Feeding convergence of Gadwall, Coot and the other herbivorous waterfowl species wintering in the Camargue: a preliminary approach

LAURENT ALLOUCHE and ALAIN TAMISIER

Introduction

The co-existence in time and space of several species with similar food habits leads to some fundamental questions, especially about the partitioning of food resources and the ecological and behavioural mechanisms which make it possible. The herbivorous waterfowl guild in the Camargue is a good example, where 5 species, (Gadwall *Anas strepera,* Wigeon *A. penelope,* Red-crested Pochard *Netta rufina,* Pochard *Aythya ferina* and Coot *Fulica atra)* have to share a given amount of resources during the 6–7 months of the winter and migration periods.

The aim of this article is to present new results on the food habits of Gadwall and Coot (Allouche 1983). Comparison with those of Wigeon (Campredon 1982) and with the available information on the other two species (Red-crested Pochard and Pochard) will lead us to a better understanding of the problem.

A full analysis of the partitioning of food resources would require their evaluation, the determination of their availability, as well as the examination of food consumption, feeding behaviour and habitat, and food habits. Only the last aspect (food) is analysed here, so that the conclusions must be considered as preliminary. The other aspects will be studied later.

The Camargue (Rhône Delta, France) is a 100 000 ha zone where the wetlands (70 000 ha at a maximum) are fresh, brackish, and saline. Most of the freshwater marshes are managed for hunting purposes. From June–July Rhône water is pumped into the marshes (preventing them often from a natural summer drying up) and into new impounded areas. This management has been increasing for the last 20 years: the inundated surfaces are increasing and now include areas which rarely used to be wet. Generally speaking, the water level is rising through the winter season.

According to monthly counts (September to March, 1964–65 to 1983–84), of the total ducks and coots (mean maximum about 150 000 individuals) 40% are herbivorous species, Coot being the most abundant (Fig. 1). During the last 20 years, we have observed an important increase in the numbers of Gadwall (2 000 to 7 000) and a gradual decrease of Pochard (7 000 to 3 000). On the other hand Coot are very abundant in (August–) September–October whilst the others are almost absent (Fig. 2).

Material

64 stomach contents of Gadwall and 113 of Coot were analysed. They were collected by P. Campredon, J-Y. Pirot and A. T. from hunters' bags during the 1979–80 and 1980–81 hunting seasons which last in the Camargue from August 15th to February 28th (Table 1). This sampling method includes several biases: the hunting clubs where most stomachs came from are not fully representative of the biotop diversity of the Camargue; hunting is selective, females and juveniles being usually the most vulnerable; more than 95% of Coot, rather a diurnal feeder, were collected in the morning. However, the death hour of the sampled individuals was usually late enough to provide significant results.

Because of the relatively small total numbers of stomachs, we decided to group all the individuals of a species together in three periods, without any age- or sex-distinction. All the oesophagus samples were analysed, but only every other gizzard.

Methods

We used several criteria to compare the diets of both species:

a) Relative abundance of food items, seeds and vegetative parts of distinct plants were expressed as percentages of the total numbers of items. The very few animal prey were kept aside. Since oesophagus and gizzards were analysed separately the percentages are a mean of both results. They were calculated from dry weight of all seeds and of the

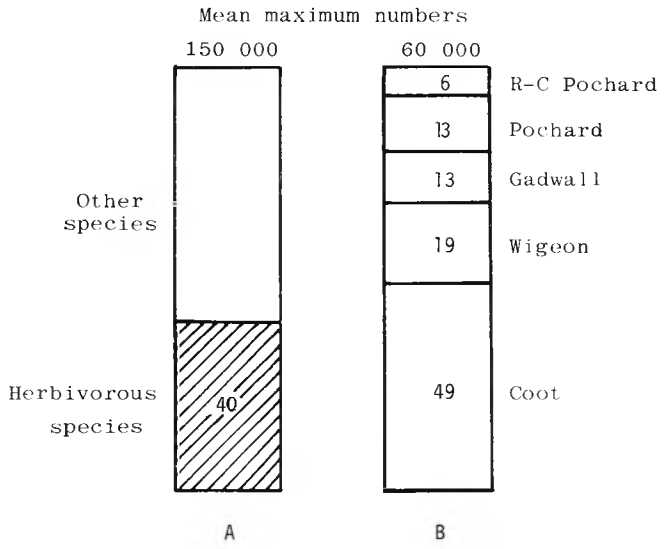

Figure 1. Mean composition of the populations of ducks and coots wintering in the Camargue. Monthly counts (September to March, 1964-65 to 1983-84). A) Herbivorous species versus other species. B) Detailed composition of the herbivorous waterfowl guild.

