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Journal
International Journal of Comparative Psychology, 9(3)

ISSN
0889-3675

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Publication Date
1996

DOI
10.46867/C43W3J

International Journal of Comparative Psychology, Vol. 9, No. 3, 1996

TEMPORAL PATTERNING OF ORAL STEREOTYPIES IN RESTRICTED-FED FOWLS: 1. INVESTIGATIONS WITH A SINGLE DAILY MEAL

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ABSTRACT: In two experiments, 24 immature female broiler breeder fowls housed in two 12-cage battery units in identical rooms received a single daily ration which they ate in 10 min, according to a programme of food restriction. From regular 15-min videorecordings, measurements were made of times spent in mutually exclusive activities (sitting, standing, head out, pacing, preening, object pecking, drinker activity). In Experiment 1, feeding time was 09.00 h in one room and 13.00 h in the other, and all birds were videorecorded in every hour of the (14-h) photoperiod on two alternate days. Differences in behaviour before and after feeding were independent of feeding time. In both rooms, head out and pacing increased before feeding, and object pecking and drinker activity (oral stereotypies) commenced immediately afterwards and then declined. Individual variation in the oral stereotypies was significant, and individuals' mean levels of both stereotypies together were consistent on the two days, but their hourly patterns were less so. Experiment 2 tested the notion of homeostatic control of oral stereotypies, by feeding all birds at 09.00 h and measuring their responses to removal of drinkers and empty feeders (main targets of the stereotypies) for either 0, 1.5 or 3 h before 15.00 h. Each cage tier received each treatment once, over three alternate days when all birds were recorded on video between 12.00 and 18.00 h (lights off). During removal of feeders and drinkers, partial suppression of object pecking and total suppression of drinker activity were balanced by corresponding increases in sitting, head out and preening. After the return of feeders and drinkers, preening declined and both stereotypies showed evidence of post-inhibitory rebound, but there was no difference between 1.5 and 3 h removal treatments. The results concur with earlier evidence indicating that preening can substitute with oral stereotypies, and it is suggested they may demonstrate homeostasis in total (substitutable) oral activity over the whole test. Conceivably, homeostasis of arousal may underlie changes in broiler breeder behaviour before and after feeding time.

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INTRODUCTION

In commercial conditions, parent stock (breeders) of meat-type chickens (broilers) are fed on restricted rations during the growing period in order to limit body weight at sexual maturity, and thereby improve health and fertility (Hocking et al., 1989). Birds fed on the recommended rations, which are provided once a day and eaten in <15 min, eat only a third as much as they would with free access to food, and are highly motivated to feed at all times (Savory et al., 1993). They are more active than ad libitum-fed control birds, and show increased pacing before feeding time and increased drinking and pecking at non-food objects afterwards. Their expression of these activities is often stereotyped in form and is correlated positively with the level of food restriction imposed (Kostal et al., 1992; Savory et al., 1992; Savory & Maros, 1993). Similar behavioural responses have been studied in breeding pigs, which are also subject to routine chronic food restriction (e.g. Appleby & Lawrence, 1987; Rushen, 1985; Terlouw et al., 1991).

When restricted-fed broiler breeders are housed individually in cages, they show oral stereotypies in the post-feeding period directed towards their drinker, empty feeder and parts of the cage (Kostal & Savory, 1994). Two further experiments with caged restricted-fed birds are reported here. In the first, two groups were studied which differed in the time their daily meal was provided, to see whether differences in behaviour before and after feeding are independent of feeding time. This was found with restricted-fed pigeons, whose peak of spot pecking after feeding remained the same when feeding time was shifted by 12 h (Palya & Zacny, 1980), and pigs' oral stereotypies also commence after feeding, whether they are given one meal a day or two (Jensen, 1988; Rushen, 1985; Terlouw et al., 1991, 1993).

Proportions of time spent performing oral stereotypies vary greatly among individual broiler breeders (Kostal et al., 1992; Kostal & Savory, 1994), and another objective here was to see how this variation is expressed in relation to time of day. From two observation days, measurements of repeatability were made of individuals' hourly patterns and mean levels of stereotyped behaviour, because the ways in which an activity varies within and between days can provide information about underlying control processes (e.g. Savory, 1993).

