

DIFFERENTIAL INTENSITY OF MOORHEN (*GALLINULA CHLOROPUS* (RALLIDAE) FEEDING AT DAWN AND DUSK IN SPRING

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SUMMARY: Feeding intensity of moorhens (*Gallinula chloropus*) in Scotland is indexed by combining frequency of feeding activities with rates of pecking measured on three substrates. Scottish moorhens peck fastest on a grass/herb sward and slowest on water, with mud intermediate. The foraging pattern over spring, with a March peak, is influenced more by changes in pecking rates than by frequency of feeding activities. Because frequency of feeding and rates of pecking are both higher before sunset than after sunrise the hypothesis of equal feeding intensity at dawn and dusk is discarded. Factors possibly contributing to this result are: reduced energy expenditure at night; diurnal variation in the proportion of time taken up by other, especially social, activities; regulation of bodily heat losses; and diurnal variation in availability of invertebrates and in concentrations of nutrients in plants.

INTRODUCTION

Time and energy spent by a bird searching for food during the day relate to bodily mass and surface area, required diet, and the structure of the community to which the bird belongs. Growth, and natural constraints such as weather, diurnal period, and changing season, modify availability of dietary components and the birds' pattern of activity, bringing shifts in the amount of time and energy allocated to bodily care, reproduction, feeding, and so on. In the Rallidae, which includes a range of herbivorous and omnivorous species, diurnal patterns of foraging, shaped by diet and modified by season, could comprise:

- (a) continuous even effort during the day;
- (b) one or more periods of concentrated feeding superimposed on more or less continuous low-intensity feeding;
- (c) one or more periods of concentrated feeding with no significant feeding in between.

Published information on diurnal changes in the intensity of feeding in rails is, however, scarce. In the large flightless takahe (*Notornis mantelli*, preliminary data (Mills, 1973) indicate that feeding may occupy over 90% of the day (over 21 hours) with a fairly constant rate of feeding throughout. In the smaller, flighted, pukeko (*Porphyrio p. melanotus*), examination of stomach contents and direct observation suggest that peaks of feeding occur. Contents

of stomachs collected at three periods—sunrise plus three hours; about midday; and during the three hours before sunset—declined in quantity over the day (Carroll, 1966), suggesting that pukekos forage most in the morning and least in late afternoon. The early morning specimens were, however, shot mostly in summer, midday ones through the year, and late afternoon birds mostly in winter and spring, so the data were probably affected by unequal sampling. Craig (1974) considered that there were two major feeding times for pukekos, in the early morning and late afternoon; but pilot analyses of activity frequencies and pecking rates (J. D. Wright, *pers. comm.*) suggest that in autumn pukekos feed more or less continuously between dawn and dusk, but with greatest intensity in the afternoon rather than the morning. A parallel to this may possibly be found in Tasmanian native hens (*Tribonyx mortierii*) which emerge late on cold winter mornings (Ridpath, 1972) thus suggesting the need for a "warming-up" period. The omnivorous weka (*Gallirallus australis*) is said to become more active at dusk (Falla *et al.*, 1966) while A. Anderson (*pers. comm.*) observed that in Scotland in 1963 the moorhen (*Gallinula chloropus*) fed almost continuously during daylight in winter and early March, but in summer fed intensively in the morning, and only sporadically thereafter. For the same species in Florida, Bent (1926) noted peaks of calling in early morning and late afternoon, and almost no calling at night. Calling, however, does not necessarily indicate active foraging.

Available evidence, therefore, suggests that in some rails foraging increases periodically during the day, often near the start or finish of daylight, but is relatively more intense at one or other of these times, i.e., the birds feed more vigorously at one end of the day than they do at the other. Since dawn and dusk bracket the dark hours when foraging may diminish in frequency or cease, birds could stock up with heavy feeding at dusk and/or refill empty stomachs with heavy feeding at dawn. Whichever situation obtains, both external causes and the bird's own physiological mechanisms merit examination. Increased feeding could, for instance, be linked directly to food availability. Preferred invertebrates, for example, may fluctuate in abundance during the day, and the attractiveness of different plants, or parts of plants, may alter diurnally according to changes in the location and concentration of metabolites and complex compounds. In short, rails may feed intensely when it is most profitable.

