Etho-ecological studies of Teal wintering in the Camargue (Rhone Delta, France)

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Through the numbers of its wintering ducks and their specific diversity, the Camargue is one of the most important wintering areas for West Palaearctic Anatidae. The population of Teal *Anas crecca* is particularly well represented there and was studied from 1964 to 1972. The results obtained have been published in detail (Tamisier, 1972b) and are presented in summary here. An ecological sketch of the Camargue (Hoffmann, 1958), a detailed phytosociological analysis (Molinier & Tallon, 1970) and a study of edaphic (soil) and climatic factors (Heurteaux, 1970) should be read usefully for a total understanding of the importance and uniqueness of the Camargue as a whole.

I. Analysis of the population

Origin

Teal are ringed intensively in the Camargue (Station Biologique de la Tour du Valat) and from 50,000 Teal caught (1952–1970), 10,000 recoveries have been obtained, 7,000 from hunters. These data give a good idea of the origin of the population.

Most of the Teal wintering in the Camargue come from an area covering Finland, the Baltic Republics, the Leningrad' and Novgorod's provinces and White Russia (Hoffmann, 1960; Wolff, 1966; Shevareva, 1970). The majority of Teal in this breeding area winter in the Camargue. The Camargue is the terminal stage of their migration, except for a few birds continuing towards W and SW. However, during cold spells, many Teal leave the Camargue and reach the French and Portuguese Atlantic coasts as well as some more inland areas.

Fluctuations

Variations in numbers are determined by the different migratory movements and by the effects of mortality. The former are the more striking. Teal arrive in the Camargue from July and their numbers increase progressively until November when numbers are maximum (mean 40,000; maximum 80,000 in 1972). The first departures occur in January and the last Teal leave the Camargue by April (Figure 1). These fluctuations of numbers are similar to those for the other species of ducks. The total number of Anatidae wintering there ranges from 120 to 150,000 birds.

The effects of mortality on the numbers are less spectacular. This mortality is mostly due to hunting which removes 20,000–25,000 Teal each shooting season (15 August–31 March) in the Camargue. The mortality rates evaluated by means of composite and dynamic life-tables (Hickey, 1952) are 65% for juveniles and 45% for adult Teal annually. These rates are always higher for females than for males. They have tended to increase since 1955 because of the increase in hunting pressure. This occurs mostly during the 2 first and 2 last months of the winter season. Natural mortality is very slight, masked by the major effects of hunting pressure (Tamisier, 1970a).

Structure of the population

Sex-ratio always favours males: 70% is the mean and by August it is 80–85% (earlier migration of males). These ratios from counts *in natura* are higher than those from ringing. The comparative values show that the traps are $1\frac{1}{2}$ times more attractive for females. The higher proportion of males is usual in the other wintering areas and it is to be expected in the Camargue which is the terminal stage of this population. This weakens the hypothesis that females winter more to the south than males. If the sex-ratio is equal at hatching (which is probable, but not checked), one would think that females have a higher mortality rate (they are actually more vulnerable to all the mortality factors), and/or have a different range, being less attracted than males by the large wintering areas from where most of the data are obtained. In fact, they have distinct requirements and such differences can reduce intraspecific competition (Blondel, 1971).

Age-ratios obtained from ringing data indicate a proportion of 80% juveniles during the first months of wintering in the Camargue. Calculated from life-tables the percentage of juveniles decreases strongly, from 65 to 45%, between the beginning and the end of the annual cycle: the very narrow age-pyramid (Figure 2) indicates the heavy action of mortality factors (mostly hunting) during the first year. The mean life span of Teal

