SEASONAL VARIABILITY IN FEEDING RHYTHMS OF FOUR SPECIES OF DUCKS

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Rhythms of feeding activity in four species of ducks were investigated in outdoor pens using data obtained from photocells at feeding boxes. Patterns of food intake showed a 24 hour period, with the daily rhythm synchronized by sunrise and sunset throughout the year. Analyses of phase angle differences and activity patterns revealed interspecific differences in exploitation competition. These differences were more evident in diving ducks than in dabbling ducks. Variability in food intake, which reflected seasonal changes, appeared to be synchronized by length of photoperiod. The amount of food consumed was low during last summer and early fall. A rapid increase in food consumption observed in late fall and early winter during the period of pair formation was believed to be the result of increased activity related to social and/or breeding behavior. Transfer to an ultradian rhythm occurred at this time. During incubation, a bigeminus pattern of activity with the night phase suppressed was recorded.

dabbling ducks; diving ducks; feeding rhythm; activity pattern; seasonal cycle; food consumption; circadian and ultradian rhythm

INTRODUCTION

Information on activity patterns in wild ducks has been based primarily on visual observation. Such observations indicate that feeding occurs mostly during daylight; however, night feeding is very difficult to observe. Usually feeding was recorded as part of the overall behavioral sequence. Frequently such records covered periods of a few days or months, but not the entire year. An automatic device to monitor feeding activity was investigated by S w a n s o n et al. (1972). A small radio transmitter, mounted on the upper mandible, changed its pulse rate when the bill was tipped vertically. However, no published data obtained using this device were located.

Regulation of feeding by exogenous synchronizers is not well understood in wild ducks. In view of the difficulty in monitoring feeding behavior continuously in the wild over the entire year, we established an automatic recording system for use on ducks in captivity.

This paper reports on seasonal changes in feeding behavior of captive mallard (*Anas platyrhynchos*), gadwall (*Anas strepera*), crested pochard (*Aythya ferina*) and tufted duck (*Aythya fuligula*).

METHODS

Two species of dabbling ducks, mallards and gadwalls and two species of diving ducks, crested pochards and tufted ducks were selected to examine interactions between species occupying the same habitat. All incubated ducks were raised in a group indoors near Č. Budějovice, Czech Republic (49° 0′ N, 14° 30′ E) until approximately one month of age, when they were placed outdoors in separate 3 x 6 m pens. Food was a granulated monodiet used for domestic ducks, available *ad libitum* in automatic feeding boxes. Water, maintained in basins 0.5 x 0.5 x 1 m, was changed every day or every other day, but at different times of the day. Feeding activity was recorded using a system of photo cells placed at the entrance of the feeding boxes (Figala et al., 1990). Food intake was recorded and analyzed in one hour intervals.

On April 1, an adult mallard drake was placed in the pen with the mallard hen. The first egg was laid on April 12th. A nest was built and incubation began May 1. On April 29th the drake was transferred to a separate, nearby pen so that visual and acoustical communication was possible. Incubation lasted for 35 days, when the hen abandoned her unfertile eggs (Figala et al., 1990). A similar procedure was followed with the crested pochard. The pair remained together until May 31st, but no eggs were laid.

The time within the 24-hour cycle when the amount of feeding increased sufficiently to rise above the threshold line was selected as the onset of intake. Similarly, the time when feeding fell below the threshold was selected as the time of cessation (Figala, Muller, 1972). Bimodal rhythms were characterized as bigeminus when the first peak was higher than the second, and as alternans when the second peak was higher (Aschoff, 1962).

The pattern of food intake in different hourly periods (tested by coefficient of variance) shows the preferred feeding time. However, time differences may exist between the peak of foraging and the lowest point of variance.

RESULTS

FEEDING ACTIVITY

Mallard

Seasonal changes in food intake by a mallard drake are shown in Fig. 1. The food intake peaks occurred 2 to 4 hours after sunrise and, during the summer of the first year, shortly after sunset. During fall (October and November) feeding activity shifted into the night hours. Feeding during March did not have clear peaks and the rhythm showed a tendency to shift into an ultradian pattern around the threshold. The feeding rhythm in the second year exhibited a negative phase angle in relation to sunrise. Length of feeding activity was remarkably constant and did not follow the length of photoperiod in the summer. The increase in length of foraging activity in November appeared to be determined by sunset. The end of activity followed the time of sunset until February.

Food intake in the mallard hen (Fig. 2) exhibited a peak in the morning hours with a negative phase relation to sunrise throughout the 18-month period. This activity time, of intensive food intake, was from 6 to 9 hours long. The end of feeding activity time was not synchronized with sunset and night feeding peaks did not occur.

In July of year one, the foraging activity showed two peaks of activity (alternans pattern). Since this pattern did not occur in July of year two, we believe it was a function of age. The two extremely high peaks of activity in daylight in May are believed to be related to incubation by the hen.

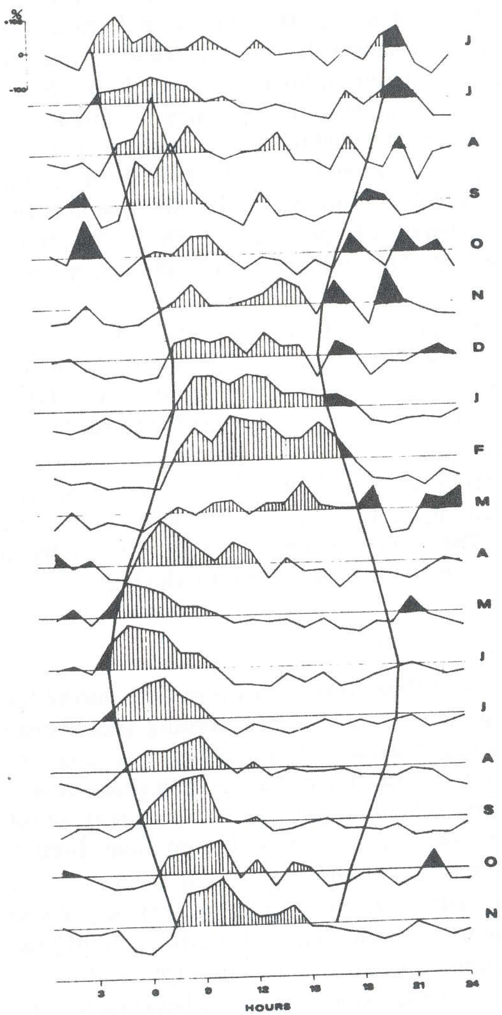
Gadwall

Feeding activity in the young male (Fig. 3) occurred primarily during the night from August through January. At that time the feeding peak began shifting slowly to the time of sunset and the activity pattern became alternans (February, March). In early April the phase changed again with peak feeding occurring shortly after sunrise. This bigeminus pattern continued (except for June) until November. Night feeding activity occurred from June through August, but was greatly reduced during the fall.

Similar changes in feeding activity were observed in a female gadwall (Fig. 4). Feeding activity was common at night, but the time of the night peak varied considerably. However, morning peaks were synchronized with sunrise. In January and February a high correlation was observed between feeding and length of daylight, i.e. feeding followed very close the length of daylight.

Crested Pochard

Monthly averages of the daily feeding rhythm in a crested pochard drake (Fig. 5) showed a night and a morning feeding period. Peak feeding occurred after sunrise (negative phase angle values). This peak seemed to be well synchronized by sunrise during late summer and fall in the first year and



1. Seasonal changes in feeding activity of a captive male mallard

For Figs. 1 - 18: the horizontal curves show percent deviation from the monthly average for each hour and the curved vertical lines indicate sunrise and sunset

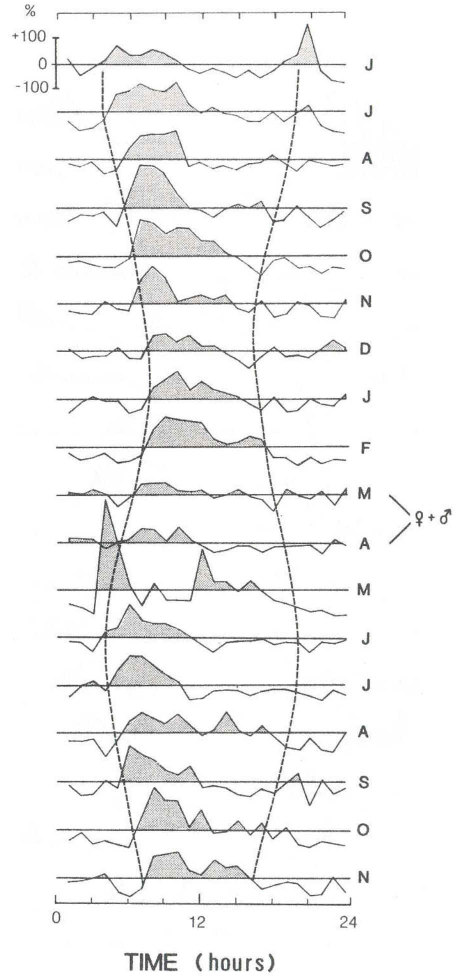
For Figs. 1 - 9: the black areas represent feeding activity higher than the monthly average threshold during the night hatched areas during the day

during fall in the second year. The daylight feeding activity during December and January was correlated with length of the photoperiod.