In New Zealand, ongoing work on the takahe (*J. Mills, pers. comm.*) and pukeko (Fordham and Wright, unpublished data) centres on food and foraging patterns because these reflect habitat requirements. At this early stage in knowledge of rallid feeding ecology it is important to compare a variety of species. For this reason, the moorhen was examined briefly during a visit to Scotland. Attention focused on the two-hour periods after sunrise and before sunset, because these times involved marked changes in light intensity and appeared likely to be important feeding times.

The moorhen inhabits a wide range of freshwater habitats (Voous, 1960) but also moves into cultivated or other land in bordering zones. For instance, Anderson (1965) found in winter that birds would feed in stubble fields and pasture more than 1 km from their breeding territories. Apart from brief mention of food items by Bonhote (1907), Bent (1926), Witherby *et al.* (1938-41), Howard (1940),

Voous (1960), and Wood (1974), which indicate omnivory involving a wide selection of vegetative, seed, and fruit material from aquatic and land plants, and numerous small invertebrates, there are no data on feeding in relation to other features of moorhen life. Activity categories can, however, be recognised from Wood's (1974) behavioural descriptions.

The present paper discusses feeding intensity of adult moorhens in late winter and spring 1975 indexed by scoring activity frequencies, and combining the frequency of feeding with the rate at which birds pecked. The hypothesis of no difference in feeding intensity after sunrise and before sunset was tested. Food eaten was not measured.

STUDY AREA

Observations were made at Culterty Field Station (Lat. 57° 20' N) owned by the University of Aberdeen in Newburgh, Aberdeenshire, Scotland, where a small breeding population of moorhens, described by Anderson (1965), was present all year on two ponds. Natural inward drainage and use of a sill varied the area of water and exposed pond floor periodically. Pond margins carried a mixed sward of plants flattened by the grazing, trampling and resting of numerous waterfowl. In winter the most common sward species were visually assessed to be *Plantago lanceolata*, *Potentilla anserina*, *Matricaria inodora*, *Sagina procumbens*, *Agrostis stolonifera*, and *Festuca rubra*. By late spring the sward was enriched by *Poa annua*, *Prunella vulgaris*, *Rhinanthus minor* ag., *Odontites* sp., and *Filipendula ulmaria*, while *Juncus articulatus*, *J. conglomeratus*, and *Aster novi-belgii* were locally common.

A food supplement of c. 3.5 kg barley and c. 0.25 kg standard layers' pellets was scattered in the ponds each morning for the 30-40 resident waterfowl (mainly geese and ducks) and up to 40 doves, (*Columba livia*), amongst all of which there was

TABLE 1. Meteorological Records at Culterty Field Station. Newburgh. Lat. 57° 20' N.

	Mean Monthly Temperature °C				Rainfall (mm)				
	5.08 cm below ground			Grass minimum		Monthly total			
	Range of means			Range of means		Range of means			
	1974-75	since 1964		1974-75	since 1964		1974-75	since 1964	
Dec	2.9	1.1	3.5	-1.2	-4.5	0.0	30.9	13.0	104.6
Jan	2.5	0.6	3.0	-2.8	-3.4	0.5	70.9	40.1	99.1
Feb	3.1	0.5	2.8	-0.3	-3.5	0.6	15.3	16.9	70.6
Mar	3.0	1.6	3.8	-2.5	-1.9	1.1	42.0	10.6	75.1
Apr	6.1	4.1	7.1	1.4	-4.1	1.9	102.6	21.6	55.0
May	9.5	8.8	11.9	1.8	1.7	4.6	22.8	28.1	112.0

vigorous competition for the food. Moorhens fared very badly in this scramble. Moreover, as spring progressed and sunrise advanced the food was not available until long after observation periods ended, accordingly its influence on feeding pattern was considered to be unimportant.

Meteorological data from December 1974 to May 1975 (Table 1) provide an index of the weather in

winter and spring for comparison with the preceding ten years. Temperatures and precipitation in the winter months were average except that February was warmer and drier than usual. In March the air temperature was cooler than usual, while April was exceptionally wet (from a snow storm early in the month) and May drier than usual.

TABLE 2. Frequency of activities from February to May 1975.

