Activity and time budget of Tufted Ducks on Swiss lakes during winter
JEAN-CARLO PEDROLI

Introduction
Alternation of day and night produces a change of activity for most living organisms adhering to a rhythm and following a regular pattern. Changes in the other environmental conditions were shown in the case of ducks by Nilsson (1970) and Tamisier (1972) to produce only minor alterations in the activity pattern, alterations which it is important to know in order to determine a habitat’s quality. When the activity rhythm is altered too much by environmental conditions, producing higher energy consumption, the birds are forced to leave the wintering ground to seek others more favourable. The present study concerns the activities of Tufted Ducks Aythya fuligula wintering in Switzerland.

Most Swiss lakes were recently colonized by Dreissena polymorpha, a bivalve mollusc which rapidly invaded the whole of the bottom of the littoral zone. This increase of biomass in the benthos attracted very high numbers of wintering Tufted Ducks. (Pedroli 1981a, b, c.)

Description of Lake Neuchâtel
Lake Neuchâtel (Figure 1) belongs to the great lake region of central Europe, which was once covered by alpine glaciers. Its coordinates are 46°53’N and 6°51’E and the altitude is 429-3 m above sea level. With a total length of 38-3 km and a maximum width of 8-1 km, it is the largest subjurassic lake. The surface is 214-6 km², the mean depth 64-2 m and the maximum depth 153 m. There is a large littoral zone (0-9 m) covering 58-86 km², 26-6% of the surface, a favourable characteristic for aquatic birds.

The substratum of the littoral zone comprises sand and mud (50-84 km²) and gravel (8-02 km²). The gravel is concentrated in three deposit regions, Bas-lac, Vaumarcus and Yvonand, which are the main feeding and resting areas of the ducks, because of the high density of D. polymorpha.

Figure 1. Lake Neuchâtel—geographical sketch.
Field studies were conducted from 1975 to 1979. The diurnal part of the time budget was established in the winters 1976–1977 and 1977–1978 on the three main concentration points of Tufted Ducks on Lake Neuchâtel: Bas-lac, Vaumarcus and Yvonand. Every 15 to 30 minutes the individual behaviour of 100 birds, randomly selected within a flock, was observed by telescope and recorded on a dictaphone, according to the following categories: resting, preening, swimming and diving (time spent under water). The data were collected throughout the winter under various meteorological conditions. The nocturnal part of the time budget was established during winter 1977–1978 in the same way, using a night vision scope.

The electronic part was by RCA, USA; amplification power 40,000×, cathode S 20; the optic part by Zoomar, BRD, objective 180 mm, aperture 1:1-3. A minimum residual light was required, which limited our investigation to the Bas-lac region, those of Vaumarcus and Yvonand being too dark.

The observations were extended in 1978–1979 to Ouchy on Lake Geneva, today colonized by D. polymorpha, where day and night behaviour could be established, and on Niederried reservoir, not yet colonized and for which only day activity could be observed.

Our results are based on data from 1,259 groups of 100 birds: 856 diurnal and 106 nocturnal on Lake Neuchâtel; 145 diurnal and 66 nocturnal on Lake Geneva; and 106 diurnal on Niederried reservoir. The time budget of a bird flock was expressed as a percentage of each activity.

During these instant observations of flocks every 15 to 30 minutes, flight produced by sporadic disturbance was not considered. In several cases, however, continuous observation for 232 hours allowed us to note the flight activity of the ducks, its causes and duration.

Bi-mensual ground or aerial counts of the total wintering Tufted Duck population of Lake Neuchâtel were conducted, to find the number of bird-days for each concentration place, and the fluctuation within and between winters.

Results

Diurnal activity
The activity of Tufted Duck on the three main feeding and resting grounds of Lake Neuchâtel was similar (Figure 2). Resting was the main activity everywhere. The time devoted to preening was also similar in each place. Diving, the feeding activity of the ducks, occurred only seldom. During daylight, there were two periods of higher activity with swimming, and sometimes diving, in the morning when birds had finished their nocturnal feeding and late in the afternoon when birds initiate, their feeding. Data collected from Lake Geneva and the Niederried reservoir were also similar to those from Lake Neuchâtel.

