9.3 (11)	377.2 ± 9.0 (18)	340.6 ± 14.2 (16)	305.5 ± 6.0 (32)	319.6 ± 5.7 (26)	8.242(7/118) ***
		Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	F
M Ad		-1.587 (1)	0.360 ± 1.171 (8)	-0.535 ± 0.444 (4)	0.778 ± 0.851 (9)	0.667 ± 0.638 (2)	-0.638 ± 0.996 (10)	-0.031 ± 0.771 (10)	-0.201 ± 0.114 (4)	2.84(7/40) *
M Juv		-0.133 ± 1.122 (9)	-0.323 ± 0.981 (21)	-0.105 ± 0.918 (9)	0.352 ± 0.857 (8)	0.909 ± 0.493 (5)	0.094 ± 0.942 (5)	0.542 ± 1.749 NS		1.46(6/52)
F Ad		-0.806 ± 0.978 (4)	-0.282 ± 0.875 (6)	0.011 ± 0.564 (4)		1.258 ± 0.559 (5)	-0.409 ± 0.318 (2)	-0.084 ± 1.074 (5)	-0.176 (1)	2.79(6/20) *
F Juv		0.240 ± 0.743 (3)	-0.471 ± 0.917 (20)	0.726 ± 0.771 (8)	0.317 ± 0.985 (7)	0.447 ± 0.567 (6)	-0.204 ± 1.246 (8)	-0.031 ± 1.074 (10)	-0.065 (1)	1.74(7/55) NS
Total Ad		-0.963 ± 0.916 (5)	0.085 ± 1.068 (14)	-0.262 ± 0.553 (8)	0.778 ± 0.851 (9)	1.089 ± 0.599 (7)	-0.600 ± 0.911 (12)	-0.049 ± 0.844 (15)	-0.196 ± 0.099 (5)	4.76(7/67) ***
Total Juv		-0.040 ± 1.022 (12)	-0.395 ± 0.941 (41)	0.286 ± 0.930 (17)	0.335 ± 0.885 (15)	0.657 ± 0.563 (11)	-0.089 ± 1.107 (13)	0.064 ± 1.127 (12)	-0.065 (1)	2.26(7/114) *

Tamisier *et al.*

July-August have finished their recuperating phase before the last Teal arrive at the end of October. Yet any differences in chronology that occur at the specific, population or individual level, do not obscure the similarity in the chronological succession of the three periods and the fact that energy demand is always lower at mid winter.

Adaptive behavioural mechanisms

Several authors argue that it is advantageous for a bird to be heavier (usually fatter) than average for its size because this provides better resistance to cold (Baldassarre *et al.* 1986) and to starvation caused by reduced food availability, through snow or ice (Le Maho 1984, Robin *et al.* 1991). Heavy birds probably are less affected by the environmental conditions they encounter in winter (Afton 1980, Dufour *et al.* 1993). Within some theoretical limits, it may also be advantageous to be heavier if this involves higher muscular size and hence better flight ability, since this can reduce predation risk and allow better defense of territory as shown by Alisauskas & Ankney (1985) for the American Coot. More generally, positive correlations between body weight and winter survival have been found, for example, in Green-Winged Teal *Anas crecca carolinensis* (Bennet & Bolen 1978), Black Duck *A. rubripes* (Reinecke *et al.* 1982) and Canvasback *Aythya valisineria* (Haramis *et al.* 1986). In other words, despite some controversy (i.e. Lima 1987 from a theoretical point of view, Krementz *et al.* 1989, Dufour & Ankney 1990, Krementz *et al.* 1990 from field data), heavier than average birds in winter have a higher probability of surviving until the following breeding season.

Furthermore, courtship behaviour and pair formation start earlier for the heaviest birds (American Wigeon, Wishart 1983) or for ducks that can benefit from the best feeding conditions (Black Ducks, Brodsky & Weatherhead 1985, Hepp 1986). Courtship of heavier Chilean Teal *Anas flavirostris flavirostris* is more complete than for lighter ones (Standen 1980). Paired birds forage

more efficiently, as shown for Bewick's Swans *Cygnus columbianus bewickii* (Scott 1980). They are dominant over unpaired birds and juveniles in gaining access to food when conditions become harsh. Examples are Wigeon in the Camargue when an increase in water level makes feeding energetically more expensive (Campredon 1982), or Gadwall in Louisiana which face a seasonal reduction in food resources (Paulus 1983). In these situations, subdominant individuals are forced to leave and spend extra energy to fly to another, presumably suboptimal, habitat. Dominant birds stay put and take advantage of the available resources in the face of reduced intraspecific competition (Campredon 1982, Jorde *et al.* 1984). Similarly, a selective turnover of mostly unpaired Teal has been observed from marked birds on the main roosting sites of the Camargue where paired Teal remain in very large numbers. Unpaired individuals may be forced to use smaller roosting waterbodies (Pradel *et al.* submitted) as already suggested for females (Tamisier 1974).