There was evidence from the first experiment suggesting that the stereotypies might be regulated in a homeostatic way (i.e. a steady state maintained through compensatory changes in behaviour). There is also evidence from other species that stereotypies may have de-arousing consequences (Brett & Levine, 1979; Dantzer & Mormede, 1983;

Dantzer et al., 1988; Jones et al., 1989). Conceivably, homeostasis of arousal (Delius, 1970; Odberg, 1993) might underlie changes in behaviour of restricted-fed animals before and after feeding time. This notion was tested in the second experiment, by measuring broiler breeders' behaviour during and after removal of the main targets of their oral stereotypies - the drinker and empty feeder. To provide evidence of homeostasis, temporary suppression of the stereotypies should be followed by "post-inhibitory rebound" (Kennedy, 1985) in those activities, and the size of the rebound should compensate for the duration of suppression. Such deprivation dependent rebounds have been demonstrated in fowls with feeding, drinking, dust-bathing and various comfort movements (Marks & Brody, 1984; Nicol, 1987; Savory, 1981; Vestergaard, 1982; Wood-Gush & Gower, 1968). They all imply some degree of homeostasis, and are consistent with models of motivation based on "psycho-hydraulics" (Lorenz, 1950) and accumulation of "action-specific energy" (Wennrich & Strauss, 1977).

The situation with broiler breeder stereotypies is complicated by the fact that they may be substitutable with another form of oral behaviour - preening. It was the only activity to increase consistently when either the drinker or empty feeder was removed in a previous study with penned birds (Kostal et al., 1992), and in another study with caged birds, drinking, pecking at the cage and preening were each dominant in different tiers of a battery system (Savory et al., 1992). It has long been recognised that effects of some motivational states on behaviour can be non-specific (Fentress, 1973), and various activities seen in frustrating situations may have de-arousing consequences (Brett & Levine, 1979; Dantzer & Mormede, 1983; Delius, 1970; Hutt & Hutt, 1970). For these reasons, the apparently substitutable forms of oral behaviour of restricted-fed broiler breeders could have common internal causation and consequences (Savory & Maros, 1993). In the second experiment here, neither pecking at parts of the cage nor preening could be prevented, so in analysing responses to drinker and feeder removal, attention was given to total oral behaviour, and substitution of activities during the removal periods, as well as to any rebound in behaviour afterwards.

EXPERIMENT 1: METHODS

Subjects and husbandry

Twenty four female broiler breeders (Ross 1, Ross Breeders Ltd., UK) were kept in a multi-unit brooder and fed ad libitum to 2 weeks of age. They were then moved to a pen and fed once a day at 09.00 h according to the restricted feeding programme in the Ross 1 Parent Stock Management Manual (authorized by UK Home Office Licence). At 8 weeks, 12 of the birds were housed individually in a 12-cage battery in a light-proof room, and these continued to be given a daily ration of "grower" pellets (150 g/kg protein and 11.0 MJ/kg metabolisable energy) at 09.00 h and will be referred to as early-fed (EF) birds. The other 12 were similarly housed in an identical battery in another identical room, and were fed thereafter on the same diet/ration at 13.00 h and will be referred to as late-fed (LF) birds. Each battery consisted of three tiers of 4 cages. Each cage measured 30 x 45 x 41 cm (w x d x h) and had solid sides, back and ceiling, and a front with vertical bars through which the bird could feed from a metal feeder and drink (ad libitum) from a 1 litre plastic container situated adjacently in a large common trough running along the outside of each tier. The drinker was filled with water daily at feeding time. Birds could see neighbours on the same tier when their heads were out of the cage fronts, but not birds on other tiers. In each room the lights were on from 06.00 to 20.00 h, and ambient temperature was maintained at 21° C.

Measurements of behaviour

At 12 weeks of age, after 4 weeks in the cages, mean body weight was 1.28 kg and the daily ration of 58 g pellets was all eaten in 10 min. The behaviour of all 12 birds in each room was recorded on videotape for 15 min (half past to quarter to) in every hour of the 14-h photoperiod on two alternate days. The recording was done remotely with equipment in a third room, and involved no disturbance to the birds.

From the videorecordings, measurements were made in each 15-min period by noting each bird's behaviour every minute from a single "on the dot" observation (Slater, 1978), according to one of seven mutually exclusive categories. These were: sitting (only); standing (only, with head inside the cage); head out (of the front of the cage while standing and often pushing against the bars); pacing; preening (nearly always while standing); object pecking (at the empty feeder or at parts of the cage); or drinker activity (drinking was interspersed with, and indistinguishable from, pecking at the water or drinker without drinking; all birds produced wet faecal droppings indicating polydipsia (Lintern-Moore, 1972)). The last two activities (but not pacing or preening) were stereotyped in form, according to the usual definition of stereotypies (i.e. invariable, repetitive, no apparent function (Odberg, 1978)). Computer software used for this analysis was written by LK in Turbo Pascal (Borland International, USA).