Nocturnal activity
The results from both Lake Neuchâtel, Bas-lac, and Lake Geneva, Ouchy, were similar and contrast strongly with the diurnal pattern. During the night the birds have their feeding activity, which at flock level seemed to be constant throughout the night. Between 30 and 50% of the time was devoted to diving, the remaining time being spent swimming. Sometimes birds preened, mostly in the first and last hours of the night and around midnight.

As diurnal activity was the same in each place of investigation, it is likely that night activity was similar everywhere as well. This presumption was confirmed by the number of ducks caught during the night in gill nets used by commercial fishermen, 1975–1976 to 1977–1978 at Ouchy, Bas-lac (306), Vaumarcus (78), and Yvonand (209).

The activity rhythm
Our results showed, without any doubt, an alternation of diurnal resting and nocturnal foraging activity. During daylight, resting seemed to be very continuous, interrupted only briefly for individual birds by preening. In a flock, this was randomly distributed, not being induced by a collective stimulus. In some rare cases, however, a whole bird flock began to preen, probably when favourable conditions occurred, such as a rapid rise in temperature after the disappearance of haze, or sudden sunshine on a cloudy day.

Detailed observations of small bird groups during the night showed that diving was an irregular activity, stimulated by collective behaviour. When an individual dived, other members of the group rapidly did the same, this sequence being repeated
Tufted ducks on Swiss lakes

Figure 2. Tufted Duck, daytime and night-time activity.

at least ten times. The diving also stopped rapidly and the whole bird group began to swim for several seconds. Again an individual began to dive and the whole group did the same, and so on throughout the night. This collective behaviour is probably stimulated by the noise of a bird entering the water. During these rapid diving sequences the birds vocalized which also seemed to serve as a stimulation.

During the night, the ducks did not swim from one place to another, but after a series of dives, allowing them to regulate their respiration. During the day, only isolated individuals in the flocks swam. Courtship activities were never observed. However, in some particular situations a whole bird flock showed a high agitation phase. All the ducks swam rapidly in the same direction, some birds splashed, slap-
ped their wings on the water and pursued others, uttering the same frequent vocal noises as during feeding. These vocalizations were the only ones recorded. Agitation phases with rapid swimming were observed on all the concentration points and they always occurred at dawn and dusk. This can be interpreted as a sign of the transition between resting during the day and feeding during the night. In some rare cases this behaviour was also observed in the daytime, especially after the disturbance of a flock or arrival on a new resting ground.

**Duration of the Tufted Ducks’ activities**

For winter 1977–1978 on Lake Neuchâtel (Bas-lac), and 1978–1979 on Lake Geneva (Ouchy), the time devoted to the different activities was similar (Table 1). From the data collected for Lake Neuchâtel we were able to divide the winter season into four periods:


Our results showed that the time devoted to each activity was similar for periods 1, 3 and 4. Period 2, with a higher rate of disturbance all round the lake, showed longer foraging activities (swimming and diving) and shorter resting activities.

**Number of bird-days on the three major concentration points on Lake Neuchâtel**

Our data revealed (Table 2) that the number of bird-days on the Bas-lac region was always higher than on the other two. Annual fluctuations, however, were high. Yvonand and Vaumarcus had about the same number of bird days.

**Disturbances producing flying**

For the Bas-lac region, where the ducks rest in a bird sanctuary, disturbances were minor (Table 3), in total duration as well as in frequency. Their origin was, moreover, for the most part unconnected with man, the wind playing a major role. The sanctuary is situated at the north-eastern end of the lake, where the south-west wind sometimes produces high waves. Birds resting on open water away from the shore made periodic flights to adjust their position when the wind and the waves pushed them near the shore.

