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Interaction between coot (*Fulica atra*) and waterlily (*Nymphaea alba*) in a lake: the indirect impact of foraging

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Abstract

A previously unrecorded indirect impact is described of coot (*Fulica atra*) on a floating-leaved species (*Nymphaea alba*) during the plant growing season in a shallow eutrophic natural freshwater ecosystem, Lake Grand-Lieu, western France. The bird population was counted, the proportion of petioles cut by bird was estimated and the density of the four main invertebrate groups on the leaves was measured just after the breeding season, in July and then in September 1997 in the whole *N. alba* area (739 ha divided into 15 sections). Up to $6 \pm 1\%$ of leaves were cut in July, with differences between sections (from 0.3 ± 0.1 to $16 \pm 6\%$) when about 10,000 coots fed in this part of the lake. A positive relationship was recorded between the proportion of cut petioles and coot density during the first period (excluding sections where *N. alba* was mixed with another plant species, *Trapa natans*). In September, coot abundance fell to 5000 individuals and the impact decreased to $0.3 \pm 0.2\%$ of leaves, new generations of leaves having meanwhile grown. The comparison of the mean density of invertebrates on cut and intact leaves showed a massive depletion of the beetle, *Galerucella nymphaeae*, present on the upper side of the leaves. The selection of this specific food item might explain this marked interaction, which was nevertheless insignificant in September because of high turn over rates of the plant. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

Interactions between waterfowl and plants, especially submerged macrophytes, are relatively well documented (Schutten et al., 1994; Søndergaard et al., 1996, 1998). The various

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published references have emphasised three major findings. Firstly, extensive grazing often takes place outside the plant growing season, by winter aggregations of aquatic birds (Van Donk, 1998). Secondly, waterfowl consume only a portion of what they break off or uproot. Finally, the main influence of grazing appears to derive not from what they consume but from the loss of the future growth potential of the material, compounded through the growth period (Mitchell and Perrow, 1998). The literature indicates a large range of effects from near zero (Kiørboe, 1980; Perrow et al., 1997) to a substantial decrease in standing crop or area covered by submerged macrophytes (Jupp and Spence, 1977; Lodge, 1991; Idestam-Almquist, 1998) and even to changes in composition of macrophyte communities (Lauridsen et al., 1993; Lodge et al., 1998).

In the present study, we describe an unusual indirect plant–bird interaction. We suggest that there may be an indirect impact (damage when catching prey) by waterfowl in areas when an unusually high bird population occurs. To assess this point, we quantified the impact of coot (*Fulica atra*) in the large floodplain Lake Grand-Lieu, western France, on the main floating-leaved macrophyte, *Nymphaea alba* during the 1997 growing season.

1.1. Study site

Lake Grand-Lieu is a shallow, turbid, eutrophic natural freshwater ecosystem (47°05′N, 1°39′W), composed of four major complementary functional units (see Marion et al., 1994 for a more detailed description). It covers 4000 ha in summer and 6300 ha in winter, by flooding surrounding peaty marsh grasslands. Much of the permanently flooded central area of the lake is covered from April to October by about 1400 ha of several floating-leaved species (mainly *N. alba*, *Nuphar lutea*, *Trapa natans* and *Nymphoides peltata*) forming a mosaic of monospecific patches. The summer depth is reduced to 0.7 m in this part of the lake whereas the water level generally increases up to 1.5 m in winter.

The spatial distribution of coots on the lake is strongly related to the water level regime (Marion and Marion, 1975). Coots use the peat fen and the marsh grasslands for breeding when these are flooded in spring. When the water level decreases in June, coots move mainly to the floating-leaved macrophyte area.

2. Materials and methods

2.1. Coot census

Coots were counted from boats without disturbing them (Marion and Reeber, 1997), twice during the macrophyte growth period in 1997, just after breeding (at the beginning of July and September). According to observation facilities from boat pathways, the coot density was calculated by dividing the Nymphaeid area into 15 sections covering from 10.55 to 102.90 ha (Table 1).