Night feeding activity peaked at sunset or shortly there after throughout the year. A short term rhythm appeared in January. In February and March feeding peaked at night shortly after sunset.

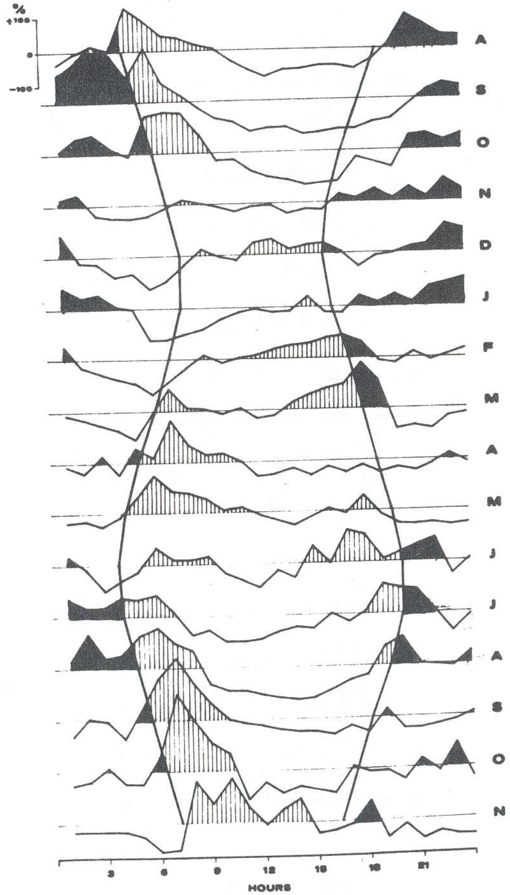
A female was placed in the pen with the male in April, May and June. The feeding rhythm during these three months did not show the typical two peak

2. Monthly feeding activity of a captive female mallard. A male mallard was placed with the female during March and April. The shift to an ultradian rhythm during these months is probably related to courtship and breeding behavior. Incubation lasted until May 31



pattern. However, daily feeding activity fluctuated near the calculated average threshold.

Feeding activity in the female crested pochard (Figs. 6 and 7) had a two peak pattern with morning and evening peaks. Regal and Connolly (1980) summarized information on social influences on circadian, ultradian and infradian rhythms, stated that mating behavior is one of the social synchronizers. Breeding behavior may have caused the bigeminus pattern of feeding to change to a short-term, ultradian rhythm.



3. Seasonal changes in feeding activity of a captive male gadwall

Tufted Duck

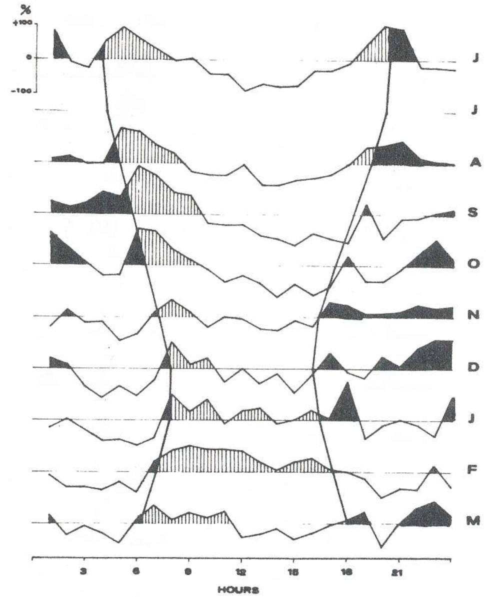
Feeding activity in tufted ducks (Figs. 8 and 9) was characterized by a ultradian rhythm with a night phase throughout most of the 16-month monitoring period. During some months peaks of feeding activity occurred near sunrise, but night peaks did not occur near sunset. Day activity occurred in August and October in the young female (Fig. 9). Morning peaks of feeding occurred only in the female during summer and fall.

VARIANCE IN FOOD INTAKE

Mallards

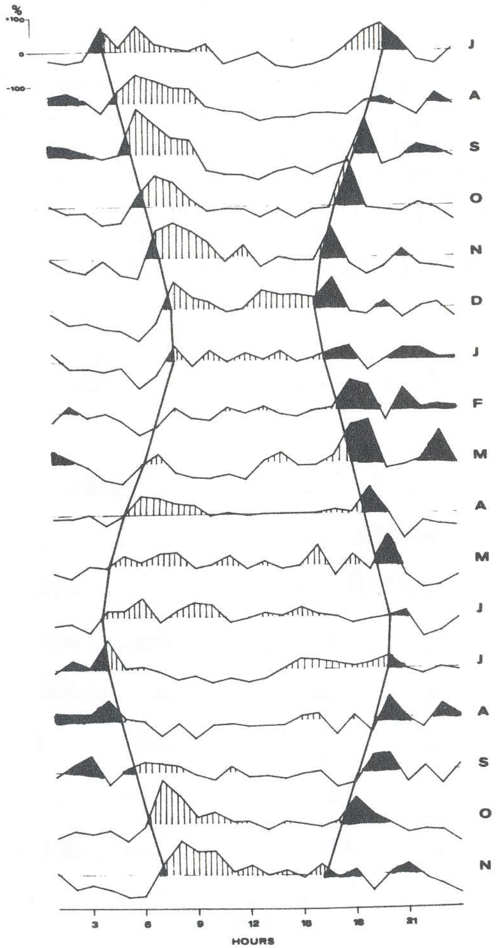
In both the male and female mallard, the lowest points on the curves (Figs. 10 and 11) indicating high regularity of food intake, occurred near sunrise and sunset, and most exhibited negative phase angles. The hen showed higher seasonal stability with the range of morning phase angle values varying from 2 to 4 hours (Fig. 11). Variation in the male varied from 1 to 6 hours (Fig. 10). From August through December during year one, the phase angle differences between the time of sunrise and the time of lowest variabi-

4. Seasonal changes in feeding activity of a captive female gadwall



lity of feeding (e.g. in late night hours) were positive for the male. Food intake variance in the evening was usually higher than in the morning and the phase relationship to sunset was variable, with values ranging up to 5 hours.

The short photoperiod in winter might have influenced regularity of food intake. The long photoperiod in summer resulted in shortening the time of regular food intake. The shift of the peak of food intake to the morning hours could be caused by a stronger synchronizing effect of sunrise compared to sunset.



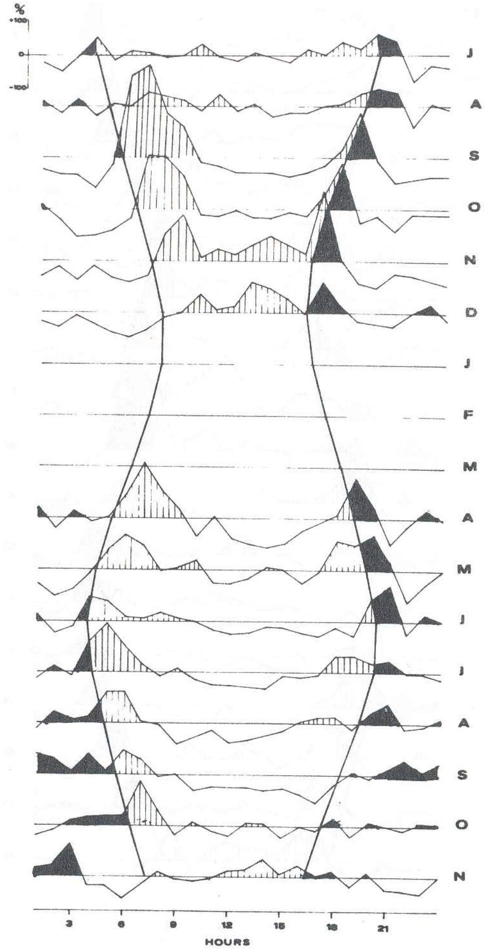
5. Seasonal changes in feeding activity of a captive male crested pochard

Gadwall

From August to January of the first year of life the gadwall male fed primarily during night hours around midnight (Fig. 12). Both the male and female (Fig. 13) showed morning feeding peaks near sunrise.

