Some considerations on the social requirements of ducks in winter

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Introduction

The increasing interest in wintering waterfowl stresses the importance of some well known topics (food, feeding habits, habitats) and emphasises a few new ones (pair formation, bio-energetics), bringing to light the correlation between nutrient reserves of ducks at the end of winter and their reproductive rate a few months later (Krapu 1981; Reinecke in press). The winter period is not only a break between two successive breeding seasons, but also can be considered a preliminary phase in the reproductive processes. The large gatherings of waterfowl in the winter quarters, as compared to their very low density on the breeding grounds, is a major difference between the two periods. The aim of this paper is to document the importance of these gatherings in ducks from several southern areas; examine the behavioural patterns associated with these gatherings; discuss their adaptive significance; and speculate about the fundamental aspects of these requirements.

The "Functional Unit System"

Several patterns are regularly or frequently observed during the main wintering time:
1) Diurnal concentrations of several thousands or tens of thousands of ducks engaged primarily (sometimes exclusively) in comfort activities. Examples include surface-feeding ducks in Sénégal, Mauritania, Mali, and Chad (Roux *et al.* 1978; Roux & Jarry 1984), Tunisia (Bredin *et al.* in press), Algeria (Skinner & Smart 1984), France (Tamisier 1974; Campredon 1981), California (Euliss 1984) and in Louisiana (Tamisier 1976), as well as for diving ducks in Sweden (Nilsson 1970), Switzerland (Pedroli 1982), and Iowa (Thornburg 1973).
2) Numbers of birds are relatively stable at every location from one day to the next.
3) Ducks tend to use traditional localities on large open areas for these gatherings (Tamisier 1974; Roux *et al.* 1978; Roux & Jarry 1984).
4) Nocturnal feeding (Tamisier 1966; Willi 1970; Roux *et al.* 1978; Campredon 1981; Pedroli 1982; Paulus 1984a) usually occurs at distinct and scattered localities where the density of ducks is much lower.

These data suggest that ducks probably use a social organization for the exploitation of their wintering grounds. A more detailed study on Teal *Anas c. crecca* in the Camargue, France, gives supporting evidence for this hypothesis (Tamisier 1979). The Camargue, a winter quarter for 40,000 Teal (mean of maximum), appears divided into three geographical sectors. Every sector includes an area of diurnal concentration (the resting area) used for comfort activities and several feeding areas scattered (2–20 km) around the resting area and used only at night. Every sector is exploited by a group of Teal relatively constant in numbers and independent of the other groups: the individuals belonging to one group regularly exploit the same resting area and the same feeding areas. This is what I term the "Functional Unit System" (Fig. 1).

This hypothesis was confirmed by a telemetric study (Tamisier & Tamisier 1981) which demonstrated the very strond fidelity of every individual to its Functional Unit. In the rare cases (3%, n = 305) where changes of resting area were observed, an immediate change of feeding areas occurred too. Teal which moved to a new resting area flew to the corresponding feeding areas the following night. They had passed from one Functional Unit to another.

Furthermore, several new aspects of this organization were demonstrated. A given individual used the same restricted feeding point constantly during the night. Individuals remained in their original group and/or the geographical sector (the Functional Unit) exploited by this group. The artificial transfer of five individuals to another Functional Unit was followed by a quick return to the original Unit from a few hours to four days later. Every individual remained on a precise location on the resting area which is nearest to the feeding area used at night.

Field observations and telemetric analysis of Teal suggest that winter quarters are divided into rather isolated sectors. Also every individual belongs to a social group

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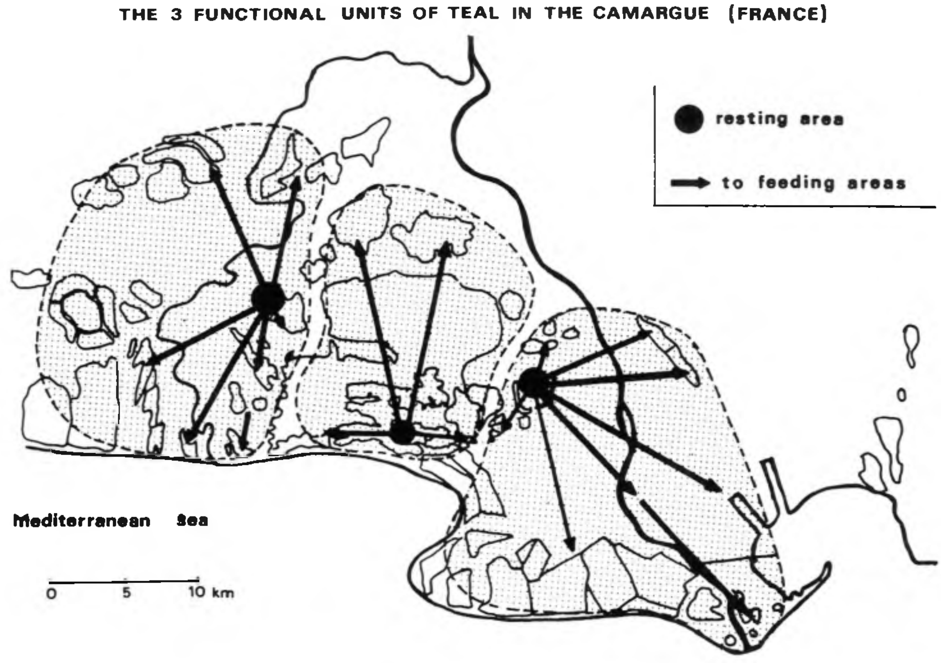