2.2. Estimation of coot impact on N. alba

Coot is known to be omnivorous, but primarily herbivorous (Cramp and Simmons, 1980), mainly consuming vegetative parts and seeds of aquatic plants (Twilley et al., 1985; Perrow

Table 1
Description of *N. alba* sections[a]

Sections	Area (ha)	Quadrats (*N*)
1	66.55	7
2	16.80	4
3	52.00	4
4	67.20	10
5	18.30	3
6	57.10	13
7	102.90	10
8	10.55	6
9	53.65	10
10	37.85	4
11	53.60	5
12[b]	41.50	9
13[b]	22.25	6
14	68.95	10
15	70.25	13
Total	739.00	114

[a] Areas expressed in ha were determined from aerial photography conducted in August 1997 applying IDRISI software, according to the method followed by Nohara (1991). The numbers of quadrats sampled are indicated in the last column.

[b] In these sections, *N. alba* occurs mixed with many small *T. natans* patches; the sections are not included in the area measured.

et al., 1997) and to a lesser extent animal prey, such as molluscs and insects (Del Hoyo et al., 1996). The proportion of animals in the diet varies according to changes in food availability during seasons and between sites (Draulans and Vanherck, 1987; Woollhead, 1994).

In the present study, direct observations showed that coot impact on *N. alba* was restricted to the cutting of leaf petioles without eating leaves. Coots cut petioles to look for invertebrates on the leaves which were generally lifted 10–20 cm above the water surface.

Therefore, we quantified the ponctual proportion of cut petioles in 114 quadrats of 1 m^2 within the 15 sections (see Table 1 for details of quadrat numbers per section) twice in the 1997 growing season (at the end of July when large flocks of coots occurred and at the beginning of September when the coot density was reduced). Coot pressure on the *N. alba* area over the whole lake for the two periods was calculated from the mean weighted section area and the percentage of cut petioles.

In order to explain the specific behaviour of coots on *N. alba*, densities of the available prey (mainly beetles, dragonfly larvae, snails and leeches) on the leaves were recorded in July and September. We counted prey in the field, on both the upper and under sides of leaves over a 0.25 m^2 area in four quadrats in each section. Animal prey on cut and intact leaves were counted separately to quantify a possible effect of coot. Data were transformed to invertebrate density per leaf.

3. Results

3.1. Abundance of coots

At the beginning of summer 1997, the coot population was unusually high with about 20,900 birds, about twice as many as usual (Reeber, 2000). The influx of coots into the macrophyte area was also high. In July 1997, about half of the bird population (10,100 individuals) was found in the *N. alba* area whereas the rest of the population was present in the other zones of the lake (5200 individuals in the *T. natans* area and 5600 individuals in both the central open water region without plants and the surrounding marsh grasslands). In September, 5000 coots still used the *N. alba* area but only a few hundred birds were recorded in the other parts of the lake. In the *N. alba* area, the mean density reached 14 individuals per hectare in July and 7 individuals per hectare in September and varied greatly between sections for both periods, from 1 to 49 individuals per hectare (Fig. 1).

3.2. Measurement of coot impact on N. alba leaves

The proportion of cut petioles was about 20 times higher in July than in September ($6 \pm 1\%$ compared to $0.3 \pm 0.2\%$ of leaves, t test $= 8.642$, $n = 114$, $P < 0.001$). Attacks were recorded in all the sections in July (0.3 ± 0.6 to $16 \pm 6\%$) while they only occurred in four sections in September (0 to $2 \pm 2\%$) when the coot population was reduced by half in the Nymphaeid area (Fig. 1). Remarkably, there was no correspondence between the same sections for the two periods (Spearman rank correlation, $rs = -0.125$, $n = 15$, $P > 0.05$).