Statistical analyses

Influence of feeding time (EF, LF) was assessed by seeing whether differences in behaviour before and after feeding were independent of the room used. This was done by calculating mean numbers of minutes in which different activities were observed in all the 15-min periods before feeding, and in all those after feeding, for each bird and observation day. These values were transformed by empirical logistic transform ($\log[(S+0.5)/(15-S+0.5)]$, where S is the untransformed value, Cox, 1970), to allow for lower variability at the limits of the 0-15 min scale. They were then compared by split-plot ANOVA, with birds as plots, to measure the significance of effects of bird, observation day, the difference between before and after feeding, and its interaction with feeding time/room. The results presented in Table 1 are back transformed means from this analysis, expressed as proportions of time.

To assess how consistent birds' *hourly patterns* of oral stereotypies (object pecking and drinker activity) were on the two observation days, measurements of repeatability were calculated for each hour after feeding time (expression of these activities was minimal before feeding). This was done separately for EF and LF birds, by expressing the between birds variance as a proportion of the total (between and within birds) variance (cf. Falconer, 1960), after transforming the data (number of minutes spent in object pecking and drinker activity together) by empirical logistic transform (see above). Hence, the repeatability value would be one if there was no within bird variation (between days), and zero if there was no between bird variation. Mean values of repeatability were then calculated from all the hourly values. To assess how consistent birds' *mean levels* of the stereotypies were on the two days, similar repeatability measurements were calculated from each bird's mean of the transformed hourly data used above.

To see whether individual expression of oral stereotypies was influenced by the behaviour of nearest neighbours (cf. Appleby et al., 1989; Cooper & Nicol, 1994; Palya & Zacny, 1980), each bird's overall mean time spent in object pecking and drinker activity, over all hours after feeding on both days, was correlated with that of its nearest neighbour (using the transformed data referred to above, from both (EF, LF) rooms). With the middle two birds in each tier, that each had two neighbours, stereotypy times of these neighbours were averaged (Appleby et al., 1989).

RESULTS

Influence of feeding time

When behaviour in the hours before feeding time was compared with that afterwards, there were highly significant differences in all the activities observed (Table 1). Thus, there was more standing, head out, pacing and preening before feeding, but virtually no sitting, object pecking or drinker activity.

Table 1. Mean (n=12) proportions (%) of time spent in different activities, before (BF) and after (AF) feeding time on two days, by individually caged restricted-fed broiler breeders fed at either 09.00h (EF room) or 13.00h (LF room), and significance of effects of bird, day, feeding time (BF versus AF), and its interaction with room, from ANOVA. Analyses of variance were done with empirical logistic transformed data, and the values shown are in the observed scale (from back transformations) expressed as proportions. *P<0.05; **P<0.01; ***P<0.001; NS, not significant (P>0.05).

	EF room		LF room		Significance of effects			
Activity	BF	AF	BF	AF	Bird	Day	BF vs AF	BF vs AF x room
Sitting	0.1	5.4	0.2	2.0	NS	NS	***	**
Standing	39.1	29.1	47.6	31.3	***	NS	***	NS
Head out	25.4	13.8	26.0	12.1	***	NS	***	NS
Pacing	5.5	3.2	6.4	3.7	**	NS	***	NS
Preening	18.7	7.0	11.9	7.1	NS	NS	***	NS
'Object' pecking	1.5	21.6	1.7	25.4	***	NS	***	NS
Drinker activity	0.8	8.0	2.3	7.7	*	NS	***	NS

Head out and pacing increased as feeding time approached, while the oral stereotypies, of which object pecking was dominant, were highest immediately after feeding and declined gradually thereafter (Figure 1). The only significant interaction with feeding time/room was with sitting, which was greatly increased with EF birds in the last hour of the photoperiod. Hence, the differences in behaviour before and after feeding were relatively independent of feeding time.