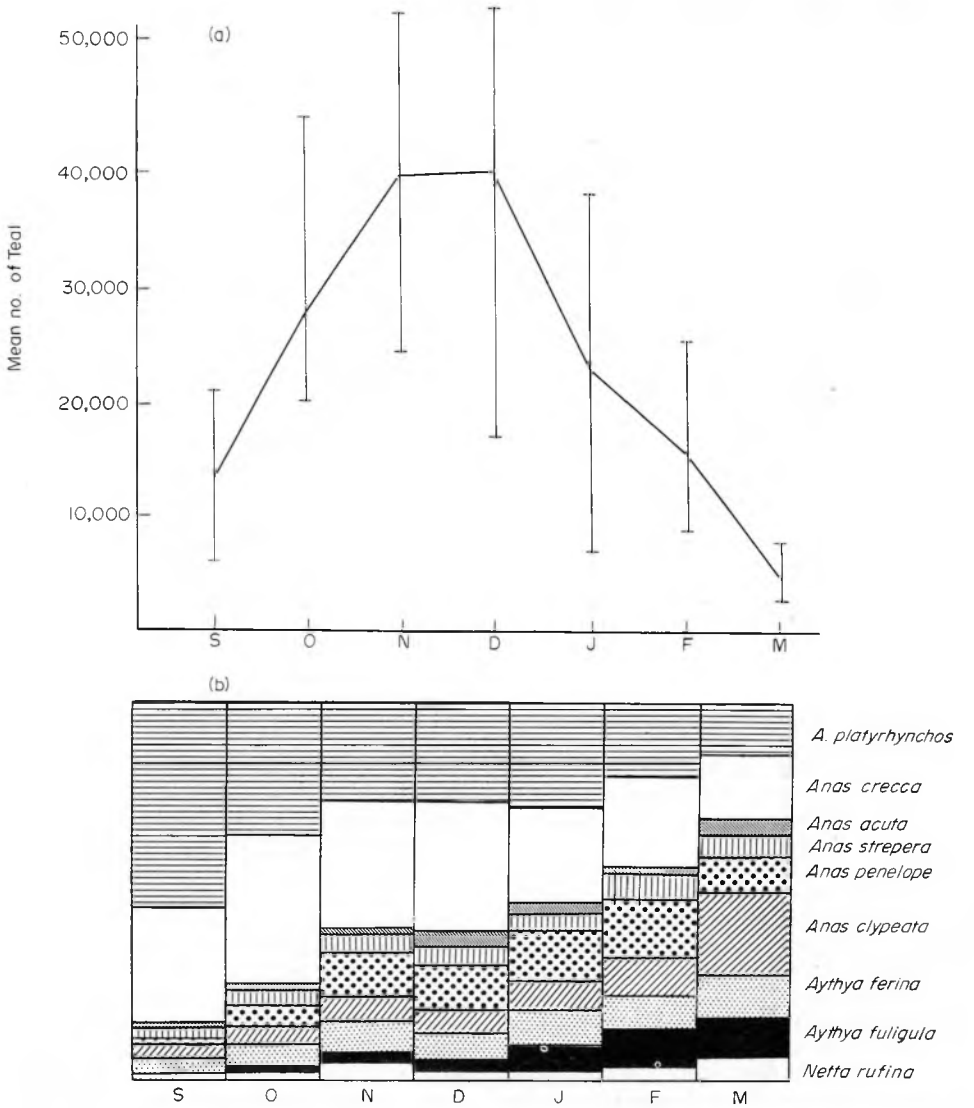

Figure 1. (a) Mean number of Teal in the Camargue (1964–1965 to 1971–1972). Vertical lines show the maximum deviations. (b) Relative abundance of the different species of ducks (total 120,000–150,000 birds). Surface feeding ducks are predominant and Teal the most abundant except in August and March. The monthly variations of total numbers parallels that of the Teal.

ranges from 1 to 2 years while their theoretical mean age is probably 9–10 years (Tamisier, 1970a) and their potential longevity is 17 or 18 years (Ryabov, 1960).

II. Daily rhythms

The two phases—diurnal and nocturnal—of the daily cycle have distinct behavioural aspects (Tamisier, 1972a). By day, wintering Teal are gregarious and concentrated on large open waters called 'remises' where they sleep, preen and rest. They feed very little. At night, they leave their resting places and scatter on nearby marshes for feeding (nocturnal observations have been made on moonlit nights and in darkness with an infrared telescope).

Analysis of the activities

Resting occurs on the water or on the shores

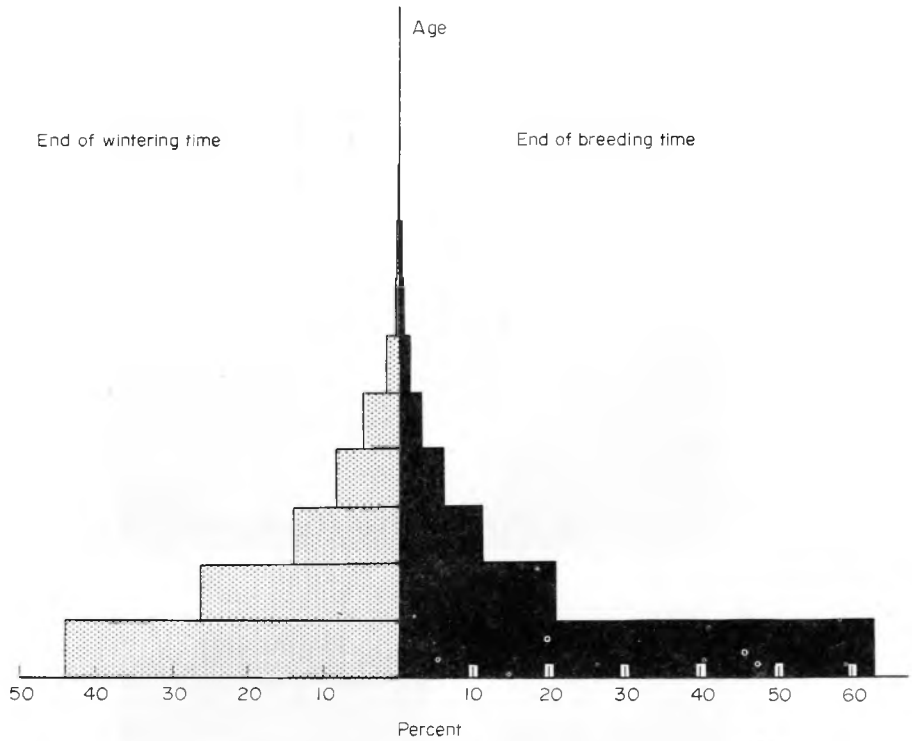

Figure 2. Age-pyramids of Teal. Hunting is the main mortality factor, particularly for juveniles (65% for first year Teal in the Camargue).

where Teal sleep while keeping frequent contact by sound and sight with other individuals. They often stand on the ground, roost on clumps of vegetation or perch in trees. They sleep for 6–10 hours per day.