In July, less than half of the sections (six) had a proportion of cut petioles lower than 5% of leaves, and three adjacent sections (S1, S2 and S4) were characterised by a high impact (from 12 ± 14 to $16 \pm 6\%$ of leaves), where coot densities were relatively high (from 14

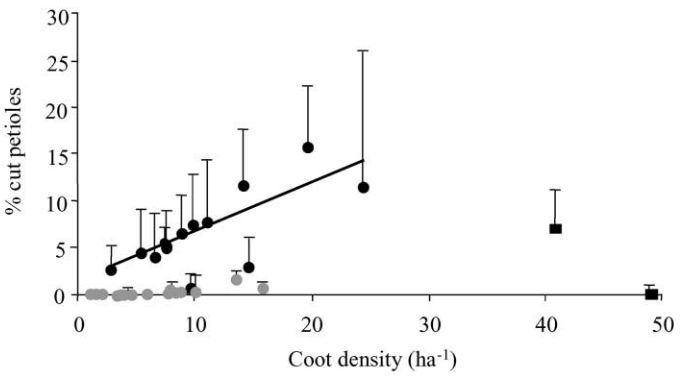

Fig. 1. Relation between coot densities (ha^{-1}) and the proportion of cut petioles (mean ± S.D.) in the 15 sections of Lake Grand-Lieu in both periods. In July, the linear relation was calculated from all sections except S12 and S13 (black squares) where coot density was biased by the presence of many small *T. natans* patches ($y = 0.52x + 1.21$, $r^2 = 0.46$, $n = 13$, $P < 0.05$). The proportions of cut petioles in July and September are indicated, respectively in black and grey circles.

to 24 individuals per hectare). In contrast, two sections (S12 and S13), characterised by the presence of many small *T. natans* patches had the highest density of coots (49 and 41 individuals per hectare). Here the proportion of cut petioles on *N. alba* was only moderate (<8%). So there was no significant relation between the density and the pressure of coot in the overall sections ($rs = 0.329$, $n = 15$, $P > 0.05$). When these two sections, S12 and S13, were excluded from the data set, a significant relation appeared between coot density and the impact on *N. alba* leaves ($r^2 = 0.46$, $n = 13$, $P < 0.05$, Fig. 1).

3.3. Relation between attack on N. alba leaves by coot and prey density

The main invertebrate species present on *N. alba* leaves were insects (primarily the beetle *Galerucella nymphaeae* and a few dragonfly larvae), snails (*Lymnaea*, *Planorbis*) and leeches (*Haemopis*, *Erpobdella*). Other invertebrates (caddisflies and fly larvae) were less abundant. Table 2 gives the average densities of these prey taxa on intact leaves in both periods, and on cut leaves in July only when the impact of coots was significant. Beetles (all development stages) were found on the upper side of the laminae while the other invertebrates were present on the lower surface. On intact leaves, beetles were the most abundant prey both in July and September, followed by snails and leeches while only few dragonflies were found. Overall, the density of invertebrates on intact leaves was higher in September (3 individuals per leaf against 2.50 individuals per leaf than in July) owing to higher densities of beetles in the second period (Wilcoxon test $W = 1.988$, $n = 15$, $P = 0.047$).

The density of snails was higher in July than in September ($W = 3.294$, $n = 15$, $P = 0.01$), whereas no difference was observed in the abundance of leeches and dragonfly larvae between the two periods ($W = -1.817$, $n = 15$, $P = 0.07$ and $W = -1.413$, $n = 15$, $P = 0.158$, respectively, for the two taxa). The impact of coots, as measured by the comparison between intact and cut leaves in July (Fig. 2), showed a high removal of beetles, whose density was reduced to 75% (Wilcoxon test $W = -3.18$, $n = 13$, $P = 0.001$), while the density of invertebrates located on the under side of the leaves was not significantly different ($W = 0.874$, $n = 13$, $P = 0.382$ and $W = -1.255$, $n = 13$, $P = 0.209$, respectively, for snails and leeches).