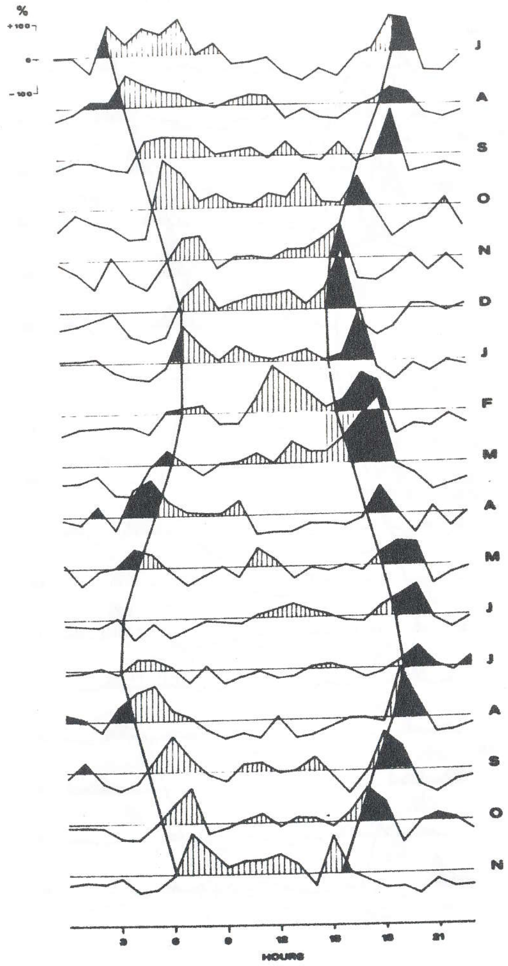
In February the feeding rhythm of the male shifted from the late night hours to the time of sunset, and remained in this phase until November. The morning phase angles had negative values. The shortest phase angle diffe-

6. Seasonal changes in feeding activity of a captive female crested pochard



rence appeared to be a function of season, with the strongest influence of the photic Zeitgeber occurring near the time of equinox in March and October (Fig. 12). The largest phase angle differences between sunrise and the times of minimum of variance were in June and July, which might correlate with the weak synchronizing effect of the Zeitgeber in summer.

Food intake by the female (Fig. 13) was synchronized by sunrise and sunset, with primarily negative phase angle differences.



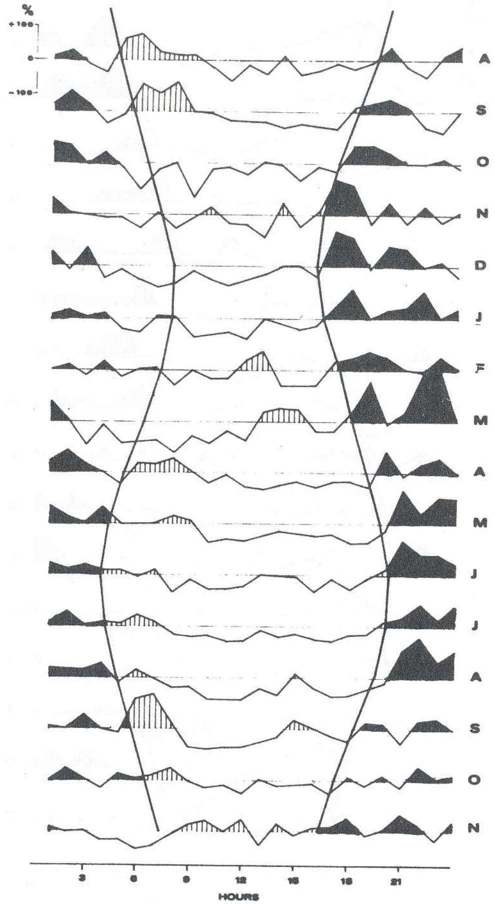
7. Seasonal changes in feeding activity of a captive female crested pochard

Crested Pochard

The minimum variance in food intake by the male (Fig. 14) occurred near sunrise and sunset, usually with a negative phase angle difference, throughout the 18-month period. Positive phase angle values occurred in June and August of the second year.

From April through June feeding activity of the male and female (Fig. 15) were measured simultaneously at the feeding box. In May and June the time of food intake correlated with length of photoperiod. After removal of the pen, feeding activity of the male was again synchronized by the photoperiod.

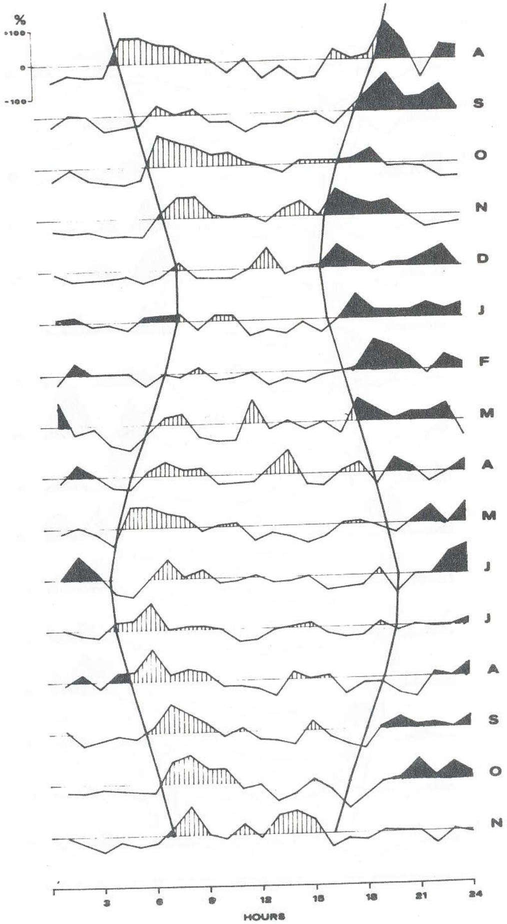
8. Seasonal changes in feeding activity of a captive male tufted duck



Similar to the male, the minimum variances in food intake in both females (Figs. 15 and 16) were near sunrise and sunset throughout the year. An additional minimum variance in food intake occurred about noon (open circles in Figs. 15 and 16), but showed no definite regularity.

Tufted duck

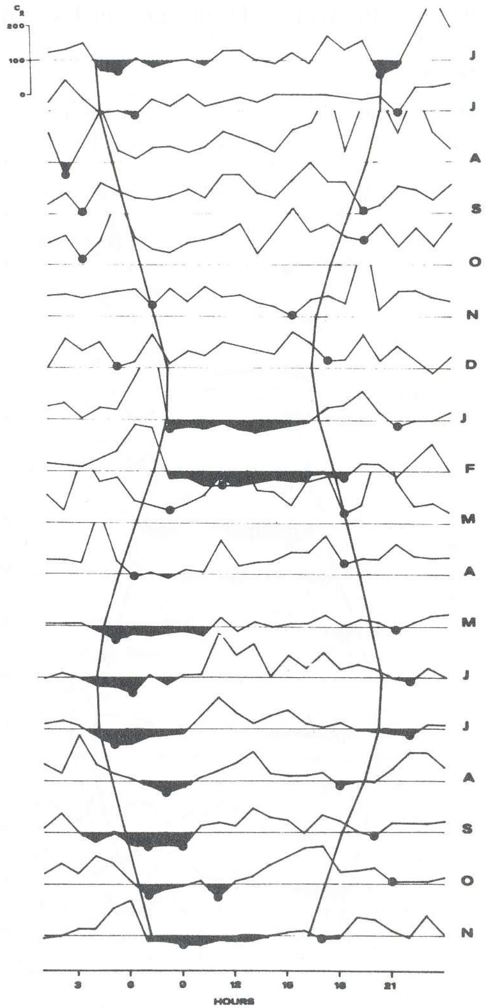
Daily variation in food intake in tufted ducks exhibited both daylight minimum values (black dots) and night minimum values (open circles) in



9. Seasonal changes in feeding activity of a captive female tufted duck

both the male (Fig. 17) and female (Fig. 18). The time if the lowest variance in food consumption corresponded generally with the peaks of the ultradian activity pattern. Tufted ducks showed less evidence of a synchronizing effect of photoperiod than the other species.