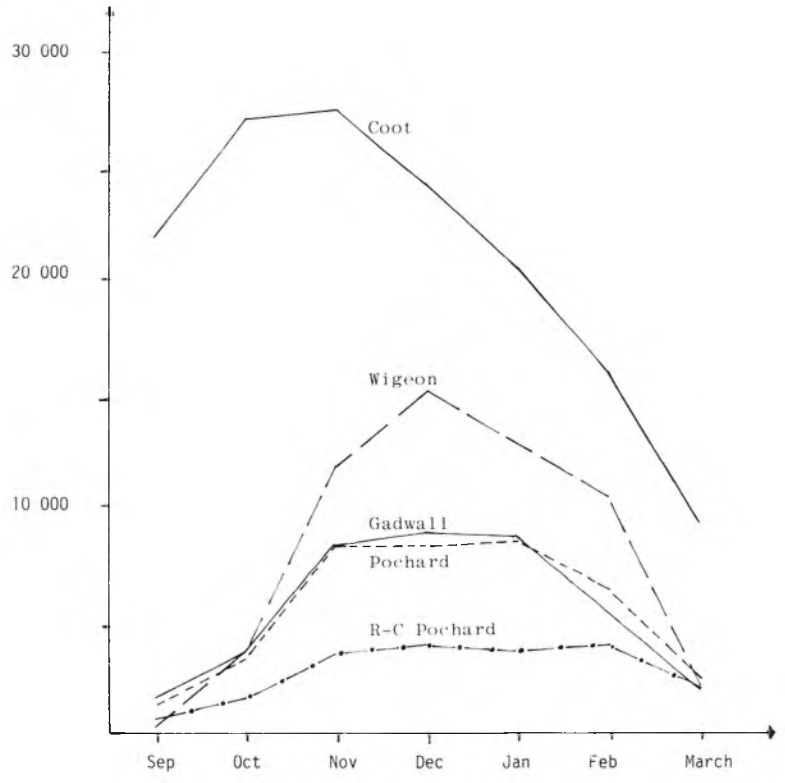

Figure 2. Monthly variation of numbers of the 5 herbivorous species (1964-65 to 1983-84).

Table 1. Distribution and numbers of stomach contents collected in the Camargue.

Period	I			II			III
Month	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.
Gadwall	4	24	9	2	8	4	13
Coot	10	17	13	21	15	19	18

vegetative parts found in the gizzard (cf. Campredon *et al.* 1982); for the vegetative parts found in the oesophagus the percentages derive from the following Abundance Index:

$$\Sigma \text{ Li li ni}$$

where Li is the central value of the class i (there are 8 size classes: 0–1, 1–3, 3–5, 5–10, 10–20, 20–30, 30–50 and > 50 mm.), li is the mean width of the items belonging to the class i. This mean has significantly distinct values according to the length and the nature (stems or leaves) of the fragments and of the species concerned (see Allouche 1983); ni is the number of items in the class i.