Figure 1. The Camargue (France) as a winter quarter for 40,000 Teal is divided into three geographical sectors (the Functional Units) which are used by three distinct social groups of Teal. Every sector includes a diurnal resting area for comfort activities and several nocturnal feeding areas.

that exploits a specific sector. These are essential components, geographical and social, of the Functional Units. While only shown for Teal in the Camargue, this concept gives some meaning to observed behavioural patterns of other duck species at other temperate and tropical winter quarters.

Adaptive significance

We are facing two main points: diurnal gregariousness mostly for comfort activities and nocturnal feeding on separate localities (Fig. 2). Gregariousness, which has been demonstrated for other species (see Krebs 1978), may be an anti-predator response for ducks, too (Tamisier 1974). Large flocks of ducks permit a collective vigilance which lowers individual vulnerability (Stinson 1980) towards diurnal predators (eagles, falcons, hawks, and more recently large gulls).

Gregariousness also allows an "information centre" to exist whose function is mostly related to feeding (Ward & Zahavi 1973). Any individual knowing where to feed goes directly there and it is advantageously followed by those which failed to feed the time before. The direct flight of Teal from the resting place to their usual feeding location is probably conspicuous enough to be seen by the "hesitating" ducks. Moreover, since the distribution of ducks on the resting area reflects the distribution on feeding areas it is advantageous for a "hesitating" duck to settle in a group rather than to stay alone, and to choose a part of the resting area where numbers are high in order to increase its probability of finding a feeding area. This hypothesis, while not actually demonstrated (see Degroot 1980, for an experimental analysis) is usually linked to the unpredictability of food. The "information centre" will be meaningful in cases where food is clumped (in space or time) and much less useful when food is predictable. In fact food is rarely constant in the wild, but more or less unpredictable.

Gregariousness should therefore occur in species which are dependent on the most unpredictable food resources. For ducks, availability of food (mostly seeds and vegetative materials) is directly dependent

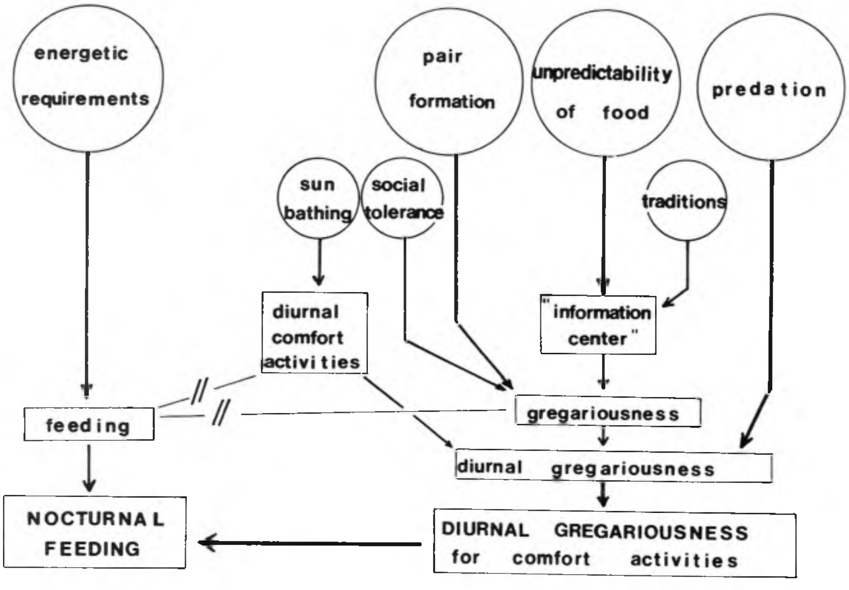

Figure 2. The adaptive significance of the "Functional Unit System": a interpretative model.

on the water level. Water depth is variable during the winter and even over a few days because of the flatness of the winter quarters and rapid drying up (wind and evaporation) after heavy rains. Thus food is unpredictable both in time and space. In response, ducks have adopted a social strategy through the "information centre" to optimize the use of feeding places.

It can be argued that, from an individual point of view, a duck has no advantage in giving away the "information" to conspecifics which become competitors for food. But the balance between advantages and disadvantages is provided by frequent shifts in opportunities for a given individual, which may change from being a duck who knows to a duck who does not know the location of the available unpredictable feeding areas.

So, the "Functional Unit System" appears as an elaborate strategy favouring the optimal partitioning of food resources while minimizing intraspecific competition. Moreover, traditional use of the same resting area as an "information centre" considerably increases these advantages.