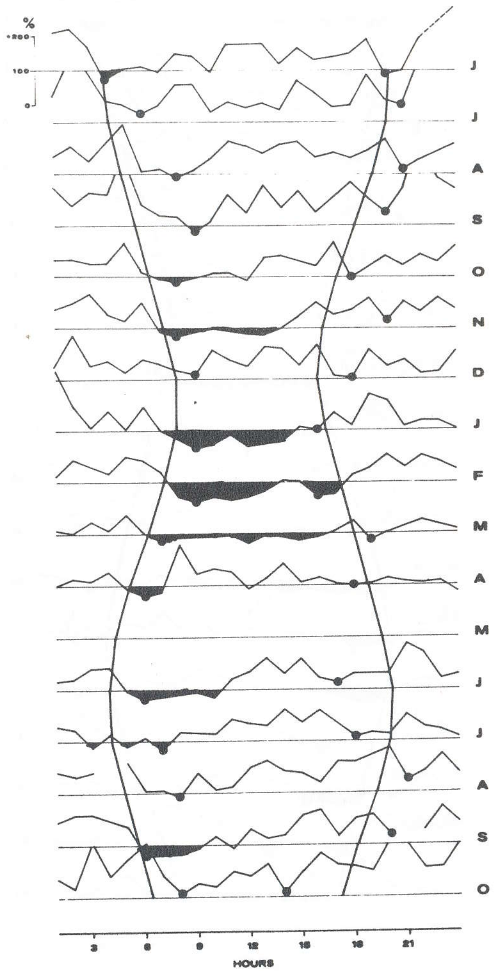
10. Monthly variability of daily food intake in a male mallard. Black dots near sunrise and sunset indicate times of high regularity of feeding



AMOUNT OF FEEDING ACTIVITY AS A FUNCTION OF THE SEASON

Mallards

The amount of foraging activity by both male and female mallards (Fig. 19) decreased in August and September. Food consumption increased in subsequent months peaking in December for the female and in February for the male. At that time the feeding frequency of the female was twice as high as in the male. The increase in food intake by the female in April is



11. Monthly variability of daily food intake in a female mallard. Black dots near sunrise and sunset indicate times of high regularity of feeding

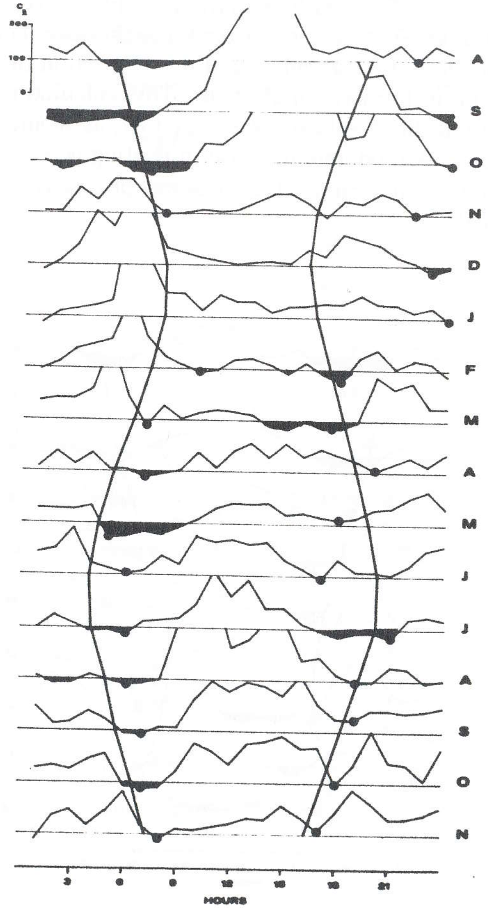
closely related to the higher ovarian activity preceding the laying period. Incubation activity dramatically reduced feeding by the female.

A low level of food intake was observed in the male during March and April. Food intake increased in May. In subsequent months food intake varied, but showed a tendency to decrease.

Gadwall

Seasonal change in the amount of food intake by gadwalls (Fig. 20) showed a gradual increase from September through December in the male and

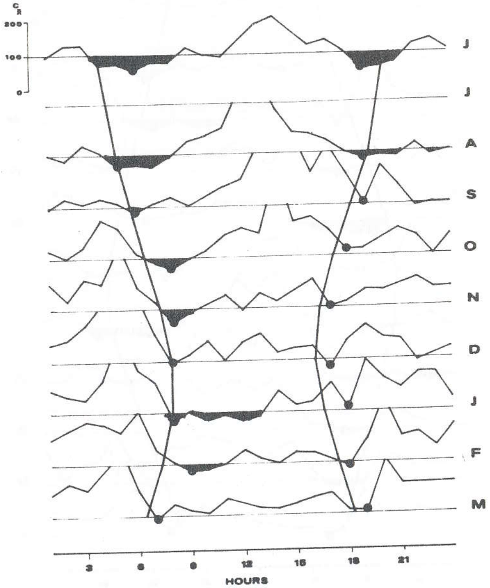
12. Monthly variability of daily food intake in a male gadwall. Black dots near sunrise and sunset indicate times of high regularity of feeding



from July through February in the female. The rapid decrease in food consumption in the female in February and March could be related to the factor which caused her death in April. The increase in food consumption by the male in July is similar to the increase observed in the mallard drake.

Crested Pochard

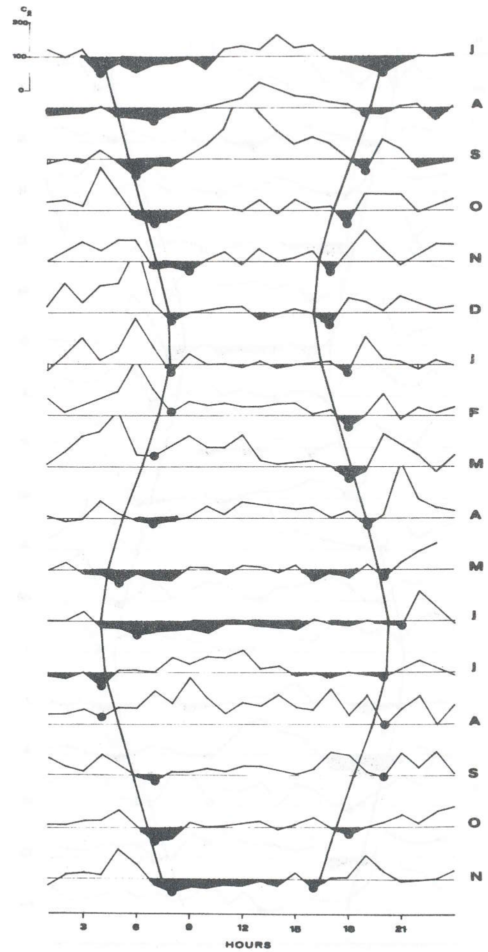
Seasonal changes in the number of total visits to the feeding box in both crested pochard females were characterized by low values during fall (Fig. 21), by increases from April through June (resp. July), and then by decreases. The yearly pattern of feeding activity in the crested pochard drake did not show a clear seasonal amplitude. Feeding activity of the male from April to June was calculated by subtraction of the increased amount of food intake in the two single hens. This calculation suggests that the number of visits to the food box was very low, as would be expected at this season in drakes. A moderate increase in feeding activity by the drake occurred during summer and early fall. This increase was less than that observed in the females.



