THE TIME COMPONENT IN WATERFOWL DIET ANALYSES

Bob J. ZUUR

ABSTRACT - Five species of waterfowl (Mallard *Anas platyrhynchos*, Teal *A.crecca*, Tufted Duck *Ayrhya fuligula*, Pochard *A.ferina*, and Coot *Fulica atra*) showed daily fluctuations in the absolute and relative abundance of consumed food types. If these fluctuations are not taken into account in diet analyses, dietary differences usually attributed to demographic, seasonal or other variables may actually be due to the normal daily feeding patterns. Some species fed largely at night (the Mallards and the Pochards) and the importance of nocturnally consumed foods will be underestimated in normal diet analyses. The Teal had apparently altered its feeding behaviour to feed outside the peak shooting time. It is recommended that the population investigated be sampled throughout the day, and that the feeding times be weighed in subsequent analysis according to the amount of food consumed and not according to the number of birds shot.

The integral of the time/food curve is an ideal way of describing a diet, although this may be difficult to apply in practice. It is pointless and misleading to present diets calculated from incomplete and uneven data as "exact" percentages.

KEY WORDS: waterfowl / food / circadian rhythm / diet analysis.

Major advances in the analysis of the diets of waterfowl have been made over the last two decades. Originally, the relative importance of the various food components was taken to be proportional to the total weight or volume of food found in the gizzards of the examined birds. Biases incurred in the limitation of the analyses to gizzard rather than oesophageal contents (Swanson & Bartonek 1970) and in the use of simple volumetric, gravimetric or frequency of occurence data (Swanson *et al.*, 1974) have been illustrated previously.

While analysing the crop and gizzard contents in a number of waterfowl from the Lake of Constance in the north-east of Switzerland, I noticed that the abundance and variety of the food varied regularly through the day. Although it is widely known that most waterfowl species feed

Schweiz Vogelwarte
CH 6204 Sempach
SWITZERLAND

within well defined times of the day, and often on different food at different times of the day, this aspect has received very little attention with respect to diet analyses in the past. When combined with the temporal incompleteness and uneveness of most waterfowl samples, this factor can lead to errors in the calculation of their diets.

This paper examines the diurnal variation in the abundance of different food types in the digestive tract of several waterfowl species overwintering on a bay on the Lake of Constance, it illustrates possible errors made when this factor is ignored in diet analyses, and proposes methods by which these errors may be reduced.

MATERIAL AND METHODS

The contents of the crops and the gizzards of 270 waterfowl of five species were analysed for this study. The birds were shot by amateur hunters during the winter shooting seasons of 1979/80 and 1980/81 on the Bay of Ermatingen on the Lake of Constance (Fig. 1). This bay supports a rich faunal benthos made up predominantly of Chironomid larvae (2-4 g dry weight per m^2 in winter) and Tubificid worms (08-10 g/m^2)(Zuur & Suter, in press). Although an abundant aquatic flora develops in summer (mainly Pondweeds-Potamogetonaceae), most of these plants die back in winter, leaving only their seeds and overwintering tubers to be of significance. Owing to the shallowness and marked seasonal water level fluctuations of the bay, this benthos provides a relatively easily available food resource for dabbling ducks. The diving ducks are better supported by the beds of the Zebra mussel *Dreissena polymorpha* to be found in the Bay of Constance (5 km to the east).

The species, the date and time of shooting were recorded for each specimen collected. The crops and gizzards were removed by the hunters as soon as possible after shooting. The combined crop and gizzard contents (1979/80) or the entire organs (1980/81) were preserved immediately in seperate bottles containing 10% Formalin. Later, the contents were washed through a sieve with a 1 mm mesh size, and sorted on a white tray under a binocular microscope. Animals were identified by the authour using Brohmer (1979) and more specialized keys, while the more important seeds were identified by Dr. S. Jacomet, University of Basle, Switzerland.