AFTER SUNRISE										
Activity	Feb		Mar		Apr		May		Spring Total (Mar-May)	
	No.	%	No.	%	No.	%	No.	%	No.	%
¹ Feeding	79	39.7	75	40.3	47	25.3	46	33.6	168	33.0
² Look at ground	16	8.0	22	11.8	9	4.8	11	8.0	42	8.3
³ Look about	26	13.1	16	8.6	17	9.1	22	16.0	55	10.8
⁴ Bodily care	20	10.1	11	5.9	19	10.2	9	6.6	39	7.7
⁵ Agonistic	12	6.0	28	15.1**	36	19.4*	14	10.2	78	15.3***
⁶ Courtship	11	5.5*	6	3.2	3	1.6	9	6.6	18	3.5
⁷ Alarm	4	2.0	2	1.1	--	--	--	--	2	0.4
⁸ Other	31	15.6	26	14.0	55	29.6***	26	19.0	107	21.0**
Total	199	100.0	186	100.0	186	100.0	137	100.0	509	100.0

BEFORE SUNSET										
Activity	Feb		Mar		Apr		May		Spring Total (Mar-May)	
	No.	%	No.	%	No.	%	No.	%	No.	%
Feeding	62	34.6	84	42.0	100	45.5***	55	34.4	239	41.2*
Look at ground	12	6.7	22	11.0	17	7.7	19	11.9	58	10.0
Look about	23	12.9	36	18.0*	23	10.5	20	12.5	79	13.6
Bodily care	14	7.8	9	4.5	12	5.4	24	15.0*	45	7.8
Agonistic	23	12.9*	12	6.0	22	10.0	10	6.2	44	7.6
Courtship	2	1.1	3	1.5	16	7.3*	14	8.8	33	5.7
Alarm	1	0.5	1	0.5	2	0.9	1	0.6	4	0.7
Other	42	23.5	33	16.5	28	12.7	17	10.6	78	13.4
Total	179	100.0	200	100.0	220	100.0	160	100.0	580	100.0

Significantly higher frequencies (by χ^2 with Yates' correction) at sunrise or sunset are indicated: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Components included in activity categories:

1. Peck at food while standing or walking.
2. Look at ground with head and neck turned downwards while sitting, standing, or walking. This posture invariably preceded feeding.
3. Look round while sitting, standing, or walking.
4. Preen, scratch, stretch, wash.
5. Swan, churn, charge, splatter, mutual retreat, challenge, fight-from Wood (1974), plus escape. Swanning was observed on land as well as water (cf. Wood, 1974) when two rival birds met, and led either to a charge or mutual retreat. "Escape" described the hasty retreat of birds defeated in a territorial dispute.
6. Meet and pass, bow, nibble, courtship-chase, stand-arch, squat-arch, copulation, post-copulation-from Wood (1974).
7. Alarm-from Wood (1974)
8. Sit, swim, fly, drink, collect nest material. Although nest-building occurred, it was rarely visible and so was excluded from analyses. The "normal" posture (Wood, 1974) was not adopted here because the main accompanying activities such as sitting or swimming were considered to be more relevant. No activity was assigned to the "other" category if (for example) agonistic or courtship components were clearly recognizable.

METHODS

Moorhens were observed with 8 x 40 binoculars from a permanent hide for three days per month between February and May, 1975. Observation covered the two hours starting at sunrise (as given by the 1975 Nautical Almanac-HMSO) and the two hours ending at sunset. Most birds watched were within 40 m of the hide, while some were less than 20 m distant. Activity for each bird was categorized at 5-minute intervals and the frequency of each activity scored by hour, period of day and month. This indicated the proportion of time spent on any particular activity since the probability of scoring an activity depended upon how much time the bird spent on it before switching to another, and not the interval between observations, unless that interval coincided with the natural periodicity of an activity. The assumption made here was that a 5-minute interval did not parallel any natural periodicity of behaviour and therefore the summed frequencies of activities were equivalent to the proportion of time spent on each activity by an "average" bird. Categorization of courtship and agonistic "displays" largely followed Wood (1974), while other activities and major groupings of activities followed those used for the pukeko (Fordham, unpublished data) (See Table 2).