13. Monthly variability of daily food intake in a female gadwall. Black dots near sunrise and sunset indicate times of high regularity of feeding

Tufted Duck

Seasonal changes in food consumption in tufted ducks shown by the number of visits to the food box show sexual differences (Fig. 22). A rapid decrease in food consumption was recorded in the young male in August and September. A continuous decrease of the amount of feeding activity was observed in the female from December through March. Both the male and



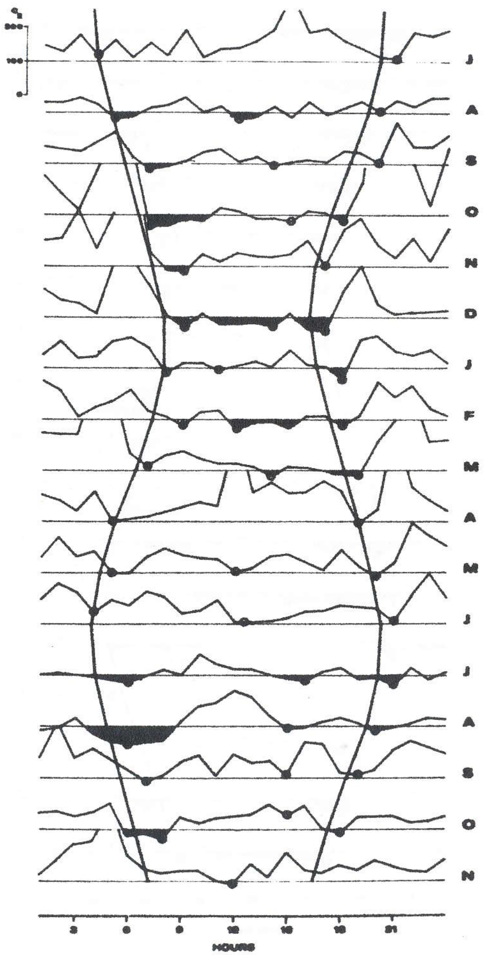
14. Monthly variability of daily food intake in a male crested pochard. Black dots near sunrise and sunset indicate times of high regularity of feeding

female increased their food intake slowly until they reached the high seasonal peak in October.

DISCUSSION

FEEDING RHYTHM IN DUCKS

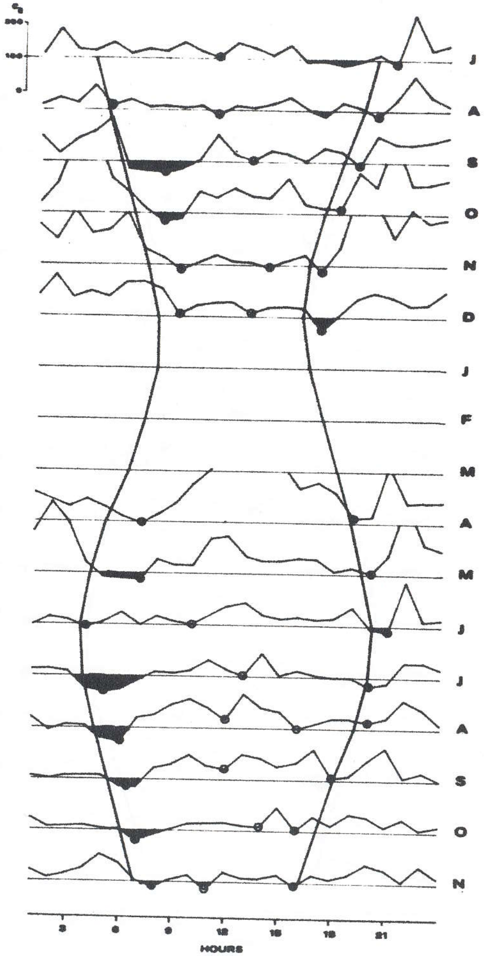
Feeding activity in free-ranging ducks has usually been recorded as a part of time-defined periods. These have included resting time and the manner of



15. Monthly variability of daily food intake in a female crested pochard. Black dots near sunrise and sunset indicate times of high regularity of feeding

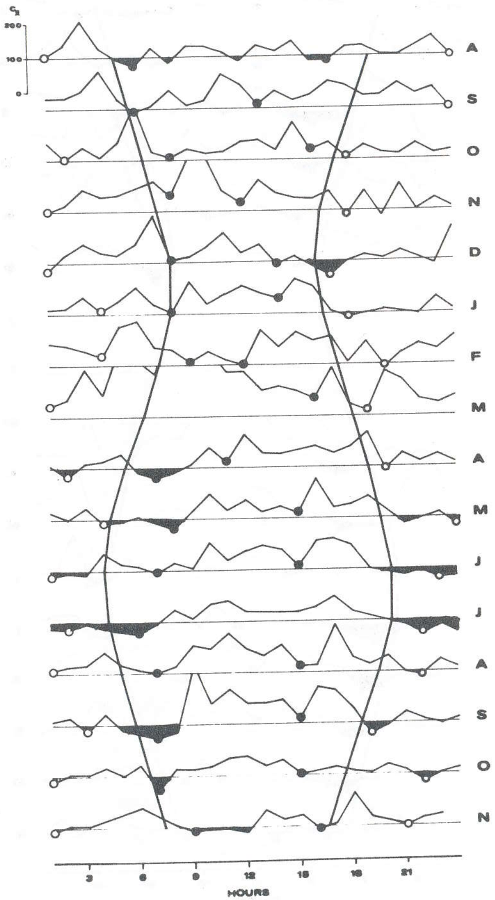
resting, locomotion in the territory, social and sexual interactions, comfort behavior, and other ethological displays. Such information has been obtained primarily during daylight and from only selected portions of the annual biological cycle. It is clear that different authors bring divergent information from different geographical areas.

Feeding activity in ducks is often described as being arrhythmic and independent of cyclic exogenous factors. K l í m a (1966) did not report diffe-



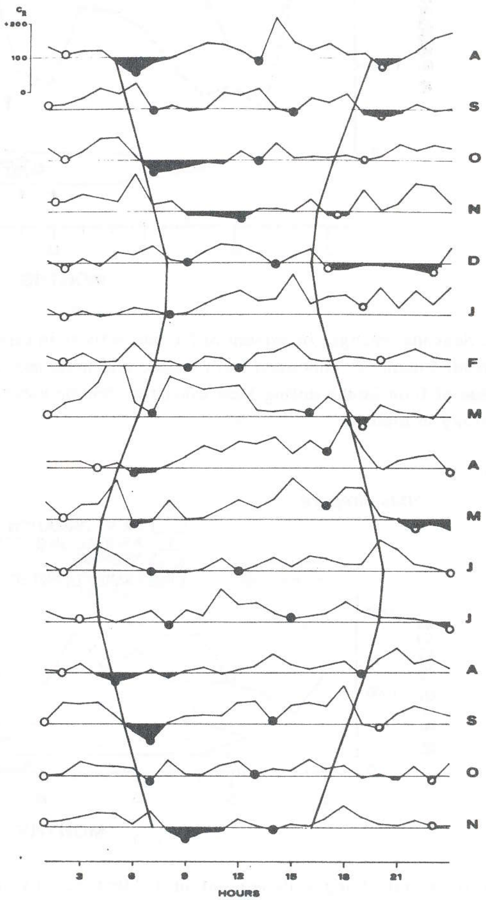
16. Monthly variability of daily food intake in a female crested pochard. Black dots near sunrise and sunset indicate times of high regularity of feeding

rences between day activity and night activity in the crested pochard. Polyphasic or ultradian rhythms have also been reported (for example R a i t a - s u o , 1964). D a a n (1981) reviewed feeding activity in diving ducks, Genus *Aythya* and related species, which find food at the bottom of lakes and marshes. He suggested this feeding behavior as a reason for night phase activity. On the other hand, F o l k (1971) and S i e g f r i e d (1974) described feeding activity of *Aythya fuligula* and *A. affinis* during daylight. T a m i s i e r (1972) stated that feeding activity in green-winged teal, (*Anas crecca*) occurred mostly at night during September. Tamisier showed an



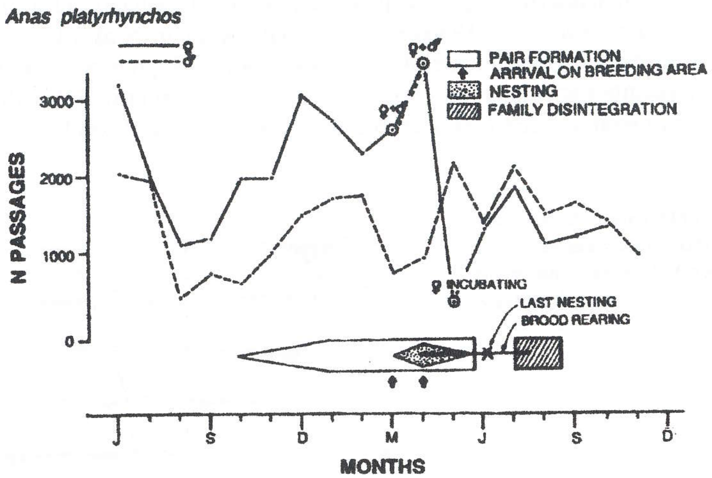
17. Monthly variability of daily food intake in a male tufted duck. Black dots near sunrise and sunset indicate times of high regularity of feeding

influence of short photoperiod and low ambient temperature, especially in February and March, when the ducks were feeding during the day. Nevertheless, in the next publication, T a m i s i e r (1978-1979) described a major night phase of feeding activity in green-wing teal from September through March in their wintering area in Camarque. On the other hand, Q u i n l a n and B a l d a s s a r r e (1984) reported that the main peak of feeding in green-wing teal in Texas occurred in late afternoon in September and October and in December and January. H o l z i n g e r (1977) reported that the peak feeding in green-winded teal occurred between 8:00 and 19:00 hours.