Preening occurs mostly standing on the shore close to the water. It lasts at most 3 hours during the 3 first months of wintering (moulting period) and very little thereafter.

Swimming appears as a diversion activity allowing a constant adjustment of the distribution of the Teal on the remise, in reaction to environmental pressures (disturbances by predators, drift by wind, etc.). It involves both courtship activities and social displays. Its duration ranges from 0·1 to 6·5 hours per day.

Feeding occurs only on very shallow waters (less than a few centimetres) in which Teal walk slowly, filtering the mud with their bill. This behaviour is most effective: 80% of the time spent is used in filtering the mud, only 20% in walking. It occurs most frequently (70%) during nocturnal feeding and Teal appear well adapted to it. Other feeding behaviour (head under water, head and neck under water, up-ending) are less effective and occur mostly during diurnal feeding. Daily feeding time varies according to the month (8–13 hours per day). It is independent of the duration of darkness.

Schematically, diurnal rhythms show three successive phases.

(a) Pre-wintering (August–September). Teal, 80% being juveniles, arrive in the Camargue: their weights are low, their energy requirements are very high: the daily feeding duration is long (12·7 hours in August; 10·4 hours in September). The vital moult involves a daily preening time of 3 hours. All these physiological conditions require a long resting time (8·5–10 hours). The daily cycle is completely occupied with indispensable activities.

(b) Wintering (October–December). Teal are in a phase of physiological equilibrium with high weights and little or no moult. The climatic conditions are mild (except sometimes in December) and energy loss is slight. Swimming can occupy a long time (3–6 hours).

(c) Post-wintering (January–March). Low temperatures, sexual activities and preparations for spring migration result in a substantial increase in energy requirements (more than 12 hours feeding) and of sleeping

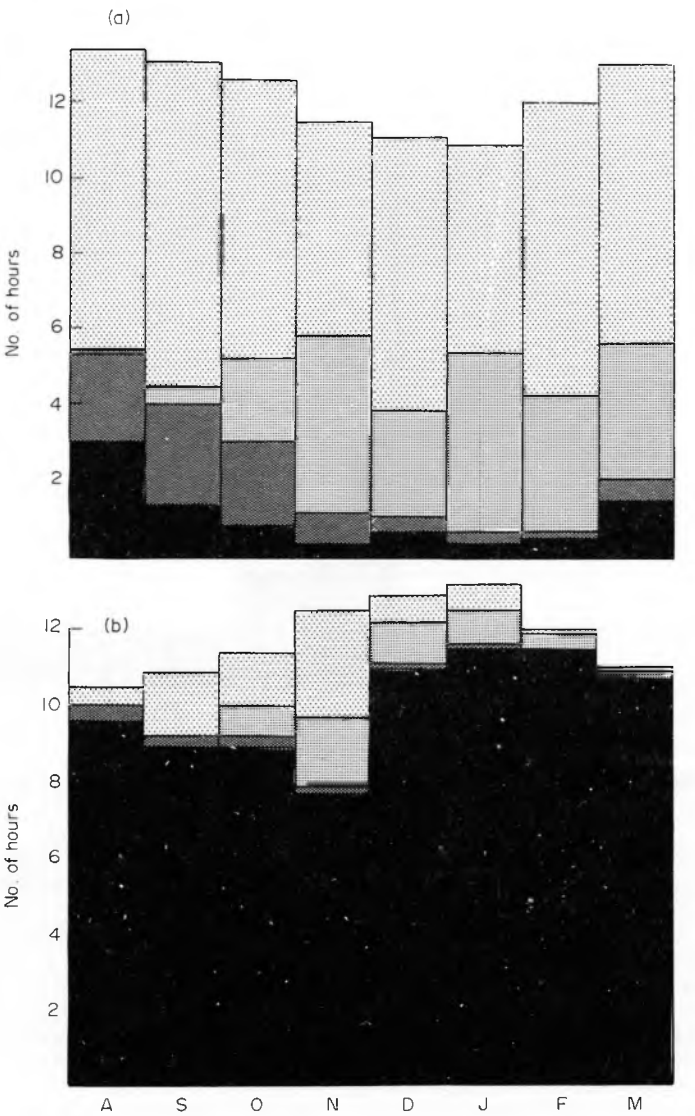

Figure 3. Periodicity of activities according to months. The time spent by day (a) on the remises and by night (b) on the feeding grounds varies as the daylength. Lightly stippled, sleeping; heavily stippled, swimming; cross-hatched, preening; solid, feeding. Feeding is mostly nocturnal and comfort activities are mostly diurnal. But in August, February and March, the daily feeding time is longer than the night length and Teal have to feed partly by day. (After Tamisier, 1972a.)

and courtship time. The daily cycle again is fully occupied with vital activities (Figure 3).