When ice covered the bird sanctuary, the ducks sometimes rested on open water near Neuchâtel, the feeding ground of the Bas-lac region. Boat traffic was dense (hunting, fishing and sport) and produced the major disturbances.

For Vaumarcus and Yvonand disturbances were similar but considerably greater than those of the bird sanctuary. Again boat traffic was the main source of disturbance.

### Table 1. Average duration (in hours) of the different activities of the Tufted Duck.

<table>
<thead>
<tr>
<th></th>
<th>Lake Neuchâtel, Bas-lac</th>
<th>Lake Geneva</th>
</tr>
</thead>
<tbody>
<tr>
<td>Resting</td>
<td>10-2</td>
<td>8-1</td>
</tr>
<tr>
<td>Preening</td>
<td>1-3</td>
<td>0-8</td>
</tr>
<tr>
<td>Swimming</td>
<td>7-6</td>
<td>9-2</td>
</tr>
<tr>
<td>Diving</td>
<td>4-9</td>
<td>5-9</td>
</tr>
</tbody>
</table>

* Period of pisciculture fishing for Coregonus sp.

### Table 2. Tufted Duck disturbances and duck-days on the resting sites of Lake Neuchâtel

<table>
<thead>
<tr>
<th></th>
<th>Observation (minutes)</th>
<th>Disturbances (minutes—%)</th>
<th>Duck-days</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fanel</td>
<td>5,845</td>
<td>8-2</td>
<td>0-1</td>
</tr>
<tr>
<td>Neuchâtel town</td>
<td>365</td>
<td>23-0</td>
<td>6-3</td>
</tr>
<tr>
<td>Yvonand</td>
<td>2,440</td>
<td>47-5</td>
<td>1-9</td>
</tr>
<tr>
<td>Vaumarcus</td>
<td>5,315</td>
<td>115-0</td>
<td>2-2</td>
</tr>
</tbody>
</table>
Seasonal fluctuation in bird numbers on the three concentration points on Lake Neuchâtel

Figure 3 summarizes the situation for the winters 1975–1976 to 1977–1978.

Tufted Ducks which arrived in October always concentrated first in the Bas-lac region, where they rest in the bird sanctuary during the day and feed in the vicinity of Neuchâtel during the night. From October to November, the number of ducks there increased, while no birds were present in Yvonand and Vaumarcus. By this time, all round the lake, gill nets were beginning to be set up to fish for spawning Coregonus sp. For the Bas-lac region, these nets were set in shallow water near Neuchâtel at the end of the afternoon, before the arrival of the ducks from the bird sanctuary, and taken out of the water in the morning, after their departure. In this way, the movement of the boats did not disturb the birds. However, frequent storms forced fishermen to take in their nets during the night, disturbing the feeding ducks. These nocturnal disturbances were probably responsible for the decrease in the number of birds in the Bas-lac region, and the increase all round the lake, especially in Yvonand and Vaumarcus. Nocturnal disturbances finished at the end of December, when Coregonus fishing is over.

In winter 1975–1976 and 1976–1977, our data showed that the number of birds again decreased during the Christmas and New Year period in the Bas-lac region, whilst they increased in Yvonand and Vaumarcus. This was not the case, however, during...
the winter of 1977–1978. In the first two winters, the bird sanctuary was covered with ice over Christmas and the New Year. For the first few days the ducks rested on open water in the vicinity, but after a while, when the ice was thick enough, the whole region was invaded by skaters, and the birds were driven away. From January until March, the birds were on all three regions, hunting and fishing activities having ceased.

Discussion

Information on time budgets of ducks is rare. For the period of reproduction, Folk (1971) in Czechoslovakia studied the diurnal activity of Tufted Ducks, and showed that this species then forages during daylight. Siegfried (1974) obtained similar results in Canada with Lesser Scaup Aythya affinis. Klima (1966) in Czechoslovakia found for Pochard Aythya ferina a regular alternation of feeding and resting activity throughout the 24-hour period. The nocturnal observations were, however, made with rudimentary equipment (a motorcycle light). In spite of the absence of valid nocturnal data on the activity of the Aythya species during reproduction, feeding certainly occurs during the day.