Spatial variation in invertebrate density was considerable: beetle density ranged from 0.25 ± 0.05 to 3.35 ± 1.60 individuals per leaf in July and from 0.85 ± 0.50 to 3.20 ± 2.20 individuals per leaf in September among sections. This variation was not correlated with coot density (Fig. 2).

Table 2
Mean invertebrate density per intact and cut leaf of *N. alba* in July and September[a]

Invertebrates on *Nymphaea alba* (*N* per leaf)	July		September
	Intact leaves	Cut leaves	Intact leaves
Beetles	1.20 ± 0.30	0.30 ± 0.20	2.25 ± 0.40
Snails	0.65 ± 0.15	1.05 ± 0.50	0.35 ± 0.10
Leeches	0.60 ± 0.15	0.55 ± 0.45	0.40 ± 0.15
Dragonflies	0.05 ± 0.01	0	0.05 ± 0.02

[a] No cut leaf was found in the second period.

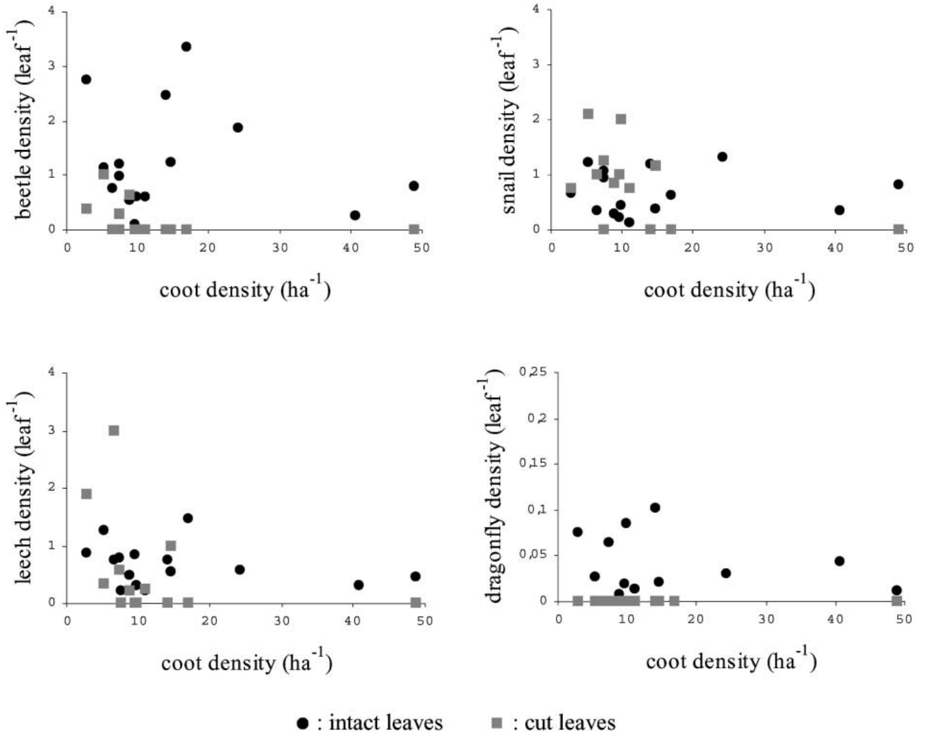

Fig. 2. Relationship between invertebrate density changes (mean value of the four quadrats) on intact and cut leaves and coot density (ha^{-1}) in the 15 section of Lake Grand-Lieu in July 1997. For some sections, no cut leaves were found.