The ingested food was classified into eight components:

- The Zebra mussel *Dreissena polymorpha*
- Other molluscs (predominantly Gastropods)
- Chironomid larvae
- Other Arthropods (predominantly aquatic insect larvae)
- Filamentous algae
- Other vegetative plant matter

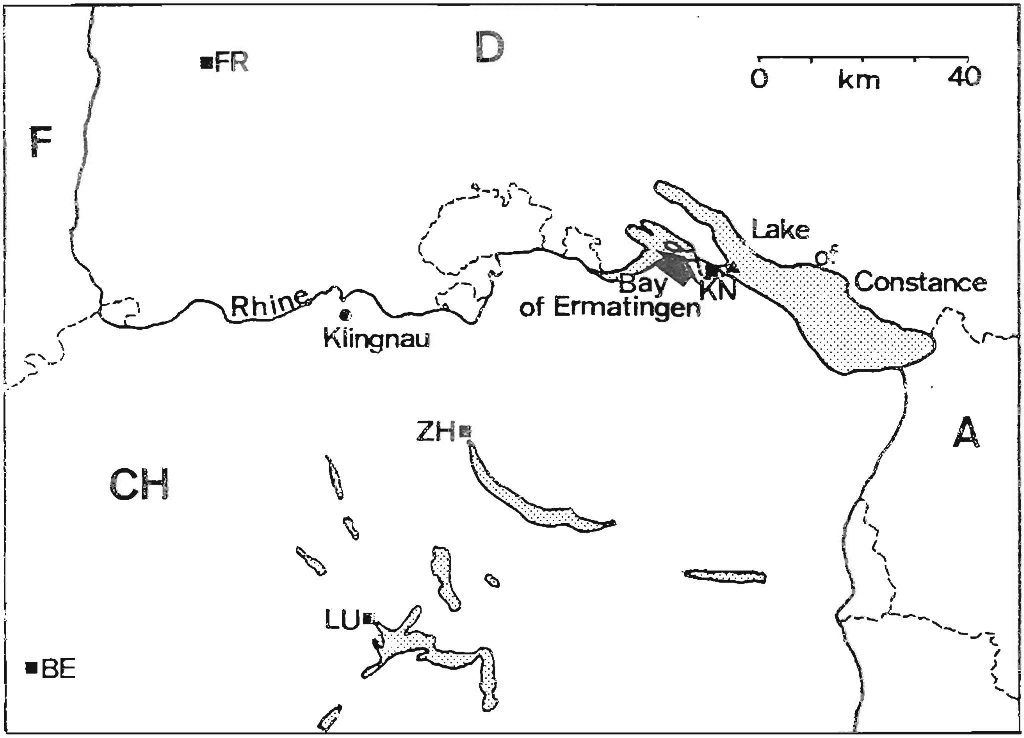


FIGURE 1 - The site of the Bay of Ermatingen in the north-east of Switzerland. The cities shown are: FR - Freiburg, KN - Constance, ZH - Zurich, LU - Lucerne, BE - Berne. The Bay of Constance is indicated by a triangle.

- Pondweed seeds (Potamogetonaceae)
- Other seeds (largely terrestrial)

The occurence of these food components above minimum criteria of freshness in the crops and gizzards were determined for each individual. These criteria described by Zuur & Suter (in press), create objective cut-off points above which only relatively recently ingested food is considered. As only the occurrence through the day and not the relative importance of the various food components were investigated in this study, the biases inherent in the "frequency of occurrence" method noted by Swanson and Bartonek (1970) were not applicable.