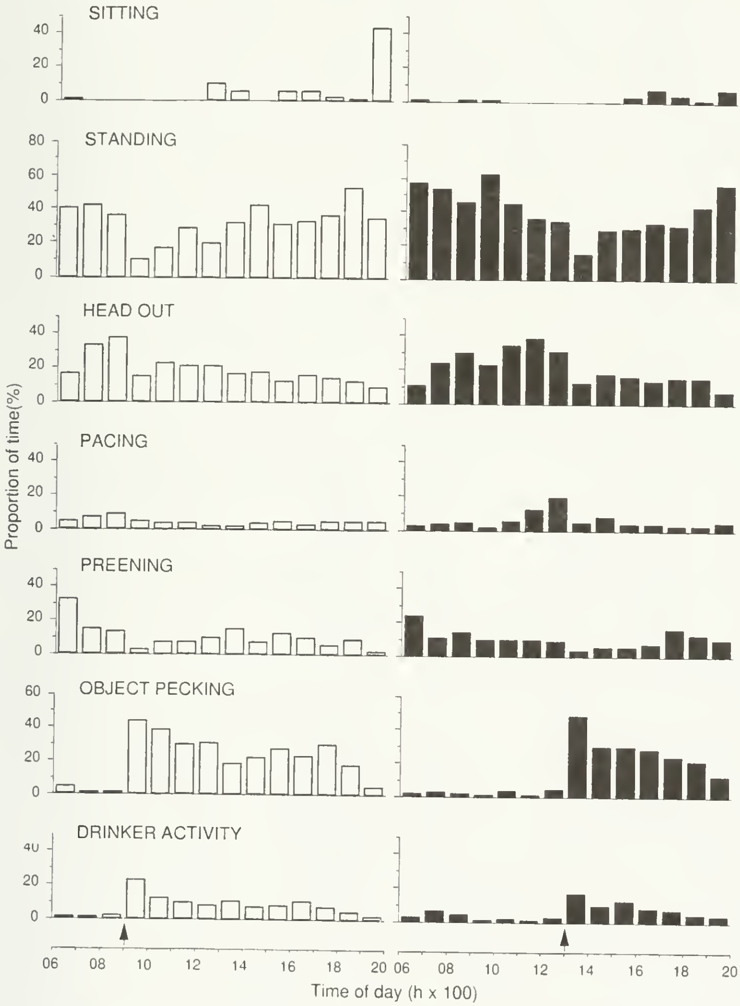

Figure 1. Mean (n=12) proportions of time spent in different activities during 15 min (half past to quarter to) in each hour of a 14-h photoperiod, from two observation days, when birds were fed at either 09.00 h (white columns, EF birds) or 13.00 h (black columns, LF birds). Arrows indicate feeding times.