In winter, Willi (1970) showed that Tufted Duck on the Klingnauer reservoir had a diurnal feeding activity, and on one occasion he was able to establish that ducks also fed during the night. The same author found Pochard had a tendency towards night feeding. After dark nights, it was shown that a part of the day was devoted to feeding, which was not the case after bright moonlit nights. Nilsson (1970), in Sweden, concluded that Tufted Ducks, Pochard and Greater Scaup Aythya marila had a nocturnal feeding activity because numerous ducks were drowned during the night in gill nets. Similar observations were made by Thornburg (1973) in the USA with Aythya affinis, Canvasback A. valisineria, Ring-necked Duck A. collaris, and Redhead A. americana.

The apparent contradictions between the nocturnal activities of the Aythya species in former studies are due to a lack of suitably-adapted equipment for nocturnal observation.

Our results on the time budget of Tufted Duck showed clearly a nocturnal feeding and a diurnal resting activity. As the present study was made on three different lakes, and revealed a similar time budget everywhere, this general figure is probably valid for Central Europe, where ducks spend winter in great concentrations. In the 24-hour cycle, Tufted Duck devoted 4-8 hours on Lake Geneva and 5-2 hours on Lake Neuchâtel to diving activities. Siegfried (1974) found for A. affinis a duration of 3 to 5 hours; Klima (1966) for Pochard 6-9 hours, and Nilsson (1970) for Goldeneye Bucephala clangula between 7 and 9 hours. Our data, therefore, tallies with these figures. It must be mentioned, however, that in our study feeding activity included only the dives.

Nilsson (1970) found for three diving duck species that nocturnal feeding activities continued during a part of the day when the temperature was low, thus increasing energy losses. Similar results were also obtained by Tamisier (1972) for Anas crecca; this species showed also an increasing foraging activity in autumn, just after their fall migration, as well as at the end of the winter, when birds had courtship activities.

Our data showed that the duration of feeding activity was more or less constant throughout the winter. The only increase was noted between the end of November and the end of December, when boat traffic on the lake produced increased disturbance, with more flight activity, high in energy cost. Tamisier (1972) noted that for Anas crecca in the case of a longer time devoted to feeding activities, the duration of swimming activities was reduced, swimming being, according to him, an activity of no great importance which took place when no other activity was needed. This opinion is questionable, especially as the energy cost of swimming is 2-6 times higher than that of resting. (King 1974; Prange & Schmidt-Nilsson 1970).

The continuous feeding process, as shown in our data, raises the question of the rapidity of the digestion. Experiments made by Grandy (1972) revealed that mussels Mytilus edulis eaten by Black Duck Anas rubripes were to be found 30 to 40 minutes later in the terminal part of the duck's digestive system.

Stimulation to feeding (diving) within a bird group, as shown in the present study, was also found for Anas crecca by Tamisier (1972), as was a collective preening phase when the temperature rose rapidly, and an agitation phase after an important change of activity.

An analysis of these details reveals a certain number of similarities in the activities and behaviour on wintering grounds,
regardless of the species, the wintering ground or the food.

The most important fact pointed out by all the authors who had adequate equipment for night observations is that most of the species of diving ducks feed during the night and rest during the day. (There is one important exception, Goldeneye.)

In the great number of cases nocturnal feeding was attributed to humann diurnal disturbances on feeding grounds, mostly located near the shore (Nilsson 1970; Thornburg 1973). This explanation, however, is not completely satisfactory.