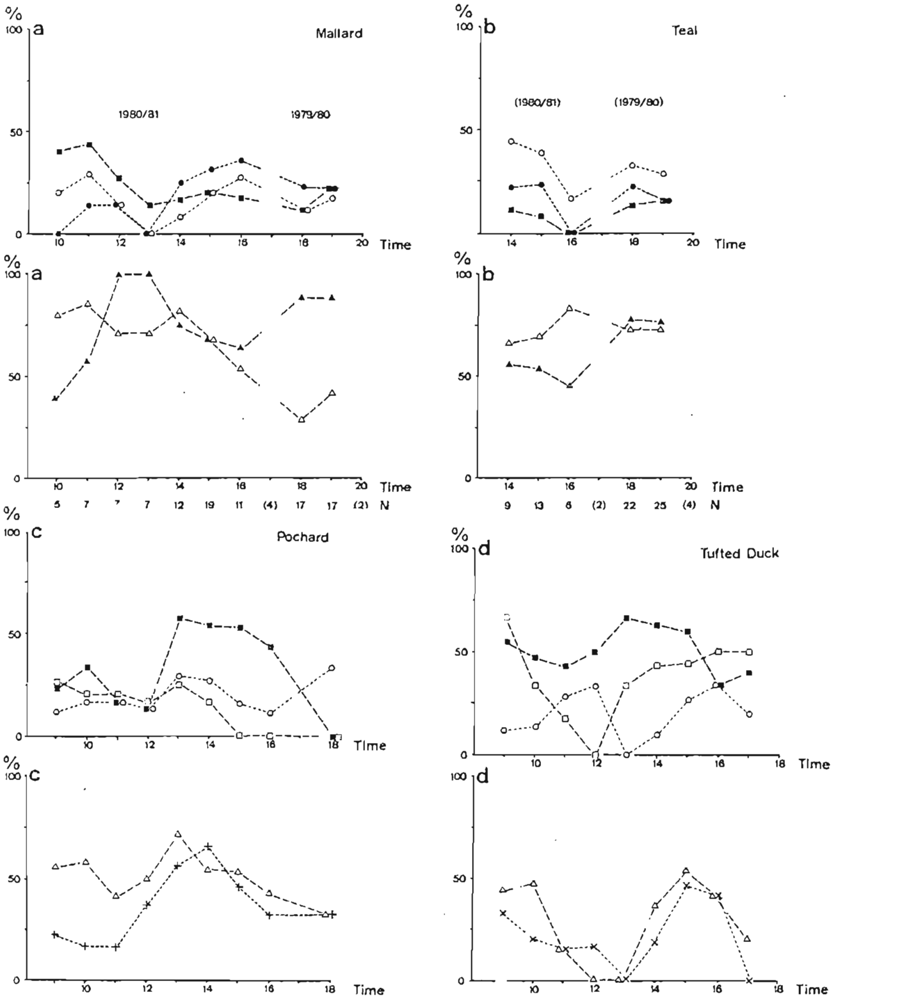
RESULTS

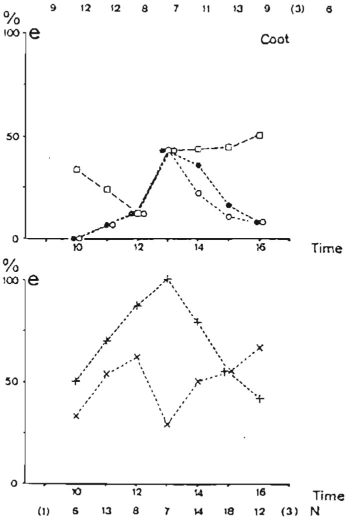
In order to minimise possible seasonal dietary variations, the analy lysis below was restricted to birds caught within a six-week period, from the middle of December to the first week of February. No birds were shot at night as this is not allowed by the hunting regulations. The Mallards (*Anas platyrhynchos*), and the Teals (*A. crecca*) from the 1979/80 season were shot later in the day than those during the following season. The other species (Tufted Duck *Aythya fuligula*, Pochard *A. ferina*, and Coot *Fulica atra*) were shot at similar times in both seasons.

The incidence with time of various food types in the crops and gizzards of the examined birds are shown in Fig. 2. The occurence of the main food types in the Mallard showed a number of interesting parallels with the feeding behaviour of this species overwintering on the Klingnau reservoir, 65 km to the west (Fig. 3a; Willi 1970). Willi noted that from October onwards, Mallards flew inland before dawn to feed in neighbouring fields, returning to rest on the lake during the morning, with few birds feeding there. This flight was repeated at dusk with the birds returning late in the evening. This evening flight has also been observed on the Bay of Ermatingen (Dr. A. Krämer, pers. comm.). The midday peak of the "other" seeds (largely terrestrial seeds such as maize, wheat, and acorns) corresponds with the return of the ducks to the lake, and the rise in the late afternoon occurs at the time of their evening departure. Aquatic animals were consumed together predominantly in the mid-morning and the mid-afternoon, with a midday activity pause not noted by Willi, but common among many waterfowl. Pondweed seeds (Potamogetonaceae) were consumed mainly during the morning.