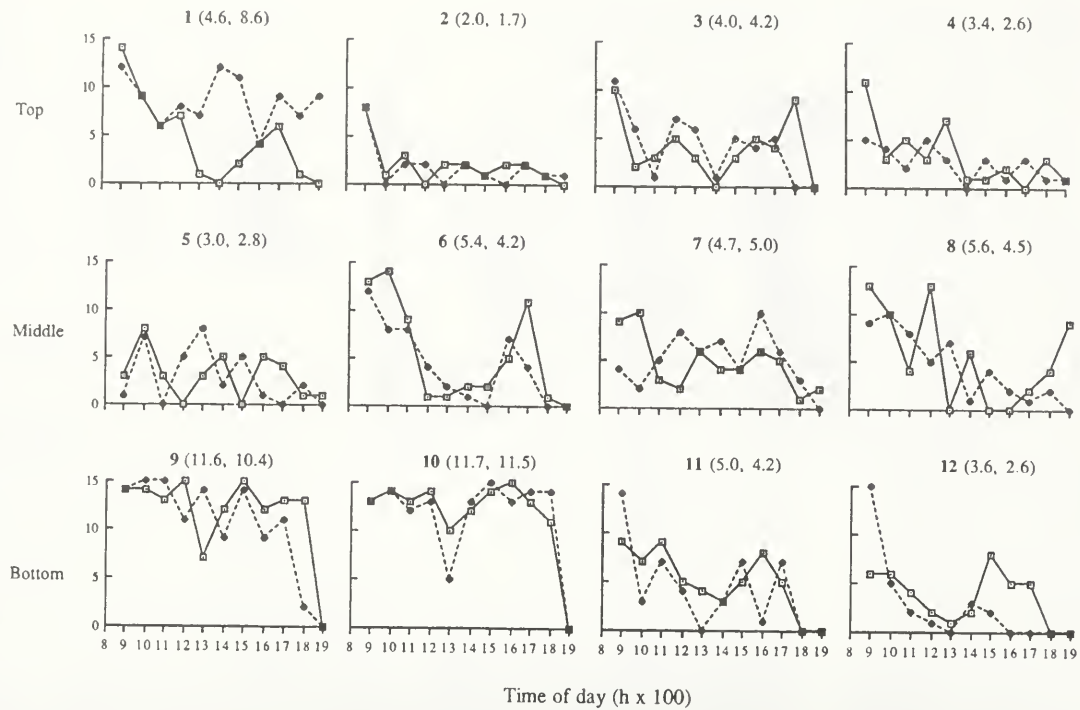

Figure 2. Total times (min) spent in stereotyped object pecking and drinker activity by each EF bird during 15 min (half past to quarter to) in each hour after feeding time (09.00 h), on day 1 (solid line) and day 2 (dashed line). Values in parenthesis after each bird number (bold) are mean times (min) spent by that bird in the two oral stereotypies, from all 15-min periods, on days 1 and 2 respectively.

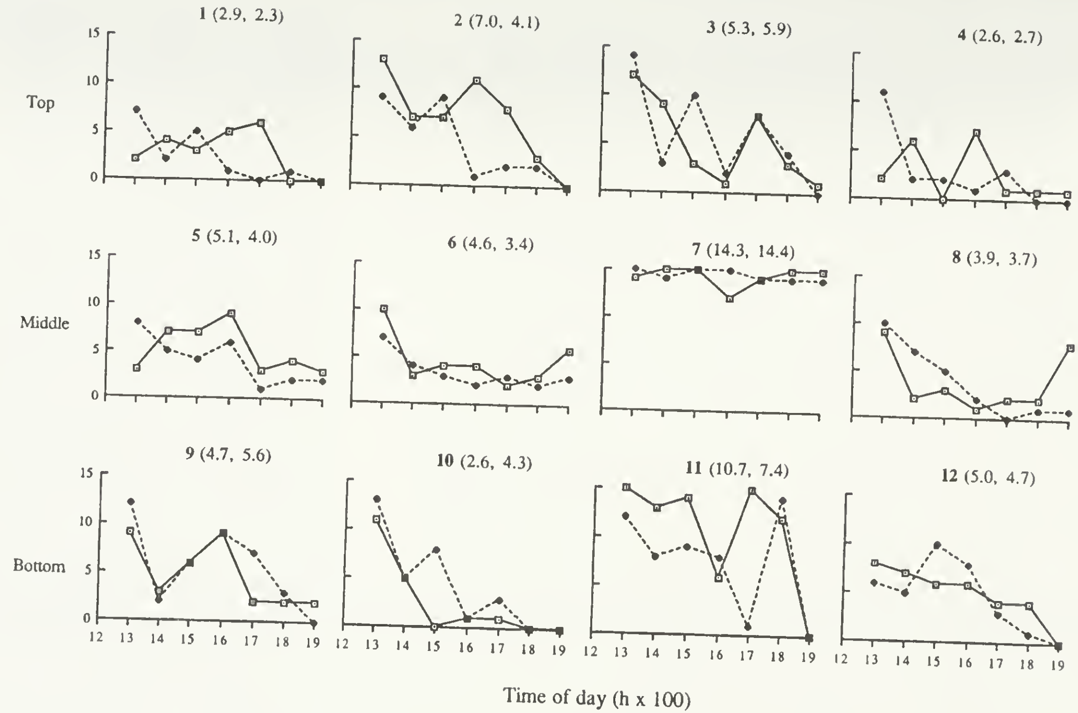

Figure 3. Total times (min) spent in stereotyped object pecking and drinker activity by each LF bird during 15 min (half past to quarter to) in each hour after feeding time (13.00 h), on day 1 (solid line) and day 2 (dashed line). Values in parenthesis after each bird number (bold) are mean times (min) spent by that bird in the two oral stereotypies, from all 15-min periods, on days 1 and 2 respectively.

Individual variation

Variation among individual birds was significant with all activities except sitting and preening (Table 1). Of the two stereotypies after feeding time, individual variation was greater with object pecking than with drinker activity, and with both EF and LF birds there were 2 birds that showed very high levels of object pecking (Table 2). When proportions of time spent in the stereotypies were added together, they ranged from 12 to 77% and 17 to 96% in EF and LF birds, respectively.