4. Discussion

The unusual plant–bird interaction described in the present study has not been previously described in the literature: an indirect impact (behaviour of cutting petioles to look for invertebrate food) of waterfowl on a floating-leaved plant during the plant growing season. The effect of the coot population varied between the two periods studied (July and September). It coincided with changes in abundance of an unusually high population of coot (4000–6000 breeding pairs in 1997 compared to 2000–3000 pairs in 1996 and subsequent years, 1998–2000, Reeber, 2000) and a movement from breeding habitats to feeding areas (floating-leaved regions of the lake). In other years, when the hydrological conditions were slightly different from those in 1997 (Marion and Reeber, 1997), the movement of coots to the floating-leaved area was less rapid and massive.

Although the effect appeared was very spectacular (in July on average 6% of the petioles was cut from 739 ha of *N. alba* at a mean leaf density of 38 m^{-2}), it probably did not affect the growth of the plant in the following months. Indeed, 2 months later, only a tiny proportion of cut petioles was noted (0.3%) corresponding to the more anecdotal phenomenon currently observed every year (0–0.5%, unpublished results). The high turnover rates of this Nymphaeid species (Rich et al., 1971; Van der Velde and Peelen-Bexkens, 1983; Twilley et al., 1985; Marion et al., 1998) resulted in rapid regeneration of the above-ground parts of the plant later in the growing season. Moreover long-term monitoring of *N. alba* in this study site did not reveal any changes in mean biomass and productivity in the previous or subsequent years (Paillisson and Marion, unpublished data).

Overall, a large difference was noted only between densities of beetles on intact and cut leaves. No relation was observed between the spatial distribution of coots and beetles in July. However, beetles were present only on the upper side of leaves of *N. alba* which were usually lifted 10–20 cm above the water surface and direct observations indicated that coot turned leaves after having cut petioles. So the depletion of beetles on cut leaves might be due to coot predation of this selected food item including losses.

A comprehensive understanding of impacts of such large flocks of aquatic birds might require further experiments especially as in July the large *T. natans* area (about 200 ha) completely disappeared, before seed production (Marion et al., 1998), when large flocks of coot (5200) were counted in this part of the lake.

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References

Cramp, S., Simmons, K.E.L., 1980. The Birds of the Western Paleartic: Hawks to Bustards, Vol. 2. Oxford University Press, Oxford.

Del Hoyo, J., Elliott, A., Sargatal, J., 1996. Handbook of the Birds of the World: Hoatzin to Auks, Vol. 3. Lynx Edicions, Barcelona.

Draulans, D., Vanherck, L., 1987. Food and foraging of coot *Fulica atra* on fish ponds during autumn migration. Wildfowl 38, 63–69.

Idestam-Almquist, J., 1998. Waterfowl herbivory on *Potamogeton pectinatus* in the Baltic Sea. Oikos 81, 323–328.

Jupp, B.P., Spence, D.H., 1977. Limitations on macrophytes in a eutrophic lake, Loch Leven. I. Effects of phytoplankton. J. Ecol. 65, 175–186.

Kiørboe, T., 1980. Distribution and production of submerged macrophytes in Tipper Grund (Ringkobing Fjord, Denmark), and the impact of waterfowl grazing. J. Appl. Ecol. 17, 675–687.

Lauridsen, T.L., Jeppesen, E., Østergaard Andersen, F., 1993. Colonization of submerged macrophytes in shallow fish manipulated Lake Vaeng: impact of sediment composition and waterfowl grazing. Aquat. Bot. 46, 1–15.

Lodge, D.M., 1991. Herbivory on freshwater macrophytes. Aquat. Bot. 41, 195–224.

Lodge, D.M., Cronin, G., Van Donk E., Froelich, A.J., 1998. Impact of herbivory on plant standing crop: comparisons among biomes, between vascular and nonvascular plants, and among freshwater herbivore taxa. In: Jeppesen, E., Søndergaard, M., Søndergaard, M., Christoffersen, K. (Eds.), The Structuring Role of Submerged Macrophytes in Lakes. Springer, New York, pp. 149–174.