It is difficult to draw firm conclusions about the Teal as the birds were only shot during the afternoon or evening (Fig. 2b). However, very few Teal feed at night during winter, the feeding peak (in undisturbed birds) occuring in the afternoon (Fig. 2b; Leuzinger 1968; Willi 1970). But relatively few of the birds examined (2 out of 53) contained more than 50 mg of food (the apparently high incidence of seeds in Fig. 2b generally refers to less than 10 seeds per duck), implying that these birds had displaced their feeding peak. This may have been due to the disturbance caused by hunting, as feeding at night has been previously associated with hunting pressure (Tamisier 1966). In the short time span investigated, it appeared that most foods were consumed together.

The Pochard showed a simple food occurence curve with all foods peaking in the afternoon, and perhaps a second peak in the morning (Fig. 2c). Willi (1970) noted that this species overwintering on the Klingnau reservoir showed three activity peaks; one in the afternoon corresponding to the food peak mentioned above, and one each during the first and second





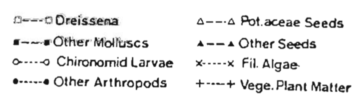


FIGURE 2 - Frequency of occurence of various food in the gizzards and crops of the examined birds according to the time of capture. The birds have been grouped into two-hour periods considered every hour. Sample size (n) is shown below, samples with less than five birds have been excluded. The Mallards and Teal shot before 1700 come from the 1980/81 season, those after 1700 from the 1979/80 season.

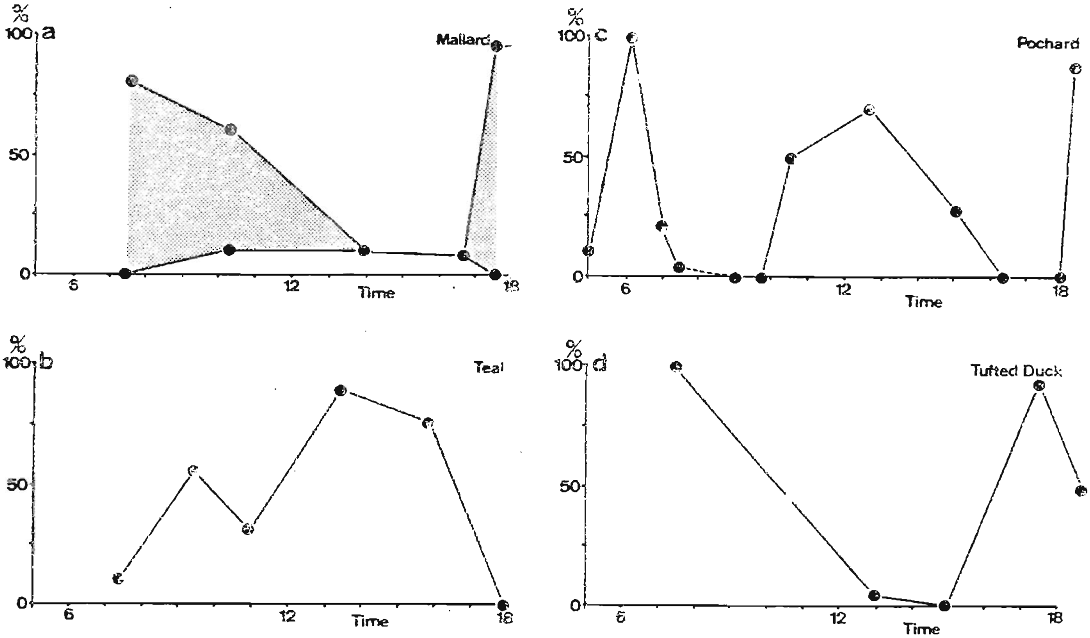


FIGURE 3 - Feeding activity in November of four duck species overwintering on the Klingnau reservoir - from Willi (1970) Ordinate is the precentage of feeding birds, the shaded area shows the proportion feeding on land.

halves of the night (Fig. 3c) during which time most of the feeding took place. The Zebra mussel was a very important element in the diet of the Pochards overwintering on the Bay of Ermatingen as most birds had well-digested shells in their gizzards (Zuur & Suter, in press), but signs of freshly consumed mussels were rare compared to those found in the Tufted Duck. This would be because Pochards feed on Zebra mussels in the Bay of Constance (5 km to the east) predominantly at night (Jacoby and Leuzinger 1972).