Total times (min) spent in the oral stereotypies in all 15-min periods after feeding time, on each observation day, were plotted separately for each bird (Figures 2, 3). In most instances, expression of the stereotypies was highest in the first hour after feeding and then declined. In the 4 birds with mean values of >50% (Table 2), levels remained high in either all hours (LF7) or all except the last hour (EF9, EF10, LF11). Patterns were more variable in birds with lower mean values. Secondary increases, following either low levels in the first hour or rapid initial declines, occurred at a similar time on both days in some cases (EF6, EF12, LF3, LF9).

The variability in hourly patterns was also reflected in regression coefficients (not shown) calculated between each bird's total time spent in object pecking and drinker activity in each 15 min, on each day, and the number of hours after feeding. All (48) coefficients except one were negative, reflecting the downward trends over time, but less than half (21) were significant ($P<0.05$).

Repeatability

There were no significant differences in behaviour between the two observation days (Table 1). With the oral stereotypies after feeding, measured repeatability values in different hours ranged from 0.11 to 0.77 in EF birds, and 0.23 to 0.90 in LF birds (Table 3). The mean repeatability values of 0.51 and 0.62 imply that variation in hourly patterns within birds (between days) was as great as that between birds. By contrast, repeatability values of birds' mean levels of the stereotypies were 0.90 ± SE 0.06 with both EF and LF birds. Thus, mean levels at which stereotypies were expressed (over all hours after feeding time) were much more consistent within birds than between birds.

Table 2. Frequency distributions of individual birds' mean proportions of time spent in object pecking and drinker directed activity after feeding time, when fed at either 09.00h (EF, n=12) or 13.00h (LF, n=12).

Activity	Feeding time	Percent time spent performing activity					
		<10	10-20	20-30	30-40	40-50	>50
Object pecking	EF	3	4	2	1	0	2
	LF	1	5	3	1	0	2
Drinker activity	EF	8	3	1	0	0	0
	LF	7	4	1	0	0	0
Object pecking + drinker activity	EF	0	3	2	4	1	2
	LF	0	4	3	3	0	2

Table 3. Repeatability of total (empirical logistic transformed) times spent in object pecking and drinker activity on Day 1 and Day 2, in each hour after feeding time, which was either 09.00h (ER, n=12) 0r 13.00h (LF, n=12).

Time of day (hx100) →	09	10	11	12	13	14	15	16	17	18	19	Mean
EF	0.39	0.76	0.77	0.58	0.25	0.43	0.67	0.59	0.59	0.45	0.11	0.51
LF	-	-	-	-	0.50	0.70	0.62	0.54	0.23	0.90	0.85	0.62

Influence of nearest neighbours

Individual expression of oral stereotypies was not influenced by the behaviour of nearest neighbours, judging from the weak correlation (r = 0.06, 22 df) between times spent in the stereotypies and those of neighbours.

EXPERIMENT 2: METHODS

Subjects and husbandry

Twenty four female broiler breeders (Ross 1) were kept in a multi-unit brooder and fed ad libitum to 3 weeks of age. They were then housed individually in cages in the same two batteries in identical rooms described in Experiment 1 Methods. Lights were on from 07.00 to 19.00 h and ambient temperature was maintained at 21°C. From 3 to 8 weeks they were used in another experiment in which the daily restricted ration (same as in Experiment 1) was provided in four equal portions at either 1 or 1.5 h intervals, commencing at 09.00 h (Savory et al., submitted). At 8 weeks their diet was changed from "starter" to "grower" pellets, and thereafter they all received a single daily meal at 09.00 h, which they ate in 10 min. The time of lights off was changed to 18.00 h.

Experimental procedure

At 13 weeks of age, after 5 weeks on the new feeding and lighting regimes, Experiment 2 was done between 12.00 and 18.00 h (lights off) on three alternate days in one week. The start of testing was thus about 2.8 h after feeding ended and presumably after food-related thirst had been satisfied. There were three treatments, where the feeders and drinkers were removed at either 14.55 h (control), 13.30 h (1.5 h removal) or 12.00 h (3 h removal), and were all replaced in their original positions at 15.00 h. All four birds on a battery tier received the same treatment at the same time, and in both rooms the three treatments were applied one to each tier on each day, according to a balanced design, so that over the three days every tier received each treatment once. When a tier's feeders and drinkers were removed, the common trough in front of it was cleaned and dried to remove any water or food particles lying in it. When they were returned the feeders remained empty and the drinkers were filled with water to about two thirds full.