The total duration of diurnal activity is always shorter than the daylength. In contrast, feeding time exceeds the night length at the beginning and at the end of the wintering season; 30% of feeding then occurs by day, around margins of the remises. This is the one case where the duration of light impinges upon the periodicity of a behaviour pattern of Teal.

Lunar phases, by contrast, have no role in this periodicity in the Camargue. During the wintering phase they shift the time at which Teal flight from resting to feeding places by 10–20 minutes, without reducing the daily feeding time. On tidal wintering grounds, however, activity rhythms are determined by variation of water level and partly by moon phases (Lebret, 1970 and personal communication).

III. Winter habitat

The analysis of group behaviour allows us to define the ecological requirements of Teal. Just as for behavioural patterns, these requirements differ radically by day and by night.

(a) *Diurnal habitat*

Because of the predation pressure by avian predators, Teal are gregarious and require large marshes able to hold some thousands of individuals. Their mean density is two to three individuals per square metre and this can be doubled when a bird of prey is approaching which will put the whole group to flight. The open water allows a permanent visual contact between all the birds. On the edges of the marsh Teal preen and sleep, often standing. A slightly sloping shore (less than 1/1,000) is indispensable. Thus, whatever the water level, large and shallow surfaces are available for the ducks which prefer, moreover, those exposed to sun (best for preening and resting). There, densities can reach thirty to forty individuals per square metre and females are always more numerous than males having somewhat different requirements. But the birds are never in contact for Teal are 'distance-birds' (Hediger, 1950). The fringing vegetation (tamarisk *Tamarix gallica* and glasswort *Salicornia* sp.) is equally used for perching up to 2 m above the water. Finally, the fineness of the soil is required to allow feeding by the Teal.

Teal choose the resting place according to requirements which vary with the season. In the pre-wintering period, preen (relation to moult), sleeping and partly diurnal feeding being important, the remises should offer large, fine-particled beaches. In the wintering period, swimming and sleeping need large open waters. For the post-wintering period, for courtship and partly diurnal feeding, Teal seek around the remises enclosed fine-particled marshes with a well-vegetated border. This biotope looks something like the breeding habitat on which they have been 'imprinted' in the early days of their lives (Tamisier, 1970b).

During the whole wintering cycle, such successive requirements could mean that several localities would have to be used as remises. But as soon as they reach the Camargue, Teal select those remises which will remain favourable at best during all three phases of the wintering cycle. This selection implies a knowledge of the seasonal variation of the biotopes, and is acquired by tradition.

The 40,000 Teal which, on average, winter in the Camargue are mostly found on only four remises. The two most important places are Marais des Bruns, used by 20,000 birds with a maximum of 35,000, and Tour du Valat, holding 5,000–10,000.

(b) *Nocturnal habitat*

This is fundamentally defined by the feeding behaviour and by the nature of the diet.

Diet of Teal (*Figure* 4). From 300 analyses (Tamisier, 1971b) it appears that Teal are mostly seed-eaters, taking oospores of Musk-grasses Characeae, seeds of Bulrushes *Scirpus litoralis* and *lacustris*, of pondweed *Potamogeton pusillus*, of wigeon grass *Ruppia maritima*, of water milfoil *Myriophyllum spicatum*, of seablite Salsolaceae, besides agricultural

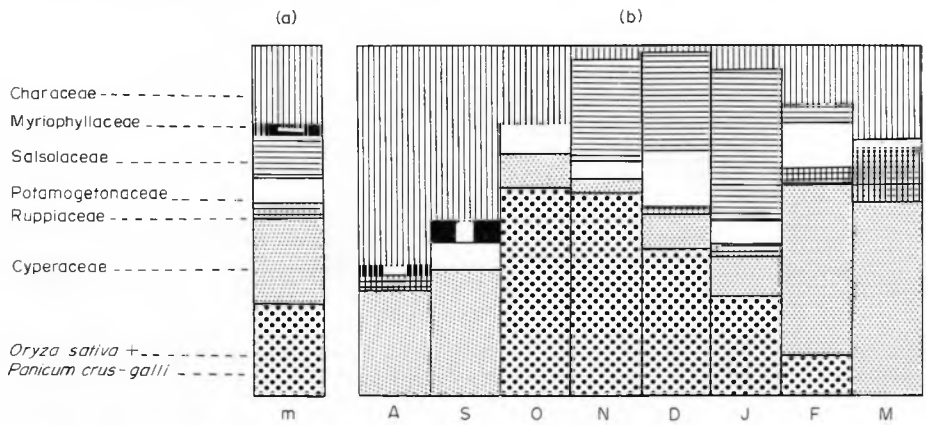

Figure 4. Diet of Teal. Winter mean (a) and monthly variation (b) by dry weight of seeds. (After Tamisier, 1971.)

grain such as rice *Oryza sativa* and cockspur *Panicum crus-galli*.