Although Willi (1970) noted that Tufted Ducks on the Klingnau reservoir were almost completely day-active. W. Suter (pers. comm.) notes that they fed to a significant extent at night near Stein-am-Rhein at the western end of the Untersee. The Zebra mussel is the main food of the Ermatingen Tufted Ducks and is probably consumed in the Seerhein immediately to the east or in the Bay of Constance. Feeding in these regions occurs predominantly during the night (H. Jacoby pers. comm.). The peak occurence of this mussel and of most other food types in the guts examined is early in the morning and mid-afternoon (Fig. 2d), corresponding to the feeding peaks noted by Willi (1970; Fig. 3d). Chironomid larvae appear to be consumed primarily at midday and in the late afternoon, probably while the birds are resting in the Bay of Ermatingen, as this is an abundant food resource here.

Coots are primarily day active, feeding in the morning and late afternoon, sleeping with the approach of darkness (Hurter 1972; Glutz von Blotzhein *et al.* 1973). Zebra mussels appear to have been consumed predominantly during these times (Fig. 2e). This probably applies only to those coots shot in the eastern part of the bay, relatively near to the stocks of this mussel in the Seerhein (it does not occur in the bay itself), as feeding flights equivalent to those made by the diving ducks and the Mallards, are of less importance for the Coot (H. Jacoby pers. comm.). Vegetative plant matter was consumed predominantly over the middle of the day (Fig. 2e).

DISCUSSION

The primary aim of most diet analyses is to determine the variety and relative importance of all consumed foods. It has been seen, however, that some of Europe's most important waterfowl species have marked periods of feeding activity and may feed on different foods at different times of the day. Birds for analysis should therefore be collected at all times of the day. Swanson and Bartonek (1970) suggest that only actively feeding birds should be collected, but this assumes that all feeding times and places are known and that hunters can select these birds.

However, as most dietary analyses examine birds shot by amateur hunters, this is only very rarely possible. Very few birds will be collected at night, for example, and therefore the importance of nocturnally ingested foods, such as maize and mussels for the Mallard and the Pochard respectively, will be seriously under-estimated. Even normally diurnal species can create problems - it appeared that the Teal had altered their feeding behaviour to feed outside the period that most were shot. Crop and especially gizzard contents were unlikely to have been fresh and biases against easily digested items must be expected (Swanson and Bartonek 1970). Coots tended to eat plant material over the middle of the day, and mussels

Coots tended to eat plant material over the middle of the day, and mussels and filamentous algae in the morning and afternoon (Fig. 2e).

Hence birds collected at the same time of the year but at different times of the day may be expected to show differences in the relative abundance of the foods they had consumed. Coots shot in the morning or in the afternoon had consumed more mussels and less plant material (eg. grass) than those shot over midday (Fig. 4). Although filamentous algae was often found in the crops and gizzards, it was only rarely consumed in significant amounts.