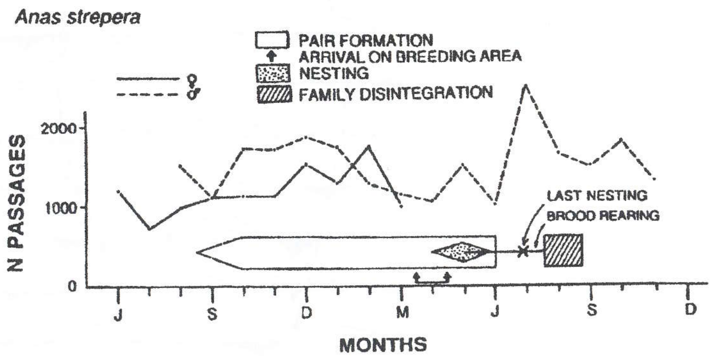


18. Monthly variability of daily food intake in a female tufted duck. Black dots near sunrise and sunset indicate times of high regularity of feeding

This short review indicates the complexity of existing data and reveals the difficulties of comparing our data from captivity to results obtained from free-ranging ducks.



19. Seasonal changes in amount of feeding activity in captive mallards. During March and April recorded data were obtained from female and male consumed food at the same resource. Low value of food intake during May caused by female incubating eggs. Legend indicates common biology in mallard

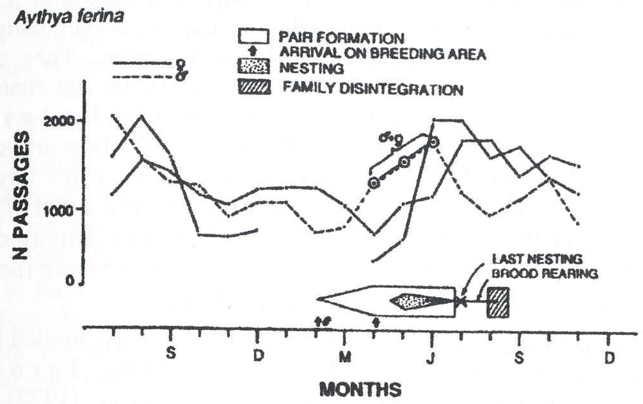


20. Seasonal changes in amount of feeding activity in captive gadwall. Legend indicates common biology in gadwall

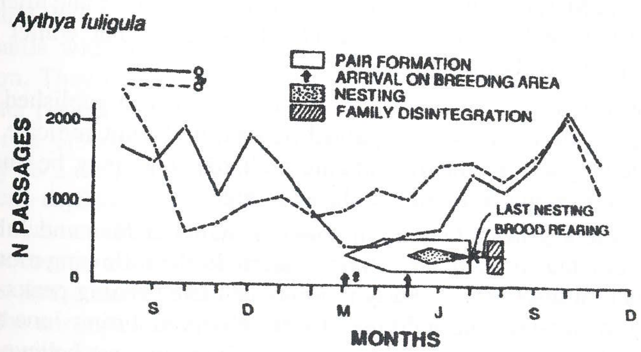
RHYTHM OF FORAGING ACTIVITY

Mallard

Feed activity in both the drake and hen mallard appeared synchronized with sunrise, with the peak of feeding following sunrise. The rhythm of



21. Seasonal changes in amount of feeding activity in captive crested pochard. During April, May and June recorded data were obtained from female and male consumed food at the same resource. Low value of food intake during May caused by female incubating eggs. Legend indicates common biology in pochard



22. Seasonal changes in amount of feeding activity in captive tufted duck. Legend indicates common biology in tufted duck

feeding activity in the hen had a day phase throughout the 18-month monitoring period. The drake also had a day phase of feeding activity, especially in the second year. During fall (October - November) of the first year, we also observed a night phase of feeding which was slightly higher then the day phase, especially in October.

Many of the observations of feeding activity in free-ranging ducks have been made on wintering areas or during nesting. Raitasuo (1964) discussed a polyphasic rhythm of feeding activity. Bauer and Glutz von Blotzheim (1969) reported that feeding occurred mostly during night hours, but also in the period shortly after sunrise. They consider mallards to be a species with high plasticity whose rhythm can change with different phases of the reproductive season. Similarly, Holzinger (1977) confirmed a time shift of duck flights from feeding areas in late afternoon. He observed three peaks of foraging activity in the day during September and October. Mallards kept in captivity (Winner, 1972) under the light cycle LD 10:14 had a morning peak of locomotor activity one hour before the time of light on; and an evening peak one hour before the time of light off. Winner described this rhythm as bigeminus.

Evening mallard flights from lakes for feeding have been studied by several authors. Bossenmeier, Marshall (1958), Jorde et al. (1983, 1984), Swanson (1977), Swanson et al. (1972), Sargeant (1976), Titman (1981), Winter (1959) and Wright (1959) agree that these flights occur primarily in daylight conditions, and that they may be initiated by light intensity. Timing of this evening flight has a negative phase angle difference with sunset. Baldassarre and Bolen (1984) observed two main peaks of mallard feeding flights between September and March, with the flights occurring near sunrise and after sunset. Willi (1970) and Jorde et al. (1984) believed that winter feeding flights occurred mostly during daylight.

Our data from captive mallards correspond in part with published data on free-ranging mallards. However, published reports do not indicate a night phase of feeding activity in free-ranging mallards. This may be due to the difficulty of observing free-ranging ducks at night.

The high night peak of feeding in young mallards in June and July (Figs. 21 and 22), created an alternans activity pattern. In the following months, the alternans pattern disappeared. Early morning and late evening peaks of feeding activity in two-year old wild ducks were observed during June and July by Ringelmann and Flake (1980). Therefore, we believe that the alternans pattern of activity with a high evening peak could be a function of age in mallards.

Gadwall

Gadwall fed more during night than mallards. The daylight phase of feeding exhibited a morning peak synchronized by sunrise. The phase angle difference was nearly constant except in winter, similar to mallards.

Paulus (1984) reported on feeding activity of free-ranging gadwall from October to April. His results showed that over 60 percent of feeding occurred at night. Paulus believed that a decrease in food intake was correlated with an increased ambient temperature. From October to April, the time used for feeding increased from 44 percent to 77 percent. These results correspond in general with our data on captive gadwalls.

Crested Pochard

Rhythmicity in the feeding activity of crested pochards was synchronized by sunrise and sunset, with negative phase angle differences. Direct observations of free-ranging pochards (Bauer, Glutz von Blotzheim, 1969) during winter indicated the beginning of the night phase of feeding in the first half of night. The early morning peak occurred a short time before dawn. Similar results were published by Galhoff et al. (1984) for the winter period. Daily onsets of feeding flight activity were correlated with outside light intensity, which was lower than 1 lux.

Holzinger (1977) discussed the low daylight feeding activity in crested pochards between 6:00 a.m. and 19:00 and 14:00 p.m. during September and October. The first peak occurred between 12:00 and 14:00 and the evening peak was observed between 15:00 and 19:00 p.m. (next high point in 17:00 - 18:00 hours).

Unfortunately the night phase of this rhythm was not recorded. Suter (1982) and Willi (1970) correlated the daylight phase of foraging rhythm in pochards with food availability, plumage molting, low temperatures or migration. They considered this species as primarily active at night during the winter period.

Klíma (1966) observed short intervals of feeding during the nesting season. Similarly Bauer and Glutz von Blotzheim (1969) reported a short term rhythm during March. They also observed high activity during the day, with the minimum between 12:00 - 14:00 p.m., and some night foraging activity.