This Abundance Index provides an approximate value of the actual volume of a given plant species in the oesophagus. The good condition of the items in the oesophagus (in contrast to their state in the gizzard) makes its calculation possible. It is an efficient alternative to the weight method (inapplicable here because of the scarce number of items) and also to that one used by Campredon (1982) for Wigeon because of the tiny size of the items.

b) Occurrence in oesophagus and gizzard

Its utilisation minimises the false importance of some abundant items taken by a few (sometimes a single) individuals.

c) Item diversity

This was measured according to the Simpson's formula (cf. Barbault *et al.* 1978):

$$D = (\Sigma p_i^2)^{-1}$$

where pi is the proportion of items of the i category. D varies from 1 to n which is the total number of classes of items (here n = 17). This value can be considered as indicative of the amplitude of the "food niche" of the species (cf. Levins 1968), a term used here only for its diet component.

d) "Food niche" overlap

This was measured according to the McArthur and Levins Index (1967, in Blondel & Bourlière 1979):

$$R = \frac{\Sigma Pij \cdot Pik}{\sqrt{\Sigma Pij^2 \cdot \Sigma Pik^2}}$$

where Pij and Pik are the proportions of items of the i category taken by the species j and k respectively. R varies from 0 to 1. The calculation of the diversity and "food niche" overlap indices do not take into account unidentified plant material. Moreover they deal with the winter as a whole and with every period. So the unity of time and location which are imperative rules for these calculations (Barbault *et al.* 1978; Pirot 1981) were roughly satisfied since we considered the successive seasons (1979–80 and 1980–81) as one (unity of time) and the Camargue as one area (unit of location). Hence the values obtained must be examined with caution.

e) Nature of the vegetable matter (stems, leaves . . .)

Only items from the oesophagus – i.e. those in good condition – were taken into account and only those of the *Potamae* family since they were the most abundant in Gadwall and Coot and constituted a rather homogenous whole in terms of pattern and toughness.

f) Size of the vegetable items

The *Potamae* found in the oesophagus were measured according to the 8 size classes defined earlier.

g) Type and size of the grit

These were measured (Campredon *et al.* 1982) since they can vary according to the diet of the species (Thomas *et al.* 1977).

Results (Table 2)

Similarities in the diets of Gadwall and Coot.

Gadwall and Coot had a very similar diet in many respects. During the winter season both fed almost exclusively on plant material, mostly on the vegetative parts of vascular plants and *Characae*. In terms of abundance and occurrence, the *Potamae* were the most important, specially the brackish to freshwater hydrophytes *Potamogeton* sp. and *Zannichellia palustris*. *P. pusillus* and *Z. palustris* were rather more important in Gadwall, and *P. pectinatus* in Coot. *Algae*, little used by Coot, were most often taken by Gadwall *(Cladophora* sp., *Chaetomorpha* sp., *Spirogyra* sp.). Conversely, seeds (mostly of *Myriophyllum spicatum, Scirpus litoralis, P. pectinatus* and *P. pusillus)* although present in both species were more abundant in Coot. In both species, the animal prey were accidental. The mean trophic diversity was low and almost identical for Gadwall (D = 7.28) and Coot (D = 6.82) and the "food niche" overlap was rather high (R = 0.64). The vegetative parts were only stems and leaves (no roots or tubers) and the items found in the oesophagus of both species were tiny, usually smaller than 3 mm long.

Differences in the diets.

Periodical variations.

Through the winter season the Coot fed more and more on *Potamogeton* sp. (mostly *P. pectinatus)* which comprised most of its food in February, and less and less on seeds. Conversely the Gadwall at the beginning of the season took *P. pusillus* and *Z. palustris* but had a more widespread diet at the end, of *Algae*, grasses, seeds, *Ruppia* sp. and some other *Potamae*. The trophic diversity of Coot was higher in the middle of the season (Table 3) whilst still low as compared to its theoretical maximum value (17). There was a gradual decrease of the "food niche" overlap through the three periods of the winter season.

Stems/leaves

The Gadwall ate leaves and stems in the same proportions. The Coot, according to the only identifiable items of the middle period, ate twice as many leaves as stems.

Size

According to the Abundance Index of ingested *Potamae*, most of the plant material of the Gadwall belonged to the 10–20 mm size class, while all classes were well represented in Coot. (Fig. 3).

Table 2. Diet composition of Gadwall and Coot (seeds and vegetative parts, % of abundance).