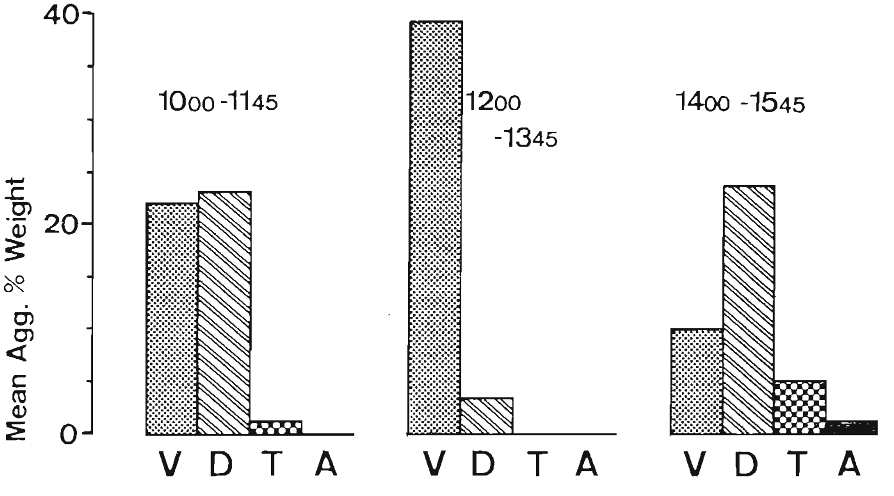


FIGURE 4 - Observed diet of Coots in the Bay of Ermatingen at three different times of the day. The ordinate is the mean aggregate percentage weight (Swanson *et al.* 1974) of the food found in the crops and gizzards of the examined birds. V = Vegetative plant matter, D = Zebra mussel *Dreissena polymorpha*, T = Winter tubers of the Pondweed *Potamogeton pectinatus*, A = Filamentous algae.

Much has been written about the changes in the diet of waterfowl between years and through the seasons. Although these changes may often reflect the changing availability of various foods, care should be exercised when making such comparisons. For example, the similarity between the crop and gizzard contents of Mallards shot at the same time but in different months was found to be greater than that of Mallards shot within the same ten-day period but at different times of the day (Table I). "C" is a measure of the overlap between two observed diets (Horn 1966) and was calculated for Table I on the basis of 19 food types. Those birds shot over

TABLE I - Degree of overlap (C. Horn 1966), in the observed diets of Mallards from the Lake of Constance at different times and dates. Values of C greater than 0.60 indicate significant similarity (Zaret and Rand 1971).

YEAR	PERIOD	TIME	NUMBER OF BIRDS	C
1980/81	Jan. 11-20	1400-1530	6	0.79
1980/81	Feb. 1-20	1400-1530	5	
1980/81	Jan. 1-20	1230-1400	5	0.54
1980/81	Jan. 1-20	1430-1530	6	

midday were found carrying more seeds and those shot in the afternoon more animal material. Admittedly, this example was selected to find a difference in the observed diets, and this may not always occur. However, before dietary comparisons are made between months or years, or between different populations or species, it must first be established that the two samples are in fact comparable and do not differ in time of collection.

Olney (1964) found that barley made up 27% of the total volume of food collected from a sample of Mallards shot during 1957/58, and almost 83% the following year. The difference was attributed to the variation in the number of stubble fields and hence to the availability of grain. A three-fold increase in the barley acreage in one year, although unlikely, would only affect the diet of the birds if the previous availability was limiting, or if alternative food supplies were limiting in the second year. As only ten of the sixty Mallards shot over the three years studied contained barley, it is certainly possible that in 1958/59 more birds were shot in the late afternoon and had therefore come into contact with barley more recently than in other years. If the time/date shooting characteristics of Olney's sample parallels that of the Mallards and Teal of the present study this is certainly possible.

Swanson and Bartonek (1970) suggest taking only actively feeding ducks for analysis. This necessarily applies only to birds shot expressly for diet analysis and assumes that all feeding times and places are known. Usually in the analysis of hunters bags very little control over the time of shooting can be made, and an allowance for the inaccessible feeding times (eg. nighttime) must be made. All the feeding times should be weighted according to the amount of food consumed during that time and not according to the number of birds shot. Of the 59 Coots examined, adult Chironomids were found in 14 birds, of which twelve were all those shot at

1300 on the 25th of March, 1980. If this sample would have been included in the analysis this food would obviously have been overrepresented.

Ideally, diets should be expressed as the integral of the time/ingested food curve, a curve similar to those presented in Fig. 2, but extending over 24 hours. The use of the aggregate percentage method in data presentation (Swanson *et al.* 1974) rather than simply the frequency of occurence of the foods will reduce the mathematical biases inherent in the latter method. Although ideal, it will only rarely be possible to determine these integrals in practise. But if this is not done, it must be realised that the errors involved in the estimations of the relative importance of the dietary components may be rather large and it is therefore pointless to list these estimations as exact percentages, and misleading to relate demographic or spatial/temporal dietary differences to easily quantified environmental variables. In many cases it may be better to be conservative and list foods simply in the categories Main, Supplementary and Opportunistic foods depending on the abundance and frequency of occurence in the crops of the examined birds.