Marion, L., Marion P., 1975. Contribution to the ecological study of Lake Grand-Lieu. Bulletin de la Société des Sciences Naturelles de l'Ouest de la France (in French).

Marion, L., Clergeau, P., Brient, L., Bertru, G., 1994. The importance of avian-contributed nitrogen (N) and phosphorus (P) to Lake Grand-Lieu, France. Hydrobiologia 279/280, 133–147.

Marion, L., Reeber, S., 1997. Effect of the increased spring water level on the bird community of Lake Grand-Lieu. Rapport Programme Life, Laboratoire d'Evolution des Systèmes Naturels et Modifiés, UMR Ecobio CNRS, SNPN (in French).

Marion, L., Paillisson, J-M., Allain, J., Carpentier, A., Marion, P., Pierres, S., Brient, L., 1998. Impact of the water level on the productivity of the floating-leaved macrophytes of Lake Grand-Lieu. Université de Rennes, SNPN, LESNM (in French).

Mitchell, S.F., Perrow, M.R., 1998. Interactions between grazing birds and macrophytes. In: Jeppesen, E., Søndergaard, M., Søndergaard, M., Christoffersen, K. (Eds.), The Structuring Role of Submerged Macrophytes in Lakes. Springer, New York, pp. 175–196.

Nohara, S., 1991. A study on annual changes in surface cover of floating-leaved plants in a lake using aerial photography. Vegetatio 97, 125–136.

Perrow, M.R., Schutten, H., Howes, J.R., Holzer, T., Madgwick, J., Jowitt, A.J.D., 1997. Interactions between coot (*Fulica atra*) and submerged macrophytes: the role of birds in the restoration process. Hydrobiologia 342/343, 241–255.

Reeber, S., 2000. Impact of the water level increase on the avifauna of Lake Grand-Lieu. SNPN (in French).

Rich, P.H., Wetzel, R.G., Van Thuy, N., 1971. Distribution, production and role of aquatic macrophytes in a southern Michigan marl lake. Freshwater Biol. 1, 3–21.

Schutten, J., Van der Velden, J.A., Smit, H., 1994. Submerged macrophytes in the recently freshened lake system Volkerak–Zoom (The Netherlands), 1987–1991. Hydrobiologia 275/276, 207–218.

Søndergaard, M., Bruun, L., Lauridsen, T., Jeppesen, E., Vindbaek Madsen, T., 1996. The impact of grazing waterfowl on submerged macrophytes: in situ experiments in a shallow eutrophic lake. Aquat. Bot. 53, 73–84.

Søndergaard, M., Lauridsen, T.L., Jeppesen, E., Bruun, L., 1998. Macrophyte–waterfowl interactions: tracking a variable resource and the impact of herbivory on plant growth. In: Jeppesen, E., Søndergaard, M., Søndergaard, M., Christoffersen, K. (Eds.), The Structuring Role of Submerged Macrophytes in Lakes. Springer, New York, pp. 298–306.

Twilley, R.R., Blanton, L.R., Brinson, M.M., Davis, G.J., 1985. Biomass production and nutrient cycling in aquatic macrophyte communities of the Chowan River, North Carolina. Aquat. Bot. 22, 231–252.

Van der Velde, G., Peelen-Bexkens, P.M.M., 1983. Production and biomass of floating leaves of three species of Nymphaeaceae in two Dutch waters. In: Proceedings of the International Symposium on Aquatic Macrophytes, Njimegen, pp. 230–235.

Van Donk, E., 1998. Switches between clear and turbid water states in a biomanipulated lake (1986–1996): the role of herbivory on macrophytes. In: Jeppesen, E., Søndergaard, M., Søndergaard M., Christoffersen, K. (Eds.), The Structuring Role of Submerged Macrophytes in Lakes. Springer, New York, pp. 298–306.

Woollhead, J., 1994. Birds in the trophic web of lake Esrom, Denmark. Hydrobiologia 279/280, 29–38.