The rate of food collection was monitored by counting the number of pecks at the substrate made in 30 seconds, as measured by an automatic timer. This interval was chosen because pilot observations suggested that often moorhens did not feed consistently for as long as one minute. Only uninter-

rupted 30-second intervals were used in analysis, and pecking movements in which the beak did not contact plants or substrate were not counted as pecks. Swallowing was found to be too difficult to record accurately, hence measurements of pecking rate could have included some unsuccessful pecks. Moorhens fed in the pond and around its margins, and in this area three substrates were recognised:

(a) pond water; (b) exposed pond floor comprising mud, stones and detritus; and (c) grass and herb sward surrounding the pond. Counts of pecks per half minute were started only when a bird had taken some pecks and was therefore judged to be "feeding". Counts were ignored if the bird was disturbed or changed activity during the 30 seconds. Each feeding bird was recorded only once during a five-minute period, but because moorhens continually shift from one substrate to another while moving about their territories, an individual would be measured again if it began feeding on a new substrate.

RESULTS

In February the mean number of birds observed in each five-minute interval after sunrise was 3.2 (range 0-6, n = 63) and before sunset 2.7 (range 0-6, n = 66), while over spring (March-May) the mean number observed after sunrise was 2.4 (range 0-5, n = 216) and before sunset 3.3 (range 0-5, n = 216). Methods of feeding varied. In water, moorhens often pecked delicately at small bubbles of scum, or reached for items below the surface, while on land items such as fresh goose faeces were sometimes

TABLE 3. *Frequency of feeding.*

AFTER SUNRISE										
	Feb		Mar		Apr		May		Spring (Mar-May)	
	First hour	Second hour								
n	129	70	90	96	109	77	74	63	273	236
Feeding	53	26	34	41	23	24	29	17	86	82
%	41	37	38	43	21	31	39	27	32	35
BEFORE SUNSET										
	Feb		Mar		Apr		May		Spring (Mar-May)	
	Penulti- mate hour	Last hour								
n	79	101	106	94	103	117	92	68	301	279
Feeding	24	38	40	44	40	60	26	29	106	133
%	31	38	38	47	39	51	28	43	35	48

Paired results were tested by χ^2 with Yates' correction -- see text.

TABLE 4. Mean number of pecks in 30 seconds-both hours combined.

AFTER SUNRISE												
Substrate	Feb			Mar			Apr			May		
	n	\bar{x}	Std Dev									
Grass sward				54	24.78	14.53	29	20.76	14.40	35	10.14	4.95
Mud				26	18.65	9.04	23	16.17	12.42	13	12.77	10.63
Water				29	10.72	5.77	22	14.68	12.03	8	8.00	5.18
Total	41*	15.29	9.50	109	19.58	12.88	74	17.53	13.22	56	10.45	6.74

BEFORE SUNSET												
Substrate	Feb			Mar			Apr			May		
	n	\bar{x}	Std Dev									
Grass sward	9	26.00	20.02	88	33.43	15.76	59	18.53	13.67	25	20.84	17.41
Mud	10	25.20	13.47	20	22.75	8.84	41	19.56	12.11	21	10.76	5.64
Water	5	31.0	12.35	8	23.38	9.59	25	10.64	5.88	25	4.20	3.23
Total	70*	23.73	14.37	116	30.90	15.06	125	17.29	12.36	71	12.00	12.91

* includes observations where the substrate was not recorded.

eaten rapidly. Stones and small turfs were scooped over, vigorous thrusts delivered at the ground, and grass and other plants were snipped with the beak, but the ingesta were rarely identifiable.

Frequency of activities

The frequency of all activities (Table 2) varied between months, and between sunrise and sunset, but not consistently. During spring, agonistic and "other" activities were significantly more frequent (by Chi square), and feeding significantly less frequent, at sunrise than at sunset; however, the differences for feeding and "other" activities were generated by April results alone. During spring, at both sunrise and sunset, swimming constituted about 92 % of "other" activities. The frequency of feeding did not alter significantly between the first and second hours after sunrise in any month or during spring (Table 3), but feeding was always more frequent in the last hour before sunset than in the penultimate hour, and for spring the difference was significant ($p < 0.001$). In spring, the frequency of feeding in the last hour before sunset was also higher than in the first hour after sunrise ($p < 0.001$, Table 3) because of a large significant difference in April ($p < 0.001$). Feeding frequency in the second hour after sunrise was not significantly different from that in the penultimate hour before sunset in any month or over spring.