ACKNOWLEDGEMENTS

I thank Dr. A. Krämer, Hunting Inspector of Canton Thurgau (Switzeland) for supplying the crop and gizzard samples and for financial support, Dr. R. Luder and Mr. H. P. Pfister for commenting on a draft of this paper, Mrs. R. Keller for typing the manuscript, and Mr. R. Lévêque for translating the Resume.

RIASSUNTO

LA VARIABILITA' TEMPORALE COME FATTORE NELLO STUDIO DELLA DIETA DEGLI UCCELLI ACQUATICI

Analisi del contenuto stomacale sono state compiute in cinque specie (Germano *Anas platyrhynchos*, Alzavola *Anas crecca*, Moretta *Aythya fuligula*, Moriglione *Aythya ferina*, Folaga *Fulica atra*) catturate in inverno in una baia del lago di Costanza (Fig. 1). Tutte le specie mostrano ampie variazioni lungo il giorno nell'abbondanza sia assoluta che relativa dei tipi di cibo (Fig. 2. Frequenza delle varie componenti della dieta in relazione all'ora della cattura. n = numero esemplari esaminati). Tali variazioni sono in relazione al ritmo di attività giornaliera delle specie (Fig. 3. Attività di alimentazione come percentuale di uccelli che si cibano. La zona in grigio indica la percentuale di uccelli che si nu-

trono sulla terra).

Se queste variazioni giornaliere non sono considerate da chi compie analisi della dieta, le differenze che di solito sono attribuite a fattori demografici, stagionali o altri ancora, possono essere dovute semplicemente alle differenze giornaliere (Fig. 4. Dieta della Folaga riscontrata in tre diversi orari del giorno. Percentuale media del peso di 4 categorie di cibo nel tratto digerente). Alcune specie si cibano in prevalenza di notte (Germano e Moriglione), ed il cibo raccolto di notte è in genere sottostimato nelle analisi della dieta. L'Alzavola pare aver alterato il suo ritmo di attività per evitare le ore di caccia più intensa. Si raccomanda di raccogliere campioni lungo tutto l'arco delle 24 ore negli studi sul cibo, e di valutare i risultati in base alla quantità di cibo consumato e non in base al numero di uccelli catturati.

L'integrale della curva quantità di cibo/tempo sarebbe la misura ideale della dieta, ma è di difficile calcolo nella pratica. E' tuttavia inutile e sbagliato presentare dati sulla dieta come percentuali "esatte" se i campioni sono stati raccolti senza un metodo adeguato.

RESUME

LA VARIATION DU TEMP COMME FACTEUR DANS L'ANALYSE DE L'ALIMENTATION DU GIBIER D'EAU

J'ai analysé le contenu de l'estomac et du gésier de cinq espèces de gibier d'eau (Colvert, Sarcelle d'hiver, Fuligule morillon, F. milouin et Foulque) tirées en hiver dans une baie du lac de Constance (Fig. 1. La Baie d'Ermatingen dans le Nord-Est de la Suisse. Les villes sont indiquées par FR = Freiburg in B., KN = Constance, ZH = Zürich, LU = Lucerne, BE = Berne. La baie de Constance est indiquée par un triangle). Les cinq espèces ont montré des fluctuations diurnes dans l'abondance absolue des sortes d'aliments ingérés, et aussi dans leur abondance relative (Fig. 2. Fréquence de divers aliments dans le gésier et l'estomac des oiseaux examinés, selon l'heure de la capture. Les oiseaux ont été groupés par périodes de deux heures et la moyenne glissante calculée pour chaque heure. La taille de l'échantillon (n) est indiquée au dessous, les échantillons de moins de cinq oisseaux étant exclus. Les Colverts et Sarcelles tirés avant 1700 proviennent de la saison de chasse 1980/81, ceux après 1700 de la saison 1979/80). Ces fluctuations étaient liées au rythme de nourrissage quotidien des oiseaux (Fig. 3. Activité d'alimentation en novembre de quatre

espèces de canards passant l'hiver sur le lac de barrage de Klingnau -d'apès Willi (1970). En ordonnée le porcentage d'oiseaux se nourris - sant; la zone ombrée montre la proportion d'oiseaux s'alimentant sur la terre ferme).