Such seeds are always present, whereas animal food occurs in only half the samples throughout all the wintering period. This is composed mostly of Molluscs (Hydrobiidae, Limnaeidae and Physidae). Chironimid larvae and Ostracods. Grit is always present: it enables the hardest seeds to be broken up and probably provides some essential mineral elements. Each individual carries seventy to eighty pieces of grit (0·5–3·0 mm) and some dozens or hundreds of smaller particles. But because of the scarcity of grit in the limonous soil of the Camargue, lead-shot lying in the depths of the marsh are used instead, giving rise to lead poisoning.

In the oesophagus, animal remains are twenty times more abundant than in the gizzard. Seeds of rice, panicum and muskgrasses also occur more frequently and in larger quantities. In these cases the Teal seem to have found very rich feeding places (mostly agricultural) and have temporarily stored their food in the oesophagus. By contrast, the seeds regularly taken in natural feeding places occur more frequently in the gizzard. Thus, seeds of *Scirpus litoralis* and *Potamogeton pusillus* occur respectively in 85 and 60% of the samples. They seem to be the typical food for which Teal are adapted: their sizes give the limits (1·2–2·6 mm) of the food particles on which Teal subsist (Figure 5). Identical results have been obtained by Olney (1963) for Teal in Britain. Smaller (muskgrasses) or larger (rice, *Panicum*) seeds are selected only when available in large numbers and then taken in enormous quantities. Animal prey are always larger, they involve a different feeding behaviour and bring some essential components of the diet, particularly proteins.

In summary, the feeding niche of the Teal is firmly defined by the physical conditions of the feeding grounds (fine mud under a few centimetres of water), by the nature of the food taken (Teal are the most specialized in seed-eating of the palaearctic ducks) and by the limitations on food particle size.

Biomasses of available food. All the feeding places have the same physical characteristics but differ in the nature and abundance of food. A total of 480 samplings were taken in the top 4 cm of mud (depth most exploited by Teal) in different biotopes and in different months of the winter. Their analysis showed that the biomass of seeds ranges from 3 to 50 g/m^2 (dry weight) (Figure 6). Most of the feeding places have biomass between 5 and 20 g/m^2. The most frequent seeds are those of Bulrush *Scirpus maritimus* and *lacustris* and *Eleocharis palustris* and oospores of Muskgrasses. Pondweeds are generally represented by *Potamogeton pectinatus* but seeds of this species are too large for Teal. In saline

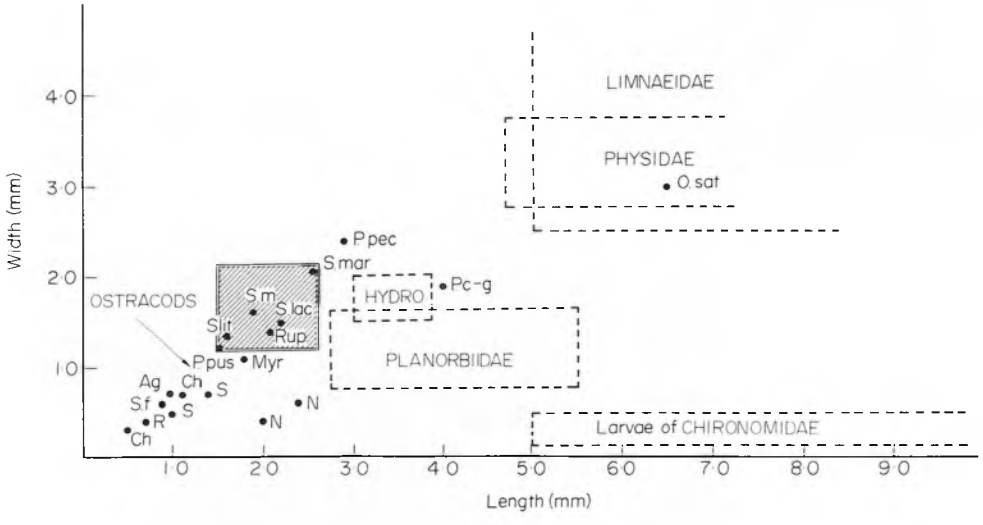

Figure 5. Limitations of food particle size of Teal defined by the size of the most frequently occurring seeds. Animal food as much as seeds of Characae, rice and *Panicum* have a marginal position. A.g.: *Arthrocnemum glaucum*; Ch.: Characeae; HYDRO: Hydrobiidae; Myr.: *Myriophyllum spicatum*; N.: *Naias* sp.; O.sat.: *Oryza sativa*; P.c-g.: *Panicum crus-galli*; P.pec.: *Potamogeton pectinatus*; P.pus.: *Potamogeton pusillus*; R.: *Ranunculus* sp.; Rup.: *Ruppia maritima*; S.: *Suaeda* sp.; S.lac.: *Scirpus lacustris*; Sc.lit.: *Scirpus litoralis*; S.mar.: *Scirpus maritimus*. (After Tamisier, 1972b.)