We recorded similar ultradian rhythms of feeding activity in captive mallards and crested pochards. This type of rhythm probably occurs only during the nesting period, and it is probably initiated by courtship.

In general, all ot the observations made in free-ranging crested pochards support with our results obtained by continuously recording feeding in captive birds.

Tufted Duck

Little is known about feeding activity in free-ranging tufted ducks. Folk (1971) reported that food intake was highest during daylight in summer. Similarly Willi (1970) believed that tufted ducks were day active with a bigeminus pattern. A night period of feeding was observed in October at the time of migration. Holzinger (1977) reported low feeding activity during daylight in September and October. However, this author did not study feeding activity during the night. Therefore, it is possible that free-ranging tufted ducks commonly feed at night.

FEEDING RHYTHM DURING INCUBATION

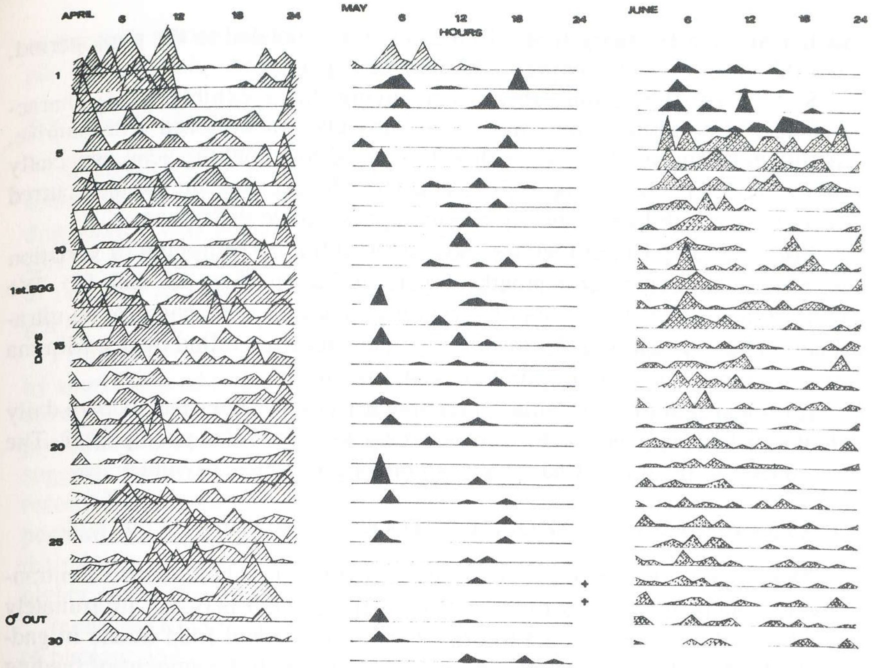
Incubation by a hen mallard began May 1, after the sixth egg was laid. The time when hen began continuous incubation was not observed; however, feeding activity stopped shortly after noon (Fig. 23). The next day the feeding rhythm changed abruptly, and the night phase of feeding disappeared. This typical bigeminus pattern lasted through the incubation period. The eggs were not fertile and the female abandoned the eggs spontaneously on June 5th, after 35 days, instead of the usual 26 days of incubation. During the 35th day the daytime feeding frequency increased. After three days the feeding rhythm shifted slowly into the night phase and became unimodal.

A reduction in feeding by wild nesting mallards was calculated by Caldwell and Cornwall (1975). They reported 78 minutes of feeding per day which represents 33.5 hours for the incubation period of 26 days. On the other hand, Afton (1979) calculated that female mallards required 23 hours of feeding during incubation. Reduction of food intake cause body weight loss in incubating hens, as reported by Folk et al. (1966), Young (1977) and others.

Direct observations on mallard hens in the wild showed that females usually left the nest twice a day during the morning and evening twilight (Winner, 1972; Krapu, 1974 in pintails).

Our continuous recording of feeding activity confirms the morning peak of feeding but the second peak occurred shortly after noon rather than in the evening. The incubating hen left her nest about three times per day.

The incubation period, usually 26 days, was prolonged to 35 days because the eggs were not fertile. Prolonged incubation has also been observed in mallards (49 days), pintails (48, 60, and 62 days) and shovelled (42 and 45 days) by Sowls (1955). It may be that incubation behavior, part of the endogenous biological oscillation of the organism, which is programmed to expire several days after embryonic development is normally completed (hour-glass-clock?). An alternative hypothesis might invoke body weight



23. Daily rhythm of feeding activity in captive mallards during the reproductive season. Male and female food intake was measured silmutaneously at the same feeding box during April. The first egg was laid on April 12, and the male was removed from the pen on April 29. Black areas represent feeding activity of the female during incubation, shaded areas indicate feeding activity following incubation. Days of expected hatching of the clutch are marked by +

loss, which could stimulate metabolic pressure to begin feeding to obtain energy. We do not have sufficient data to confirm either of these hypotheses.

SEASONAL CHANGES IN THE VARIATION OF FEEDING

Using the coefficient of variation, we analyzed variation in time of feeding during the 24 hour cycle for each month of the year in all species. In the dabbling ducks the minimum variation occurred after sunrise in most months (Figs. 10, 11, 12 and 13), with a negative phase angle difference (except in August - October and December in the mallard drake). The second lowest variation occurred near sunset with larger negative phase angle differences. Shortening of the photoperiod in winter resulted in changes in the time of regularity of feeding. The period of low variation in male and female mallard in January and February (Figs. 10 and 11) corresponded to the photoperiod, and the morning and evening minimums disappeared.

Stability of the feeding rhythms in diving ducks exhibited two characteristics. The morning minimums were strongly synchronized with sunrise, as shown by the small phase angle difference throughout the year, especially in the crested pochard (Figs. 14, 15 and 16). The evening minimum occurred near sunset, with larger, mostly negative phase angle differences.

Both crested pochard females showed an additional minimum of variation near noon during several months (open circles on Figs. 15 and 16). We believe that this daily rhythm of variability indicates a tendency for an ultradian rhythm, which is best illustrated by the data from tufted ducks. Minima of variation occurred during both day and night.

It is clear that the variability in feeding activity in ducks has its own daily rhythm which appears to be correlated by length of the photoperiod. The variability in feeding tufted ducks exhibits a polyphasic rhythm.

SEASONAL CYCLES IN AMOUNT OF FOOD CONSUMED

The amount of food intake was represented by the total number of entrances into the feeding boxes for each hour of the 24 hour period. Unfortunately we do not have enough data to draw conclusions about food intake in gadwalls. In the other species, we observed a decrease in the amount of feeding activity during summer and early fall. An increase was observed during the time of pair formation (mallard - Fig. 19, crested pochard - Fig. 21, and tufted duck - Fig. 22). This increase occurred in both mallard and crested pochard females during or shortly before the nesting period.

Many publications report increases in food intake before and during the nesting period in female ducks. A f t o n (1979) reported doubling of feeding activity in shoveller (*Spatula clypeata*) females, D e r r i c k s o n (1978) observed higher feeding activity of pintail (*Anas acuta*) females during nesting, D w y e r et al. (1979) concluded that differences in the amount of food intake by male and female mallards reflected their different roles during the nesting period, and K r a p u (1981) believed that the higher level of feeding activity in mallard hens was necessary for the production of lipids required for egg formation. In the lesser scaup, R o g e r s and K o r - s c h e g e n (1966) reported the lowest level of feeding activity during early spring. The same phenomena was found in our diving ducks during winter. T i t m a n (1981) also observed sexual differences in feeding in mallards. At the beginning of the breading season females foraged longer than males. Our measurements of the amount of feeding activity in ducks in captivity correspond closely with these observations on free-ranging ducks. Changes

in the total amount of food intake as a function of season seems to be primarily controlled by length of photoperiod.

SOCIAL INFLUENCES

An overview of social influences as synchronizers of rhythms was presented by R e g a l and C o n n o l l y (1980). Synchronization of ultradian rhythms by social interactions has been reported for several vertebrate species. Ultradian rhythms have not been studied with respect to how changes in „resting and activity" may resynchronize physiological activities (R e - g a l , C o n n o l l y , 1980).