Birds often walked, or stood, with their heads down, looking at the ground, and because this invariably led to feeding (Table 2) this activity was considered to be part of feeding. If "looking at the ground" frequencies are combined with feeding frequencies in the comparisons between hours results are identical to those just described, with the single exception of sunrise in April, when the two activities were significantly more frequent in the second hour after sunrise than in the first.

Rates of Pecking

The rate of pecking both after sunrise and before sunset on all substrates combined was highest in March, and then declined (Table 4). On separate substrates this was also the pattern after sunrise for grass sward and mud, but not water, where the April rate was highest; however, lack of data for February prevents a firm conclusion. For the period before sunset the pattern for separate substrates varied; on grass sward pecking was again fastest in March, but for mud and water pecking rate declined after February. On average, at both sunrise and sunset in spring moorhens pecked fastest on grass (Table 5) and slowest in water, with the rate for mud intermediate. Comparing sunrise and sunset over spring, pecking rates (Table 5) were significantly faster (by *t* test) before sunset than after sunrise on grass sward and on all substrates combined. After

TABLE 5. Mean number of pecks in 30 seconds in spring (March-May).

AFTER SUNRISE									
Substrate	First hour			Second hour			Total		
	n	\bar{x}	Std Dev	n	\bar{x}	Std Dev	n	\bar{x}	Std Dev
Grass sward	66	15.89	12.24	52	23.96	14.56	118	19.45	13.85
Mud	38	13.34	8.84	24	21.50	11.85	62	16.50	10.79
Water	34	11.59	10.41	25	12.16	6.15	59	11.83	8.80
Total	138	14.13	11.02	101	20.46	13.17	239	16.80	12.35

BEFORE SUNSET									
Substrate	Penultimate hour			Last hour			Total		
	n	\bar{x}	Std Dev	n	\bar{x}	Std Dev	n	\bar{x}	Std Dev
Grass sward	74	25.78	15.38	98	27.02	17.92	172	26.49	16.84
Mud	42	18.24	11.39	40	17.93	10.51	82	18.09	10.90
Water	35	11.06	9.66	23	7.43	5.42	58	9.62	8.37
Total	151	20.27	14.37	161	21.96	16.61	312	21.14	15.58

sunrise pecking was significantly faster in the second hour than in the first on grass sward ($p < 0.002$) and on mud ($p < 0.002$), no different in water, and faster when all three substrates were combined ($p < 0.061$; Table 5). There were no differences between the two hours prior to sunset in the rates of pecking on any substrate, nor on combined substrates. My attention focused on the first hour after sunrise and the last hour before sunset because of their proximity to night. Compared to the hour after sunrise the rate of pecking in the hour before sunset was faster on grass sward ($p < 0.001$) and on mud ($p < 0.05$), no different in water, and faster when all three substrates were combined ($p < 0.001$ (Table 5).

Feeding intensity

Combination of pecking rates and the frequency of feeding activity can provide an index of overall feeding intensity. The term "feeding intensity" is preferred to "feeding effort", which could involve things other than searching and catching, for example swallowing and digestion. Assumptions implicit in the index are that the frequency of feeding is equivalent to the proportion of time spent on that activity by an "average" bird, and that rates of pecking were representative of the one- or two-hour period in which they occurred. The amount of time spent feeding was obtained by expressing the proportional occurrence of feeding in terms of a number of 30-second intervals. For instance, during spring feeding occupied 31.5 % of the first hour after

sunrise (Table 3), or 37.80 30-second intervals, which, multiplied by the mean pecking rate (14.13 for combined substrates, Table 5) indicates a total 534 pecks delivered in the hour (Table 6). The total number of pecks delivered in two hours was obtained from summing the pecks in each separate hour, and not from average scores for the period.