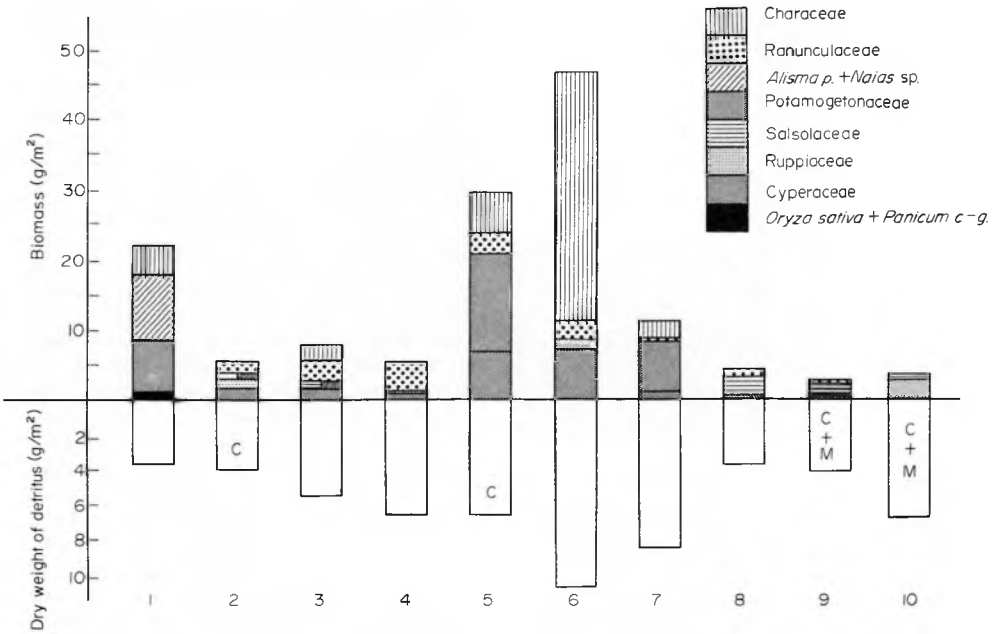

Figure 6. Biomass of seeds in the first 4 cm of mud in the feeding grounds of Teal. 1, Ricefields; 2, 3, 4, Bulrush marshes; 5, pondweed marshes; 6, Muskgrass marshes; 7, reeds; 8, 9, more or less flooded saline grounds; 10, saline marshes. Most detritus is vegetable, some are shelly (C) or mineral (M). Seeds are most available for Teal when detritus is less numerous. (After Tamisier, 1971a.)

biotopes, seeds of seablite and wigeon grass are the most abundant.

Animal food is mostly Molluscs (gastropods) and larvae of Chironomids. Saline swamps are the richest (holding on the average 20,000 *Hydrobia* sp./m^2). Fresh or brackish marshes support important concentrations of Chironomid larvae (2,000–20,000/m^2) and Physidae, Limnaeidae and Planorbiidae in lesser quantities.

Food in the soil is always mixed with vegetable detritus and sometimes shelly or mineral debris. These constituents vary in abundance and make filtration of mu ' by the ducks more difficult. Seeds are the less available the more the detritus, especially vegetable matter, is abundant.

There is little variation in the biomass present throughout the winter and the quantities available at the end of the season are everywhere generally high.

Method of exploitation of the habitat

Between the beginning and the end of the wintering season the variations of the water level are important, giving rise to large variations in flooded areas because of the flatness of the Camargue. In August and September, the water levels are low and few natural swamps are submerged. Teal at night are concentrated in a few feeding places, most hunting places artificially flooded with fresh water. This concentration (up to 100 birds/ha) results in a constant mutual disturbance of the feeding Teal. It would seem that before such artificial water surfaces were available, it was hard for Teal to feed at this period.

After the autumnal rains, the majority of the marshes are flooded and available for feeding ducks. Moreover, after the harvest (mid-October) many ricefields are ploughed and flooded with 10–20 cm of fresh water for 2 or 3 months. These numerous, rich places become very important feeding grounds.

At the end of the winter, all the marshes are filled up and Teal are markedly scattered over the feeding areas (only a few individuals/ha). Then, according to time and place, Teal exploit more or less abundant food resources. As seen earlier, the daily feeding time varies with the month as determined by the physiological condition of the birds and by climatic factors, but is completely independent of the biomass of available food. At any one time Teal using places containing a different biomass will take just as long to obtain their food (Figure 7). That

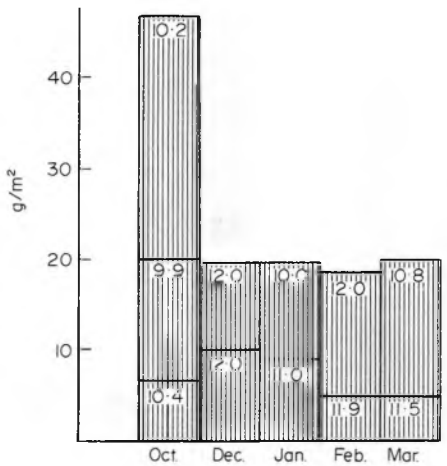

Figure 7. Independence of daily feeding time and value of feeding grounds. In any one month the daily feeding time is defined by the physiological state of the Teal and by climatic factors. It is independent of the biomass in feeding places. For instance in October, Teal feeding on three different areas (biomass: 7, 20 and 47 g/m^2) have approximately the same feeding duration (respectively 10·4–9·9 and 10·2 hours/24 hours). (After Tamisier, 1972a.)

clearly means that the quantity of food available in the poorest biotope (5 g/m^2) is sufficient for the normal feeding of Teal.