A wintering strategy

If we reconsider the three successive periods of the winter season observed in the Camargue, they appear no longer as a succession of three independent phases, but rather as a continuum in which they are linked by strong interactions (**Figure 6**). Consequently, if it is adaptive for a bird to be in good condition at the end of the winter season in order to have high reproductive fitness (cf. Ankney *et al.* 1991), the following features should be adaptive also:

- 1) to arrive early at the winter quarters and feed intensively until maximum weight possible is achieved so that some free time is made available for activities other than feeding and sleeping;

- 2) to use this spare time and energy in the middle of the winter season for courtship and pair formation;

- 3) to be paired before the end of the season in order to ensure access to food

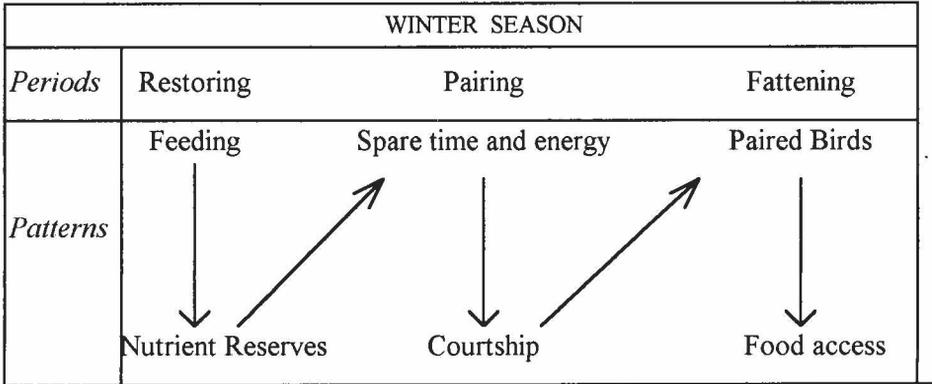


Figure 6. A model of wintering strategy for waterfowl, according to the Camargue data.

resources from a hierarchically dominant position.

This set of interactive features observed in the Camargue constitutes what we call the wintering strategy. From the first day after their arrival at the winter quarters until departure, birds should optimise their time allocation if they are to achieve the aims of this proposed strategy. This challenge is met in different ways in the different periods. During periods characterised by longest feeding times (periods one and three), birds select the most productive habitats among those available (Tamisier 1974, Campredon 1982, Pirot *et al.* 1984, Allouche 1988). Those habitats also are the most heavily hunted areas (Tamisier & Grillas 1994), therefore birds must balance the benefits of longer feeding durations for faster increase in weight against the increased risk of being killed (see Mayhew 1988).

In the middle of the wintering season, when feeding times are lowest and weights highest for most ducks, early courtship and pair formation are favoured, leading to a hierarchically dominant position for future food access and reproductive fitness, as indicated above. The cost is an immediate energetic expense in courtship and bond maintenance (Rohwer & Anderson 1988). At the end of the season, when energetic needs again are high, food is scarce and the climatic conditions are still unfavourable (see above), birds must lower energetic expenditures and increase energy input. Anti-predator

behaviour may be reduced (Campredon 1982, Allouche 1988) and warmer and wind-protected micro-habitats are selected to rest. Thus, energy conservation strategies occur at the expense of increased predation risk (Hepp 1985, Allouche & Tamisier 1989).

Because of the functional links that join the three periods of winter into an overall strategy, the selective pressures favour those individuals which attain proper energetic balance at the proper time. In other words, birds would 'start a race' once they arrived at their winter quarters and would have to be on the 'pole position' all through the winter if they were to have the highest individual reproductive fitness. The adaptive significance of this strategy was not realised until several months later.

Can our hypothesis be extended to other areas and species?

Our model relies on Camargue data related to three species and the strategy suggested here might be valid only for these species in the Camargue. More detailed analysis might still reveal some species-specific differences within this common strategy. Garganey *Anas querquedula*, which winter in Senegal, have very distinct time budgets with, surprisingly, much lower feeding durations in February-March, just before they leave for Europe and they are not known to be paired at the end of the winter (Roux *et al.* 1978). They may have a different strategy, including refuelling in temporary staging areas on the northern shore of the Mediterranean Sea. Similarly, ducks that winter further north, should have

strategies adapted to more severe climatic conditions, but also to a lower cost of migration which require fewer energy reserves. Rave & Baldassarre (1991) suggest that Green-Winged Teal wintering north of historic ranges depend on higher energy food than those wintering in Louisiana. This difference is probably strong enough to modify their strategy. Similarly, the monthly changes of carcass mass obtained in Louisiana (Rave & Baldassarre 1991) support the idea of a distinct wintering strategy as compared to the strategy proposed for Teal wintering in the Camargue. Our model emphasises that, regardless of winter quarters, there is a winter strategy, and that this strategy eventually favours those birds which have the most appropriate body condition (in terms of fitness) when they leave the winter site. At a specific level, details of the winter strategy are determined by environmental and geographical (distance to breeding range) characteristics of the winter area.