Si ces fluctuations ne sont pas prises en considération lors d'analyses de la nourriture, les différences dans l'alimentation habituellement attribuées à des variations démographiques, saisonnières ou autres peuvent être dues en réalité au rythme quotidien normal d'alimentation (Fig. 4. Régime alimentaire de Foulques dans la baie d'Ermatingen à trois moments différents de la journée. L'ordonnée représente la moyenne des pourcentages cumulés de poids (Swanson *et al.* 1974) de chaque nourriture trouvée dans les gésiers et les estomacs des oiseaux examinés. V = Matières végétales, D = Moule zébrée *Dreissena polymorpha*, T = Tubercules hivernaux de Potamot *Potamogeton pectinatus*, A = Algues filamenteuses). Quelques espèces se nourrissent surtout de nuit (les Colverts et les Milouins), et l'importance des aliments pris durant la nuit sera sous-estimée lors d'analyses conventionelles. La Sarcelle d'hiver semble avoir changé son comportement nourricier pour s'alimenter hors des heures de plus grande chasse. Il est donc recommandé d'échantillonner la population étudiée tout au long de la journée, et que dans les analyses subséquentes, h'eure du nourrissage soit liée à la quantité de nourriture consommée, et non au nombre d'oiseaux tirés.

L'intégrale de la courbe temps/nourriture est un moyen idéal de décrire une alimentation, bien qu'elle puisse être difficile à appliquer dans la pratique. Il n'y a aucune raison, et il est même erroné, de présenter des régimes alimentaires calculés des données incomplètes et inégales comme des pourcentage "exacts".

REFERENCES

BROHMER, P. 1979. Fauna von Deutschland, 14th Edition. Quelle and Meyer, Heidelberg.

GLUTZ VON BLOTZHEIM, U.N., BAUER, K.M. & BEZZEL, E. 1973. Handbuch der Vögel Mitteleuropas, vol. 5. Frankfurt/M.

HORN, H.S. 1966. Measurement of "Overlap" in comparative ecological studies. Am. Nat. 100: 419-424.

HURTER, H.-U. 1972. Nahrung und Ernährungsweise des Blässhuhns *Fulica atra* am Sempachersee. Orn. Beob. 69: 125-149.

JACOBY, H. & LEUZINGER, H. 1972. Die Wandermuschel als Nahrung der Wasservögel am Bodensee. Anz. orn. Ges. Bayern. 11: 26-35.

LEUZINGER, H. 1968. Beobachtungen zum Nahrungs- und Ruheplatzverhalten und zum Nahrungserwerb der Krickente *Anas crecca* im Winter. Orn. Beob. 65: 1-5.

OLNEY, P.J.S. 1964. The food of the Mallard *Anas platyrhynchos* collected from coastal and estuarine areas. Proc. Zool. Soc. Lond. 142: 397-418.

SWANSON, G.A. & BARTONEK, J.C. 1970. Bias associated with food analysis in gizzards of blue-winged Teal. J. Wildl. Manage. 34: 739-746.

SWANSON, G.A., KRAPU, G.L., BARTONEK, J.C., SERIE, J.R. & JOHNSON, D.H. 1974. Advantages in mathematically weighting waterfowl food habits data. J. Wildl. Manage 38: 302-307.

TAMISIER, A. 1966. Dispersion crépusculaire des Sarcelles d'hiver en recherche de nourriture. Terre et Vie.1966: 316-337.

WILLI, P. 1970. Zugverhalten, Aktivität, Nahrung und Nahrungserwerb auf dem Klingnauer Stausee häufig auftretender Anatiden, insbesondere von Krickente, Tafelente und Reiherente. Orn. Beob. 67: 141-217.

ZARET, T.M. & RAND, A.S. 1971. Competition in tropical stream fishes: Support for the competitive exclusion principle. Ecology 52: 336-342.

ZUUR, B.J. & SUTER, W. (1983). Zur Nahrungsökologie auf dem Ermatinger Becken (Bodensee) über winternder Wasservögel. Orn. Beob. (In press).

Ricevuto settembre 1982