IV. Limiting factors

Three successive phases appear from the analysis of daily rhythms. During the first (pre-wintering) and the last phase (post-wintering) the daily cycles are completely occupied with essential activities and reveal the existence of pressures upon the Teal. Indeed, during the pre-wintering time, the high metabolism of ducks forces them to a long feeding period (12 hours). The nights are short and Teal must feed partly by day, around the remises and in marginal conditions. On the nocturnal feeding grounds they lose some time by mutual disturbance because of the small size of available marshes due to a low water level.

During the post-wintering time, the daily activity cycles again are completely occupied. Thanks to the high water levels, all the swamps are full and Teal have maximum space. But their nutritional needs are high, partly because of the low temperatures. In case of a cold spell, these needs increase and, as insufficient feeding time is then available, the Teal must leave the Camargue.

Under natural conditions, it appears that the limiting factors are successively low water levels and low temperatures (generally less than 0°C). Both these factors cause an increase of daily feeding time. But natural conditions do not prevail any longer, mainly for two reasons. Firstly, water-management on hunting places creates many good areas for the earliest ducks and increases the carrying capacity of the Camargue during the pre-wintering period. Secondly, hunting pressure, partly thanks to this water-management, has increased considerably, the Teal being drawn to the places where they are shot. And Teal are mostly killed during those months when, because of their high food needs and of the shortness of the nights, Teal must leave the remises before darkness and come back after dawn in order to increase the time spent on the nocturnal feeding grounds. Hence they are much more vulnerable to hunters. During these two periods, hunting pressure is superimposed on environmental pressures. But the hunting season has been closed only on 31 March (15 March from the season 1973–1974) and all the Teal killed at this time are potential breeders. Therefore, hunting pressure now regulates the population of Teal on their winter quarter, concealing the effects of the two natural limiting factors, water level and temperature.

Spatial organization and traditions

In the Camargue there are three or four main remises for Teal. Each diurnal remise has its own nocturnal feeding grounds which are only used by individuals of this remise. Twice a day at dawn and after sunset, Teal fly from one to the other (mean distance, 15 km). A remise and its feeding grounds constitute a functional unit which is exploited by an element of the population. Exchanges between two adjacent remises do occur, but for a few individuals only. From day to day the numbers present on each remise are nearly constant. The two main remises are far enough apart to avoid any overlapping. Their feeding grounds are located in opposite directions (Figure 8).

Teal are gregarious by day and scatter at night for feeding. This gregarious habit, characteristic of most wintering Anatidae, differs strongly from diurnal flocking for feeding (Lack, 1954) and nocturnal communal roosting (Crook, 1960; Morel, 1968; Siegfried, 1971). It should have a different significance. It may be understood as a response to human disturbance, particularly hunters. However,

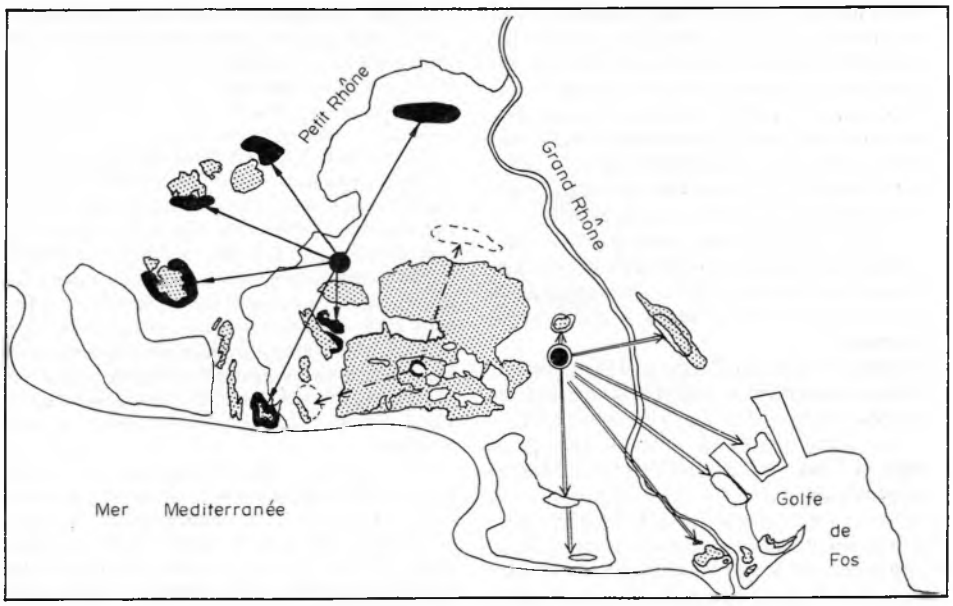

Figure 8. The 'functional units' of Teal in the Camargue. Each remise has its own feeding grounds (arrowed). The overlap between two 'units' is very slight. The mean distance between remise and feeding ground is *c.* 15 km.