On each day, the behaviour of all 12 birds in each room was recorded on videotape for every alternate 15 min, commencing at 12.05 h and ending at 17.50 h. The recording and analysis of videorecordings was done in the same way as in Experiment 1.

Statistical analyses

It was assumed that the six battery tiers in the two rooms could be regarded as independent, because all four birds on a tier received the same treatment at the same time, and they could see each other but not birds on other tiers. For the analyses, the 6-h test was divided into four 1.5-h periods (12.00-13.30, 13.30-15.00, 15.00-16.30 and 16.30-18.00 h), each containing three of the 15-min observations. There were thus two periods before feeders and drinkers were returned at 15.00 h, and two afterwards. Within each of these periods were calculated the total numbers of minutes in which each activity was seen on each tier with each treatment (4 birds x 3 x 15 min=180 maximum). These values were transformed by empirical logistic transform, and then compared by split-plot ANOVA, with tiers as plots, to measure the significance of effects of treatment, time period, and their interaction. This was done with each of the seven activities, and also with combinations of both oral stereotypies (object pecking plus drinker activity) and total oral activity (the stereotypies plus preening). The results presented in Table 4 are back transformed means, expressed as proportions of time.

Overall mean numbers of minutes spent in each activity in each time period were expressed as proportions of time (see Results, Figure 4). Significant differences between treatments within periods were identified from the above ANOVAs, using the (treatment x time) standard errors of differences between means. This was done to identify changes in behaviour during and after feeder and drinker removal. A separate analysis was done with drinker activity because it was totally precluded for either 0, 1.5 or 3.0 h, and hence, unlike other activities, was not balanced across treatments. It was analysed by "residual maximum likelihood" tests (Welham & Thompson, 1992), to compare treatment means within the two periods after return of feeders and drinkers.

RESULTS

Treatment effects over the 6-h test

The only significant (P<0.05) effects of experimental treatment over the whole 6-h test were with sitting and drinker activity (Table 4). Thus, as the duration of feeder and drinker removal increased, sitting increased and drinker activity (and total stereotypy) decreased. Preening and object pecking did not differ between treatments, nor did total oral activity. There were significant effects of time period on all activities except pacing, and significant interactions between treatment and time with all activities except standing and pacing.

Table 4. Overall mean (n=6) proportions of time spent in different activities, in all time periods (12.00 to 18.00 h), by individually caged restricted-fed broiler breeders whose feeder and drinker were removed for either 0, 1.5 or 3 h, and significance of effects of treatment, time period, and their interaction, from ANOVA. Analyses of variance were done with empirical logistic transformed data, and the values shown are in the observed scale (from back transformations), expressed as proportions. [1]Object pecking + drinker activity. [2]Object pecking + drinker activity + preening. Within rows, means with different superscript are significantly different. *P<0.05; **P<0.01; ***P<0.001; NS, not significant (P>0.05).

	Duration of feeder and drinker removal			Significance of effects		
Activity	0 h	1½ h	3 h	Treat-ment	Time period	Treatment x Time
Sitting	0.1[a]	0.3[ab]	0.9[b]	**	***	***
Standing	33.3	32.1	30.2	NS	*	NS
Head out	14.0	13.3	17.5	NS	***	*
Pacing	4.8	4.5	4.5	NS	NS	NS
Preening	15.8	14.7	14.5	NS	***	*
Object pecking	11.1	12.8	10.3	NS	***	**
Drinker activity	15.1[a]	6.0[b]	2.3[c]	***	***	***
Total stereotypy[1]	27.5[a]	23.1[ab]	17.0[b]	*	***	***
Total oral activity[2]	45.1	44.1	40.1	NS	***	***

Differences in behaviour during removal of feeders and drinkers

Feeder and drinker removal totally precluded drinker activity but not object pecking, some of which continued to be directed at the common trough in front of the cages. Object pecking was not suppressed significantly by removal of the empty feeder in the first time period (t=1.32, comparing 3 h removal with the control treatment in the same period by ANOVA, all t values have 45 degrees of freedom, P=0.05 when t=2.01), but it was in the second period with both the 1.5 h (t=2.77) and 3 h (t=2.46) removal treatments (Figure 4).