Calculated feeding intensities at different times and on different substrates (Table 6) were compared by Chi-square tests with Yates' correction against the null hypothesis of even distribution of total pecks. When tests compared two substrates the hypothesis required the assumption that both substrates were equally "available" to the birds in terms of area and/or food resources. This assumption was not tested by measurement, but as areas of water, mud, and grass sward were always freely available for selection by the birds the assumption was considered reasonable. The minimum level of significance accepted was $p < 0.05$, but in 147 of the 184 tests the level achieved was $p < 0.001$.

Overall feeding intensity on all substrates both after sunrise and before sunset (Table 6) was highest in March and then declined. The sole exception, where feeding intensity in February exceeded that in March, was on water before sunset. All but one of the differences between successive months were significant. With "looking at the ground" activity included the results were almost identical. No association between feeding and spring weather (Table 1) was apparent.

TABLE 6. Overall feeding intensity as indicated by the calculated number of delivered pecks.

AFTER SUNRISE						
Substrate	Period	Feb	Mar	Apr	May	Spring (Mar-May)
Grass sward	First hour		905	402	493	601
	Second hour		1535	1036	312	1001
	Total		2440	1438	805	1602
Mud	First hour		858	275	461	504
	Second hour		942	978	734	898
	Total		1800	1253	1195	1402
Water	First hour		479	363	157	438
	Second hour		559	578	350	508
	Total		1038	941	507	946
Combined Substrates	First hour	714	775	349	455	534
	Second hour	751	1143	900	378	854
	Total	1465	1918	1249	833	1388

BEFORE SUNSET						
Substrates	Period	Feb	Mar	Apr	May	Spring (Mar-May)
Grass sward	Penultimate hour	727	1292	1004	891	1089
	Last hour	1316	2079	1003	812	1547
	Total	2043	3371	2007	1703	2636
	Penultimate hour	918	1066	941	309	770
Mud	Last hour	1162	1215	1170	646	1026
	Total	2080	2281	2111	955	1796
	Penultimate hour	1269	1121	472	162	467
Water	Last hour	1173	786	702	183	425
	Total	2442	1907	1174	345	892
	Penultimate hour	938	1223	848	450	856
Combined Substrates	Last hour	1015	1942	1013	549	1257
	Total	1953	3165	1861	999	2113

Feeding intensity after sunrise was significantly higher in the second hour than in the first in nearly all months. Exceptions were February on combined substrates when first and second hours did not differ, and May on grass sward and combined substrates when the first hour was significantly higher. The results with "looking at the ground" included were very similar. Apart from pecking slowly in the first hour after sunrise the birds did not move about very much, and tended to walk slowly. In spring, feeding intensity before sunset rose significantly in

the last hour on grass sward, mud, and combined substrates, but not on water. Taking months separately, with each substrate the results varied, but in over half the cases (10 out of 16) feeding intensity was significantly higher in the last hour than in the penultimate hour. The results with "looking at the ground" included were very similar.

Direct comparison of the periods after sunrise and before sunset on combined substrates showed that feeding intensity was significantly higher before sunset in every month. The same result held for

separate substrates, with exceptions in May when feeding intensity after sunrise was higher on mud and water, and during spring, on water, when the two periods were not significantly different. Compared with the first hour after sunrise, overall feeding intensity in the last hour before sunset was significantly higher in all months on all substrates, except on water in May and in spring. With "looking at the ground" included identical results were achieved.

DISCUSSION

Monthly trends

The frequency of all measured activities (including feeding) at sunrise and sunset varied between February and May in no consistent pattern. In contrast, the general (combined substrates) pattern for pecking rates at both dawn and dusk comprised a peak in March and a subsequent decline. Moorhens pecked at different rates on grass sward, mud, and water, and there were no differences on any substrate between the two hours before sunset. In contrast, there were differences between the two hours after sunrise. Birds pecked on grass and mud much faster in the second hour (Table 5), whereas in water pecking rates for first and second hours were similar. In spring, when surface temperatures at dawn are commonly low and often accompanied by ice, invertebrates may be relatively more obtainable in free-flowing water than from mud or turf, and this could explain why moorhens feeding in water pecked equally fast in the first and second hours after sunrise.