the largest winter quarters suffer few (Turkey, Iran, Senegal) or no disturbance (Central delta of the Niger, Mali (F. Roux personal communication)). And there, as much as in Europe, the same alternation of diurnal and nocturnal activities occur. In effect, nocturnal feeding seems to be a direct consequence of the diurnal gregarious habit, which prevents densely grouped Teal from feeding. What, then, is the function of this gregarious habit? It appears (Tamisier, 1970b) to be an adaptation to predation pressure and is facilitated by some other factors.

Flocking of many individuals allows, by a 'multiplicity of eyes' (Miller, 1922), the best defence against predators (a Teal alone is much more vulnerable). The predators are mostly those more or less limited to wetlands (Spotted Eagle *Aquila clanga*, White-tailed Eagle *Haliaëtus albicilla*, Marsh Harrier *Circus aeruginosus*) or specializing on flocking birds (Peregrine *Falco peregrinus*). In the Camargue nowadays there is only the Marsh Harrier. But a new kind of predator, the Herring Gull *Larus argentatus*, has adapted to exploiting the niche newly left by the disappearance of the true birds of prey. The total frequency of disturbance by these two predators is high. The mean for the winter is seventy times/day, with a maximum in November of 160 times/day. Every time, 30–40% of present birds are disturbed. But the actual number of Teal caught is very slight. Predators seek among the ducks for those which cannot fly or are deficient in some way so as to make them more vulnerable. Inversely, the constant presence of predators close to the main winter quarters necessitates and favours the development of anti-predator adaptations by prey species (Murton, 1971; Zahavi, 1971).

Diurnal flocking allows the establishment of social communications, particularly expressed by the constant calls of males and females, giving each remise the function as an 'information centre' (Ward, 1965; Siegfried, 1971). This is particularly useful in the choice of feeding grounds: the best 'informed' birds lead the others to the most favourable feeding places. The communal flights of Teal on the remises could act as 'epideictic manifestations' helping this element of the population to keep in balance with the resources to be exploited (Wynne-Edwards, 1965). Facilitated by such large concentrations, traditions play a very important part in the Anatidae (Hochbaum, 1955) permitting each individual to return precisely to the same localities. Indeed the remises actually used in the Camargue are very constant from year to year. Wandering Teal in search of a suitable place are exceptional. As soon as they arrive in their wintering area, Teal seem able to go directly to their former remise. The

same applies to the feeding grounds around the remise, to every species of duck in the Camargue, and also for the remises on the great African winter quarters which have not changed for years (F. Roux, personal communication). The establishment of such traditions depends on the experience of adult birds which lead juveniles to these 'functional units' they have used previously.

The gregarious habit during the winter months is probably facilitated by the physiological conditions of Teal, the absence of sexual activity often means a good social tolerance.

In aquatic birds, the keeping of the plumage in good condition is essential and the long periods of sun-bathing are indispensable.

To summarize, the diurnal gregarious habit of Teal, determined by the predation pressure and aided by other factors, has a survival value. It forces birds to feed by night. Human disturbance seems without any effect. It appears that a similar explanation can be given for most of the Anatidae in which a winter gregarious habit is characteristic.

Summary

The Camargue, with 120,000–150,000 wintering ducks, 40,000 of them Teal *Anas crecca*, is one of the most important winter quarters for Western Palaearctic Anatidae. The previously published results of a long term study (1964–1972) about Teal are outlined.

Ringing results have shown that this population's breeding area ranges from Finland to the Urals. Most of it winters in the Camargue. Only in a cold spell do they fly westwards to the Atlantic coasts. Data are given on variation of numbers, mortality rates, sex-ratio and age-ratio.

The different types of behaviour are analysed (sleeping, preening, swimming and feeding) and their diurnal duration measured. For each month (August–March) the exact composition of the daily cycle (diurnal and nocturnal activities) is known.

The wintering period is divided into three successive phases, varying in the composition of the daily cycle. Feeding behaviour, diet, and biomass of the available food are analysed. The daily feeding duration varies through the months with the physiological condition of the Teal and with climatic factors. There is always plenty of food available.

Under former natural conditions the limiting factors of the population were probably low water levels (beginning of the winter) and low temperatures (end of the winter). Their effects are today concealed by those of hunting mortality which very likely regulates the numbers of Teal wintering in the Camargue.

Wintering Teal are gregarious by day and scatter at night for feeding. Many feeding grounds are linked to each daytime haunt, constituting a 'functional unit' always exploited by the same birds. In the Camargue three or four such units show very little overlap.

The diurnal gregarious habit is shown as an adaptation to predation pressure, and not as a response to human disturbance. It enforces nocturnal feeding. This alternation is strengthened by some other secondary factors.

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