Another advantage of gregariousness is that it brings together a large number of males and females, thus favouring pair formation. Little is known on this subject in ducks (see Weller 1965; Wishart 1983) although sexual courtship in autumn and completion of pair formation before spring migration for many species are well established. Hence winter gathering of ducks is surely important in this phase of the reproductive process and favours genetic flow. In spite of this behavioural activity, sexual hormonal activity is almost nil in winter (gonad development starts after February in Mallard *Anas plathyrhynchos* and Teal: Jallageas *et al.* 1978; Donham 1983), allowing greater social interaction between individuals.

Finally it is advantageous for comfort activities to occur diurnally because they are connected with sun-bathing, the preening and sleeping ducks rotating as the sun moves in the sky (Tamisier 1974, 1976; Roux *et al.* 1978). The significance of sun-bathing is still controversial (Kennedy 1969; Potter & Hauser 1974).

Nocturnal feeding appears to be a direct consequence of diurnal gregariousness rather than a need *per se*. In effect feeding, which lasts more than 7–8 hours per 24 hours, cannot be diurnal because comfort activities usually take the whole day. Furthermore, feeding would be hardly compatible with gregariousness because feeding ducks are less aware of a potential predator than preening, roosting, or even sleeping ducks, which open the eyes several times per minute. Moreover, if they had to feed on the area where they gather in huge numbers, they would rapidly exhaust its food resources and would have to change to another gathering area, losing the advantage of the traditional use of this area.

Discussion

This description and interpretation models the exploitation system of a wintering area by ducks. It emphasises some fundamental requirements of ducks and suggests that diurnal gregariousness and nocturnal feeding are not adaptations to human action (disturbance from hunters and farmers), but a response to the environmental variables. They have a survival value. However, the model has its own limits because nature, not being a model, cannot be reduced to it without many over-simplifications. Firstly, it relies on field data from southern winter quarters where the most typical patterns of winter strategy are to be expressed. This is all the more true as the most southern quarters are less influenced by human disturbance, making still possible to correlate the observed fundamental behaviour and the natural parameters to which they are adapted. Secondly, it gives a static view of wintering problems, whereas winter is an extreme and dynamic period between two migrating seasons. This critical period occurs gradually and is completely reached in different months according to species, location, and climatic conditions.

As a consequence the model is more flexible than it looks. The most marked distortions will happen with transient, post- and pre-migrating ducks whose food requirements are higher; with herbivorous and zoophagous species whose time-budgets can be different; during freezing periods when ducks must face higher energy demands and less food availability; and where ducks adapt to man-modified habitats (better food predictability when field-feeding) and to hunting. These points alone can explain the important differences observed in most northern winter quarters. So variations in the model illustrate a gradient from the breeding time/area to the wintering time/area. But none of these distortions will affect the persistence of the social strategy for the exploitation of a wintering area.

Furthermore, emphasis on the social origin of this organisation must not hide other parameters whose nature and importance are progressively emerging from recent studies dealing with the eco-physiology of ducks. Those parameters show the importance of requirements at the individual level. They are additive to those related to the ecological requirements already observed and are complementary to the social ones. So this social organisation provides the fundamental support which both enables and is necessary for the fulfilment of individual requirements. Since it is an adaptive response to the environmental conditions on the winter quarters, it may be important to maintain these conditions as much as possible, in particular the large open areas available for diurnal gatherings of huge numbers of ducks, and the unpredictability of food resources around. Conversely, if providing ducks with food through management practices is considered a priority goal, very immediate positive responses can be expected (for instance more healthy ducks at a given place on a given time). However in the long-term, some progressive deleterious effects on their social organisation and hence, on the fulfilment of their fundamental requirements, may also occur.

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Summary

Data collected on temperate and tropical winter quarters of holarctic ducks point out several constant patterns: large diurnal concentrations mostly for comfort activities on traditional resting areas; and nocturnal feeding usually at separate localities. A more detailed analysis on Teal *Anas c. crecca* in the Camargue, France (field observations and telemetry), supports the idea of a social organization (the "Functional Unit System"). Traditional resting grounds may serve as an "information centre" for the optimal exploitation of unpredictable food resources; comfort activities are diurnal because related to sun-bathing; and flocking, an anti-predator response, favours pair-formation. Nocturnal feeding is a consequence, of this social organisation.

As a general model dealing with the fundamental requirements of ducks in winter, it is most obvious at the more southerly wintering quarters. It is less conspicuous: the closer the wintering grounds are to the breeding areas (having many transient birds); as habitats are modified (field-feeding); as human disturbance becomes important (hunting). There is a gradient from the breeding time and area to the wintering time and area. The elaborate social organization appears

to be a fundamental support for the fulfilment of the individual's needs and is adapted to winter environmental conditions. Interest in bio-energetics of ducks (usually at the individual level) should not neglect their social requirements. Physiological results must facilitate the understanding of the adaptive significance of the social organization.

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