Hypothesis for a trade-off between wintering strategy and breeding success

Winter and breeding periods follow one another in time and are linked ecologically. We hypothesise the existence of a trade-off between wintering strategies and breeding success. Considered here only at the phenotypic level (Stearns 1989), the trade-off hypothesis relies on the fact that allocation of time and energy during the winter months can be adapted for increased fitness. As already seen according to the wintering strategy, it can be an advantage for a duck to expend most of its energy on feeding activities as soon as it arrives at the winter quarters in order to allow free time later (thanks to stored reserves) for courtship activities and be paired soon after. The cost (or one of the costs) is to maintain pair bonds for a longer period than if paired just before laying. The benefit as paired birds is to have the best access to food at a key time (the end of the winter season) when body condition predicts breeding success. So pairing in the autumn or

early winter as do most ducks, a most unusual timing compared to other birds in the northern hemisphere (Anderson *et al.* 1988), occurs not only to increase the ability of the paired female to store nutrients during the late winter "fattening" period (Rohwer & Anderson 1988) it can also be an advantage in terms of fitness because pair formation is very time consuming and pairing later (that is during the fattening period) would be hindered by lack of available time and energy. From this point of view, pairing earlier does not concern only females as proposed by Rohwer & Anderson (1988) but both males and females, as already suggested by Afton & Saylor (1982).

According to this trade-off hypothesis and at the specific level, we predict that the heaviest ducks at the time of their arrival at their winter quarters (as well as, within some limits, the first ones to arrive) are the first to pair in the course of the winter season and have the best breeding success during the following reproductive season. This fits with theoretical results of Holmgren & Lundberg (1993) who suggest that patterns of migration are partly controlled by such mechanisms of regulation between life traits occurring at distinct sites and seasons. They also point out that dominance by body mass or body condition (Sutherland & Parker 1985) and prior occupancy (Fretwell 1972) can be combined or inter-correlated (see also Scott 1988).

Finally, if this trade-off concerns life history traits occurring before the reproductive season, whilst most trade-offs mentioned in the literature deal with traits occurring after (winter survival, next breeding success), we can wonder about its year round effect. Female ducks are usually responsible for brood defense after hatching, so that the breeding season of the most productive females may be prolonged and result in poorer condition compared to unsuccessful breeders. As a consequence, they may also enter winter in worse condition (later arrival date, lower body weight and body condition). Conversely, those females that failed to breed for any reason can take advantage of this by arriving earlier at the winter quarter and competing

more efficiently for food in preparation for the next breeding season. Consequently, breeding success of individual females would be alternatively good and bad in successive years. It provides possible explanations of apparent differences in regulatory mechanisms between years, differences which have no immediate environmental links. Males usually leave females during incubation and their post-breeding energy balance is likely to be less affected by hatching success than that of females. Thus they would not be affected by these year to year regulatory mechanisms. We can criticise, however, this year-round mechanism since it can hardly be adapted to short lived species like surface-feeding ducks which must optimise the two or three reproductive seasons in which they breed. In Bewick's Swans, a long lived monogamous species, some associations have been found between size/condition and the life-time breeding success (Scott 1988, E. Rees, pers. comm.). Many more detailed analyses are needed to confirm the hypothesis.

Conclusion

The trade-off hypothesis presented here, based on observations only, deals with the phenotypic level only and is insufficient to document it conclusively. It needs to be checked at the genotypic level and at the level of the intermediate (physiological) structure (Stearns 1989). In terms of phenotypic trade-off, it should also be documented and tested, particularly at the individual level, in order to avoid biases due to reaction norms (Stearns 1989), and probably also through experimental process (Linden & Moller 1989). Alternatively, individual performances of birds in the wild might be checked according to their initial body weight during the wintering season. A first approach

might be to test, from capture-recapture data files, whether individual autumn weights predict weights at the end of the winter. A more efficient approach would consist, through the capture-recapture process, in comparing body condition of birds at the beginning and the end of the winter season by TOBEC method (Total Body Electrical Conductive Instruments, Walsberg 1988). This method, however, needs to be improved and validated. A third method could be applied to Bewick's Swans which can be identified by bill marks (Scott 1966) and for which abdominal profiles are correlated to body condition (Bowler 1995). Those birds wintering on sites like The Wildfowl and Wetlands Trust, Slimbridge, where they are individually monitored, could provide important information from data related to breeding success on the one hand, and arrival/departure dates, bodymass (from abdominal profiles) and time budgets during the winter season on the other hand during several successive years. However, this analysis might be complicated because of strong inter-correlations observed on Bewick's Swans between body condition, body mass, dominance rank and breeding success, as suggested by Scott (1988) and recent studies (E. Rees, pers. comm.). They might also help to understand year-round mechanisms as discussed above.

Within the winter season it is also important to isolate the key periods when the selection pressures are highest, and the level upon which they act. We may expect several answers according to species, strategies and years. These answers will provide new data to incorporate in the models of population dynamics on a year-round basis (Johnson *et al.* 1988) for a better prediction of reproductive success. Furthermore, they are relevant for questions which deal with conservation and winter habitat management.

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