Feeding rhythms in paired mallards and crested pochards are characterized by short shifts of phase during the daily period. We believe that changes from circadian to ultradian activity may be caused by presence of the male. Female pochards did not exhibit this change of circadian to ultradian rhythm, which suggests that the changes shown by pairs were related to courtship. We also recorded an increase in total amount of feeding activity in an isolated female pochard. S i e g f r i e d (1974) also mentioned that lesser scaup increased their feeding activity after pair formation. The number of diving periods was higher and a change in the phase of the rhythm observed.

Increased food intake by females is probably related to the effect of length of photoperiod on ovarian growth and a increase in energy required for egg production.

THE TIME NICHE AND EXPLOITATION COMPETITION

Time exploitation of the area containing the food resources requires information on phases of rhythms of activity in consumers and on the availability of food resources. A well known example would be the interaction of predator and prey. Further knowledge is needed on the synchrony in activity patterns in predators and their prey, or in a more general context, between consumers and producers. The distribution and occupation of the time niche is a very complicated process, which requires knowledge about the rhythms of activity (locomotor rhythm, feeding rhythm, etc.) in the different periods: daily, seasonal, annual, etc. The first requirement would be determination of daily activity parameters of animals in captivity. Activity data from free-ranging animals of the same species should also be collected to provide information on the effect of exogenous factors.

Many duck species are sympatric in the temperate and arctic zone. A complex type of sympatry exists in nesting territories and in wintering areas (B r a n d l , S c h m i d k e , 1983). From the point of exploitation competition, localization of the food resources in shallow water for dabbling ducks and in deeper water for diving ducks allows for similar phases of circadian rhythms. Although feeding may occur at the same time in both groups, they are spatially reported.

During summer dabbling ducks have a morning peak of feeding activity with almost constant C value. The peak of feeding activity has the same phase angle difference with sunrise throughout the year. S w a n s o n (1977) reported that both immature and adult dabbling ducks consume 98% invertebrates. Between sunset and midnight they ate mostly adult insects (89%), but during the day they consumed mostly *Cladocera* and immature *Diptera* (93%). Similar observations were made by C e r n o v (1962). During warm summer nights, the *Cladocera* move to the surface due to the low concentration of oxygen in the water. Following the increase of oxygen in the water after sunrise, the *Cladocera* migrate back to deeper water levels. Dead plankton which accumulate in the littoral zone provide a valuable food resource for dabbling ducks.

This remarkable cycle of food availability supports the hypotheses that feeding rhythms may be adapted to cyclic food abundance. The rhythm of feeding activity in our ducks in captivity should be considered in evaluated the feeding activity described by S w a n s o n (1977). Food quantity and quality were constant throughout the 18-month period. Therefore the feeding rhythms in captivity were very likely regulated by an endogenous clock. From S w a n s o n 's (1977) findings, we concluded that the endogenous feeding rhythm must be influenced or over-ridden by the exogenous factor of cyclic food availability.

T h o m a s (1982) observed much overlap in territories by mallards and pintails in England. In our temperate zone conditions, the gadwall is probably comparable to the pintail. Rhythms of feeding activity of mallards and gadwalls had morning peaks at almost the same time of day. Gadwall, however, also had a night phase of feeding.

U t s c h i c k (1980) monitored feeding rhythms of free-ranging ducks in Germany. He observed morning peaks of activity similar to those in our captive mallards, crested pochards and gadwalls.

According to T h o m a s (1982) most species of diving ducks use the same feeding or exploitation niche. On the other hand, B r a n d l and S c h m i d k e (1983) stated that competition did not occur between crested pochards and tufted ducks because of their different ecological needs. Crested pochards occupied Bavarian ponds in high altitudes, whereas tufted ducks nested on lakes and ponds at lower altitudes. Further, it is known that crested pochards seem to prefer communities with higher numbers of bird species, whereas tufted ducks seem to be more solitary. This could lead to decreased competition between these two species. P i a n k a (1980) explains this type of competition as a mechanism which forms communities and which is caused by several species exploitating the same (food) resources. Therefore, conditions exist for interspecific competition.

In contrast to crested pochards, which are well integrated into the main community of a given area, tufted ducks exhibit intraspecific competition, indicating that this species is not yet fully integrated in established central European communities. Also, the feeding strategies of crested pochards and tufted ducks are different. Crested pochards feed mainly in the transition zone between the littoral zone and deeper areas (T h o m a s , 1982), whereas tufted ducks feed primarily in deep water.

Deep lakes provide the possibility of space zonation of different duck species in relation to water depth (S z i j j , 1965). This may push tufted ducks into areas with a lower density of waterfowl species, such as small lakes with intensive fish farming (B r a n d , S c h m i d t k e , 1983). One of the basic concepts of successful establishment of a species in new geographic areas is the flexibility and adaptability of the species. A second condition for successful establishment is related to the time of feeding. The fact that tufted ducks have a night phase of the feeding rhythm may enable them to compete by using the time niche which is not occupied by their main competitor, the crested pochard. The high level of adaptability of tufted ducks has enabled them to begin to fit into the waterfowl community of central Europe in the past 50 years.

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Sezónní variabilita rytmu příjmu potravy u čtyř druhů kachen.

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Analýza informací o příjmu potravy čtyř druhů našich divokých kachen (kachna březňačka *Anas platyrhynchos*, kopřivka obecná *Anas strepera*, polák velký *Aythya ferina* a polák chocholatý *Aythya fuligula*), zaznamenaných kontinuálně v zajetí po dobu okolo 18 měsíců, poskytuje přehled o rytmicitě této fyziologické činnosti. I když se u žádného ze zkoumaných druhů neobjevuje výrazné období klidu příjmu potravy během 24hodinové periody, přesto je patrný rytmický průběh potravní aktivity, který má tvar buď unimodální (kachna březňačka), nebo bimodální s převahou typu bigeminus (kopřivka obecná, polák velký, polák chocholatý). Rytmus je řízen délkou fotoperiody a zaujímá k době východu a západu slunce většinou negativní fázový úhel, který je druhově specifický, a to po celou dobu roku.

Kachna březňačka má převahu denní fáze příjmu potravy, kopřivka obecná má vyšší podíl noční fáze potravního rytmu. Rytmus potravní aktivity poláka velkého má převážně denní, ale zčásti i večerní fázi s negativními rozdíly fázových úhlů. Polák

chocholatý má vyšší podíl noční fáze rytmu aktivity, a to v průběhu celého roku. Podle cirkadiánní fáze potravního rytmu nedochází k podstatné interferenci u kachny březňačky a kopřivky a zejména u poláka velkého a chocholatého, u kterých je využití rozdílných časových nik daleko patrnější. Tato rozdílnost přispívá k osvětlení otázky úspěšného trvalého usídlení poláka chocholatého v prostředí střední Evropy, především v interspecifických rozdílech exploatační kompetice mezi oběma uvedenými druhy.

Také variabilita příjmu potravy kachen potvrzuje synchronizaci s východem a západem slunce s negativním rozdílem fázových úhlů začátku i konce doby příjmu potravy. Cirkadiánní krokovače ukazují vysokou senzibilitu ke světelné intenzitě s rozdílnými hodnotami v ranních a večerních hodinách.

Cirkanuální změny v množství aktivity kachen jsou charakterizovány poklesem na konci letního období a v začátku podzimu a naopak jeho zvýšením v období tvorby párů. Tento mechanismus je řízen délkou fotoperiody odpovídající příslušnému ročnímu období, je s největší pravděpodobností endogenně fixován a stimuluje patrně stanovení optimálního potravního režimu během dne.

Bioscilační mechanismus může být pozvolna nebo náhle korigován kromě exogenních abiotických faktorů i faktory biotickými. Změna typu aktivity a náhlý posun fáze rytmu inicializovaný inkubací kachny březňačky změnil potravní rytmus z unimodálního na typ bigeminus s denní fází, přičemž noční fáze potravního rytmu v tomto období zcela zanikla. Výrazně se projevil synchronizující účinek doby východu slunce na vrchol potravní aktivity s nulovou hodnotou rozdílu fázového úhlu. Tento „inkubační oscilátor" pracuje systémem přesýpacích hodin, jejichž program přesahuje délku obvyklé inkubační periody (v případě hnízdící březňačky o 35 %) jako biologicky významnou časovou rezervu. Po odeznění této funkce dochází k náhlému přechodu do původního stavu potravního rytmu charakterizovaného unimodálním rytmem a noční fází.

kachny plovací; kachny potápivé; potravní rytmus; typ aktivity; sezónní cyklus; spotřeba potravy; cirkadiánní a ultradiánní rytmus

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