Diet	Winter mean		Aug–Sept–Oct		Nov–Dec–Jan		February	
	Gadwall	Coot	Gadwall	Coot	Gadwall	Coot	Gadwall	Coot
Seeds	9.9	18.2	15.3	42.6	1.2	7.4	13.1	4.7
Algae	14.6	7.5	7.4	1.5	0	16.2	36.5	4.8
Characae	5.1	5.7	0	2.7	15.3	9.1	0	5.4
Ranunculus baudotii	trace	0.1	trace	0	0	0.4	0	0
Myriophyllum spicatum	0.5	2.6	0.7	4.0	0.8	3.8	0	0
Callitriche sp.	0.1	0	0	0	0.2	0	0	0
Potamogeton pectinatus	2.5	14.0	4.0	9.0	0	19.6	3.5	13.3
P. pusillus	3.3	0	1.9	0	4.6	0	3.4	0
Zannichellia palustris	19.1	4.1	38.2	8.8	19.0	3.4	0	0
P. pusillus / *Zann.*	14.2	10.3	8.7	7.7	33.0	5.8	0.8	17.4
Potamogeton sp. / *Zann.*	4.6	20.4	11.9	4.2	0.7	14.1	1.3	43.0
Potamogeton + *Zann.* total	*43.7*	*48.8*	*64.7*	*29.7*	*57.3*	*42.9*	*9.0*	*73.7*
Ruppia maritima	1.3	1.7	0	5.1	4.0	0	0	0
R. cirrhosa	0.1	0.1	0.4	0	0	0.4	0	0
Ruppia sp.	3.6	1.5	0	0.1	1.4	3.8	9.3	0.5
Potamae sp.	1.0	1.3	0.2	3.8	2.9	0	0	0
Potamae total	*49.7*	*53.4*	*65.3*	*38.7*	*65.6*	*47.1*	*18.3*	*74.2*
Phragmites communis	0.5	0.9	0.8	0.8	0.6	1.8	0	0
Graminae	3.0	0.9	2.2	0.8	0	1.9	6.8	0
Unidentified Sup. Vascular	16.6	10.6	8.3	8.7	16.2	12.2	25.3	10.9

Grit

In Gadwall the grit was composed almost exclusively of quartz; in the case of Coot it contained also 18% mollusc shell pieces. The size of the grit was different too: most of the grit of Gadwall is included in the size class 0.25–0.49 mm, as found by Thomas *et al.* (1977), whilst in Coot 2 distinct classes (fine 0.08–0.25 and rougher 0.49–1.00) were to be found.

Discussion of Coot and Gadwall results

The comparative analysis of the food of Gadwall and Coot clearly shows an overall similarity: both species mostly feed on *Potamogeton* sp. and *Zannichellia palustris* whose stems and leaves are taken in very small pieces. Among the differences, that related to the seasonal variations looks the most interesting.

At the beginning of the season, the "food niche" overlap is at its maximum: the two species converge on the same abundant food resources. But as interspecific competition is fairly low due to the very few Gadwall (see Fig. 2) theselection of seeds by Coot can be considered as deliberate. From November to January the numbers of both species happen to be at the highest whilst the aquatic plant communities are at the lower phase of development (Stapelbroek & v.Wijck 1984; Verhoeven 1980). Coot diet then includes 50% of *Potamae* (mostly *P. pectinatus)* and Gadwall 70% (mostly on *P. pusillus* and *Z. palustris).* At the end of

Table 3. Food diversity and "food niche" overlap for the 3 successive periods and for the whole of the winter season.

Period	Diversity Gadwall	Coot	"Food niche" overlap
Aug–Sep–Oct	4.21	3.93	0.56
Nov–Dec–Jan	4.04	7.23	0.31
Feb.	3.35	3.30	0.18
Winter mean	7.28	6.82	0.64