Indeed, for palearctic ducks, alternation of nocturnal feeding activities and diurnal resting activities was noted in regions without human disturbances (central delta of the Niger, Mali, in Tamisier 1972). Moreover, morning and evening flights of ducks were already known in antiquity. Tamisier (1972, 1976) suggests that for Anas crecca in the Camargue, Green-winged teal A. c. carolinensis and Pintail A. acuta in Louisiana, the diurnal resting activity is a direct consequence of diurnal avian predation pressure. During feeding these species are more vulnerable than during resting, thus they feed at night-time when the avian predators are absent, and sleep in the daytime when the number of watching eyes ensures a better protection. Such an explanation may be possible for dabbling ducks sleeping on shallow water or on the shore. Tamisier observed numerous attacks by avian predators (Marsh Harrier Circus aeruginosus, Herring Gull Larus argentatus) on duck flocks, forcing them to fly away. In the case of Aythya ducks, which rest on open water, we never observed disturbances due to avian predators, in spite of the number of wintering Herring Gull and the regular presence of Peregrines Falco peregrinus in the bird sanctuary.

Marshall in Tamisier (1972) has another theory and considers diurnal resting of ducks as a consequence of optimal thermal conditions during the day for comfort activities (resting, preening). The collective preening phase, as shown in the present study and also for other species of duck reported by various authors, would seem to support this theory.

It does appear that nocturnal feeding of the Aythya species in winter is an adaptation of relatively long standing. Indeed, most of these species have a diurnal feeding activity during reproduction and a nocturnal one during winter. Nocturnal feeding in winter is certainly a consequence of specific requirements which are unknown, especially as not all species have eyesight adapted to searching for food in the dark.

We think that nocturnal feeding is possible only because the Aythya species eat plant matter and sedentary animals. In this connection, the Goldeneye, with a narrow bill, is an interesting example. Its diet consists mainly of mobile prey (other than fish) which it uses its eyesight to pursue and catch. Feeding activity occurs in the daytime both during the reproduction period and in the winter. This is also the case when this species feeds mostly on sedentary animals, such as D. polymorpha (Leuzinger 1972), which confirms the long-standing nature of the adaptation.

Acknowledgments
We are thankful to Dr Claude Vaucher, Prof Willy Matthey, Dr Eduard Fuchs and Dr Alain Tamisier for their valuable advices. We are grateful to Mrs L'Eplattenier for her linguistic assistance.

This study was supported by the Vogelwarte Sempach, the Basler Stiftung für biologische Forschung, the Fondation Dr J. de Giacomi, Basel and the Fondation E. et J.-P. Schnorf, Zurich.

Summary
Since the invasion of Lake Neuchâtel by Dreissena polymorpha in 1967, the wintering population of Tufted Duck Aythya fuligula has greatly increased. From 1975 to 1979 the author studied the activity and movements of these birds with a telescope and, at night, with a night vision scope, the complete daily activity of the ducks was determined. Feeding occurs mainly during the night, resting during the day. The same result was obtained on Lake Geneva, which is also colonized by D. polymorpha, and on the Niederried reservoir, not yet colonized.

On Lake Neuchâtel, the feeding area with the least disturbance was occupied first, and had, on the whole, the greatest number of wintering ducks. The movement of ducks towards the other feeding places was caused by night disturbance during the feeding.

There were some similarities of behaviour between these and other species of wintering ducks, such as the diurnal resting and nocturnal feeding and the collective restlessness at dusk and dawn.

Nocturnal feeding activity was not confirmed as being due to diurnal predation pressure.
References

Pedroli, J.-C. 1981b. Les relations entre la Moule zébrée Dreissena polymorpha (Pallas) et les oiseaux aquatiques: le régime alimentaire des oiseaux aquatiques hivernant se nourrissant de Moule zébrée. (sous presse)
Pedroli, J.-C. 1981c. Les relations entre la Moule zébrée Dreissena polymorpha (Pallas) et les oiseaux aquatiques: la phénologie des Fuligules hivernant sur le lac de Neuchâtel (sous presse)

Dr J.-C. Pedroli, Inspecteur chasse et pêche, Château 16, Ch-2000, Neuchâtel, Switzerland.