Combination of activity and pecking rate measures showed that feeding intensity at sunrise and sunset fell from March onwards, mainly because the speed of pecking declined. Moorhens lose weight between December and February, then begin to regain it in March (Anderson, 1975); females are heaviest during the laying period. The frontal shield begins to enlarge in January (Anderson, 1975) and the mean date of starting first clutches is in the first half of April (Anderson, 1965); in 1975 the first known clutch began on 24 March. The occurrence of peak feeding intensity and pecking rates in March could therefore lead directly to gains in weight and to the onset of laying, but the data are only indicative.

After March pecking could slow down if the bird's energy needs decreased as spring advanced and could be adequately met by fewer pecks; if the energy captured per peck rose, perhaps as invertebrates became more plentiful; or if feeding became gradually spread through the day. Between early February and late May the daylight period lengthened by more than nine hours, but changes in

the amount of time spent feeding at sunrise and sunset were not clearly associated with increasing day length. Day length apart, the fall in feeding intensity at dawn and dusk over spring is also related to the relative frequency of all activities (Table 2). Siegfried and Frost (1975) and Frost and Siegfried (1977) have reported division of labour and unequal expenditure of energy between male and female moorhens during breeding, which suggests that feeding rates may well differ between the sexes. This hypothesis could be readily tested. Feeding intensity differed between the three substrates, and the ranking varied between months (Table 5 and 6), but gross differences in community structure and prey species in these habitats make differences in feeding intensity on them less surprising than the difference between the beginning and end of the day.

The difference in foraging at sunrise and sunset—a possible explanation

In every month moorhens spent more time feeding and fed faster before sunset than after sunrise, which leads plainly to rejection of the hypothesis of equal feeding effort at dawn and dusk. Assuming that food gathering by moorhens stops, or at least is much reduced, during the cold, dark hours of night (Bent, 1926), it would be logical to expect especially active foraging both before dark to stock up, and again after sunrise to refill empty stomachs, but this did not happen. Some crepuscular hunting probably occurs, as in the pukeko (Craig, 1974; Fordham, unpublished data), but may be less significant in winter and early spring when twilight is short, than in late spring and summer when it is extended. The relatively small difference in May between feeding intensities at sunrise and sunset compared with larger differences earlier on (Table 6) lends slight support to this idea. On average, feeding was more intense before night than after it, and this needs explanation.

Firstly, moorhens might be metabolically adapted to low expenditure of energy at night so that after eating vigorously at dusk they survive to the following dawn without too large an energy deficit. Such a mechanism would presumably work to the limit on cold winter nights, but would be assisted by increasing the intake of animal food and by some foraging at night.

Secondly, the lower frequency of feeding activity at sunrise might be influenced, at least in March and April, by more territorial disputes and increased social activity as residents and prospective immigrant breeders re-assert their social positions after the long dark period of reduced or nil contact with neighbours.

Thirdly, effort put into feeding may be a function

of morphology and temperature regulation, and therefore be physiologically determined. Animals with a large surface area relative to their mass absorb and lose heat more rapidly than animals with a smaller area: mass ratio. Bligh (1976) stated that in the morning, when ambient temperatures are rising, small organisms will warm up and be active before larger ones, but in the evening small organisms will cool down more rapidly. Bligh went on to suggest that there has been selective pressure for the evolution of behavioural characteristics by which organisms can optimize periods of high body temperature and high activity. If this is so, then for moorhens, relatively small birds weighing approximately 250-450 g (Anderson, 1975), vigorous feeding before dark may allow essential stocking-up against heat losses soon to be experienced. At dawn, the slow start to feeding may be occasioned by the combined effects of gradual warming of the body, reduced availability of preferred high-energy foods, and the time taken up by other (e.g., social) activities.

Finally, more intense foraging before sunset could be directly related to greater availability at that time of invertebrates and *I* or to higher concentrations in plants of certain nutrients, for example soluble sugars, compared to the cool period around sunrise. As was pointed out for white-fronted geese by Owen (1972), feeding moorhens may monitor the substrate constantly and vary walking and pecking speed to match the location and availability of preferred foods.

CONCLUSION

Whatever the complete diurnal pattern of feeding proves to be in different seasons, in late winter and spring moorhens foraged much more actively on grass sward and mud before sunset than they did after sunrise. The explanations offered can be tested by simple hypotheses, and future work could well start by attacking the question "how is it that in spring moorhens feed more at dusk than at dawn?"

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