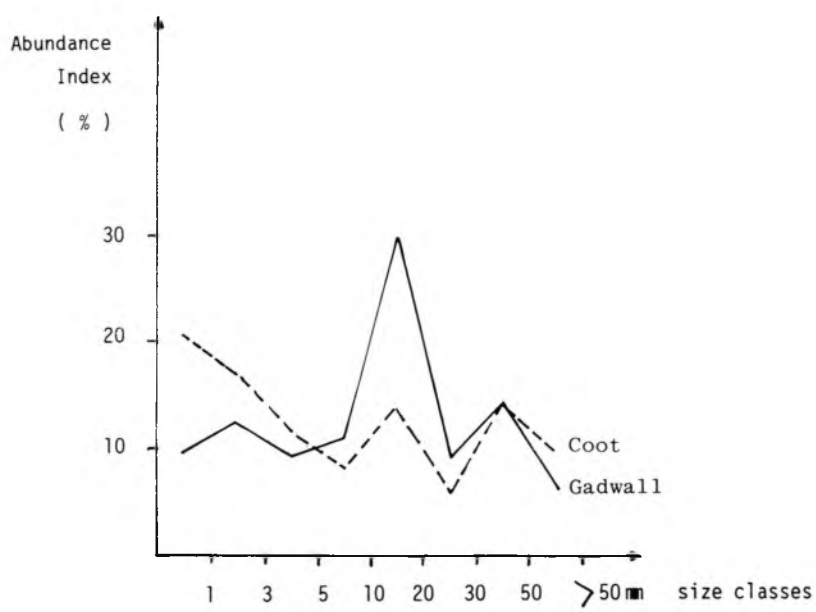

Figure 3. Size of the vegetable material *(Potamae)* found in the oesophagus of Gadwall and Coot.

the season, when the bird numbers are still high and plant development starts (Verhoeven 1980) the divergence between both diets increases (smaller value of the overlap Index) because of the pronounced concentration of Coot on *P. pectinatus* and *Potamogeton* sp., while simultaneously Gadwall spread their choice of food more widely. This divergence probably reflects food availability: the waterlevel in the Camargue is at its maximum and only Coots, by diving, can exploit the *P. pectinatus* beds which are usually located in the deepest zones. Gadwall, even by upending, can only reach the marginal fringe of the marshes (vegetative parts and seeds) or pick up floating *Algae*, which at this time of the year can constitute large masses everywhere at the surface of the water (A. Vaquer, pers. comm.).

This type of partitioning of the food resources must be beneficial for the Coots in spite of the increased energetical cost of diving for food (1.5 times; Hurter 1979).

As a whole it appears that a relative interspecific isolation occurs when the numbers are high and the food resources rather scarce. This isolation relates to 3 points:

- in terms of habitat: *P. pectinatus* (for Coot) is a brackish to freshwater plant, whilst *P. pusillus* and *Z. palustris* (for Gadwall) are freshwater plants only (Britton & Podlejski 1981; Stapelbroek & v. Wijck 1984).
- in terms of behaviour: diving in Coot, filtering the mud through the lamellae of the bill in Gadwall.
- in terms of feeding period: in the absence of detailed studies it seems that Coot are day feeders in the Camargue whilst Gadwall are mostly night feeders. So when the food resources are abundant both species might successively exploit the same places without competition.

Finally we must mention the opportunism of the Coot, capable of taking advantage of the various conditions in spite of the very peculiar form of its bill: for instance, at the beginning of the season it can pick up the seeds probably at the same time as some vegetative parts in which the seeds are caught (before they fall down to the mud where they can only be filtered by Gadwall at the end of the season).

General discussion

The eclectic winter food habits of Coots are famous wherever they have been analysed: *Characae* and animal prey on the Caspian Sea (Dementiev & Gladkov 1951); zebra mussel *Dreissena polymorpha* on the Swiss lakes (Hurter 1979; Pedroli 1981); seeds, young shoots, stems and leaves of many genera of hydrophytes *(Myriophyllum, Ranunculus, Phragmites, Potamogeton, Zannichellia, Ruppia* (Hurter 1979; Cramp & Simmons 1980). In the case of Gadwall, its food seems to be mostly composed of plant material. The few individuals analysed in Europe so far contained roots, stems, leaves and seeds of *Carex* sp., *Scirpus* sp., *Ceratophyllum* sp., *Potamogeton* sp. (Cramp & Simmons 1977) and the birds analysed in Louisiana, USA, by Paulus (1982) had fed mostly on *Algae* and the vegetative parts of *Eleocharis palustris*, *Ruppia* sp., *Myriophyllum* sp. and *Ceratophyllum* sp.

Considering this food diversity observed elsewhere, it is surprising that Gadwall and Coot in the Camargue feed mostly on the same few species of hydrophytes. Moreover we know that Wigeon, which increasingly exploit the brackish to freshwater marshes (instead of the saline ones) extended by hunting management, feed there mostly on *P. pectinatus* in addition to some *P. pusillus*, *Myriophyllum* sp. and Algae *Chaetomorpha* sp. (Campredon 1982). So the convergence of 3 herbivorous species to use the same feeding grounds and exploit the same hydrophytes might suggest a strong competition. Yet these marshes are also fairly rich in beds of *Characae, Ranunculus* sp. and *Myriophyllum* sp. (Britton & Podlejski 1981) which plants are frequently used outside the Camargue. We prefer to suggest that the *Potamae* food resources are abundant enough to stand the heavy feeding impact of the three species without giving rise to a strong interspecific competition. If it is true, this hypothesis implies also that there must be some unknown advantages in selecting Potamae rather than the other hydrophytes.

The Pochard feeds mostly in the Camargue on tubers and seeds of *P. pectinatus* (M. van Eerden and A. Tamisier, pers. obs.) whose size and density are partly correlated with the size of the beds. So an indirect competition can be suspected between this diver and the Gadwall, Wigeon and Coot, since Pochard feed on those parts of the plants necessary for the growth of the food used by the others. Yet

such a competition is necessarily restricted to the few places where the Pochard feeds and also because their numbers, at present low, are decreasing for reasons which seem to be independent of the local situation (improvement of habitat on northern winter quarters; Cramp & Simmons 1977).

Finally, the herbivorous waterfowl community includes the Red-crested Pochard whose food habits have yet to be analysed in the Camargue. This duck is usually associated with the *Characae* beds from where it takes the vegetative parts and also the seeds of *Scirpus litoralis* (Cramp & Simmons 1977), commonly found nearby. If these data are confirmed in the Camargue, they locate the Red-crested Pochard apart from the other herbivorous species of the community in terms of partitioning the resources. Given the apparent abundance of the *Characae* beds and the small numbers of this duck, we can suspect that its almost exclusive exploitation of them is not related to their non-exploitation by the other species. In other words, among five herbivorous species a single one (Red-crested Pochard) might isolate itself according to specific criteria, but the others belonging to two taxonomically distant families (Anatidae and Rallidae) show an impressive phenomenon of food convergence on the *Potamae*.

This preliminary conclusion points to the need for detailed analyses on the qualitative and quantitative aspects of the available food (distribution, biomass, productivity and energetic value of the hydrophytes), as well as on the capabilities of several species of sharing the same stock of resources (behavioural analyses). Finally we wonder whether this conclusion does not illustrate an under-exploitation of the resources, which would mean that the size of the herbivorous waterfowl community is low in relating to the carrying capacity of the Camargue.

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Summary

New data on the food habits of Gadwall *Anas strepera* and Coot *Fulica atra* in the Camargue compared to the available information on Wigeon *A. penelope*, Pochard *Aythya ferina* and Red-crested Pochard *Netta rufina* allow a preliminary comprehensive description of the relation of the herbivorous waterfowl community towards its food supply. Gadwall, Coot and most Wigeon, the three most abundant herbivorous species, are mainly dependent on the vegetative parts of *Potamae (P. pectinatus, P. pusillus, Zannichellia palustris* and *Ruppia* sp.). Those marshes in which they feed are rich in beds of *Ranunculus* sp., *Myriophyllum* sp. and *Characae*, which are commonly eaten by the same species outside the Camargue. Pochard mainly feed on the tubers and seeds of *P. pectinatus*, whereas Red-crested Pochard, numerically the less important species, probably eat the vegetative parts of *Characae* and the seeds of *Scirpus litoralis*. There is thus an impressive convergence of herbivorous species on the same family and plants *(Potamae)* without giving rise to a strong interspecific competition.

We suspect that the numerical size of this guild is low as compared to the carrying capacity of the Camargue.

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Laurent Allouche and Alain Tamisier, Centre d'Ecologie de Camargue, CNRS, Le Sambuc, 13200 Arles, France.