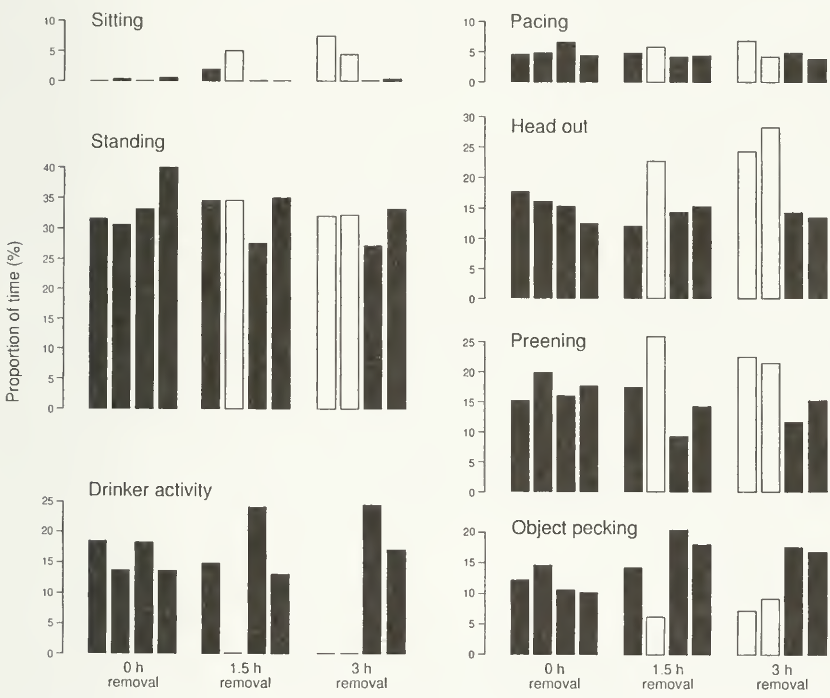

Figure 4. Mean (n=6) proportions of time spent in different activities during alternate 15 min in four time periods (12.00-13.30, 13.30-15.00, 15.00-16.30, 16.30-18.00 h), when feeders and drinkers were removed for either 0, 1.5 or 3 h before 15.00 h. White columns indicate the periods when feeders and drinkers were absent.

Sitting increased in the first period with the 3 h treatment (t=5.40), and in the second period with 1.5 h (t=2.87) and 3 h (t=3.31) removal. Head out of the front of the cage did not increase in the first period with 3 h removal (t=1.48), but did in the second period with 1.5 h (t=2.03) and 3 h (t=3.03). Preening increased in the first period with 3 h removal (t=2.05), but not in the second period with either 1.5 h (t=1.20) or 3 h (t=0.40) treatments. One bird showed high levels of preening most of the time, directed at the same part of its body, and this was the first instance in our work with broiler breeders where the preening observed was unambiguously stereotyped. There were no other significant changes during feeder and drinker removal.

Differences in behaviour after return of feeders and drinkers

In the two periods after return of feeders and drinkers, there were no differences between treatments in either sitting, standing, head out, or pacing. Compared with the control treatment in the same period, preening was reduced with the 1.5 and 3 h removal treatments in the third (t=2.26 and 2.33) but not the fourth (t=0.90 and 1.52) period. Increased object pecking in both periods (Figure 4) was significant only with the 1.5 h treatment in the third period (t=2.04, other t values 1.62, 1.94, 1.29). From the residual maximum likelihood tests, drinker activity with both 1.5 and 3 h treatments increased significantly ($P<0.01$) in the third period (c^2=6.80 and 7.38, respectively, with 1 degree of freedom), but neither differed from the control treatment in the fourth period (c^2=0.11 and 2.11). When object pecking and drinker activity were considered together, they increased with 1.5 and 3 h treatments in the third (t=2.31 and 1.98) but not the fourth (t=1.17 and 1.47) period. There was no difference in these activities between the 1.5 and 3 h treatments in either period.

DISCUSSION

When results in Experiment 1 from caged restricted-fed broiler breeders are compared with those obtained previously from grouped birds kept in pens (Kostal et al., 1992; Savory & Maros, 1993), times spent sitting (the only index of consistent inactivity) were similarly low in both environments, reflecting a positive correlation between general activity and the level of food restriction imposed (Savory & Maros, 1993; Savory et al., 1996). Times spent in preening and other forms of oral behaviour were also broadly similar, but penned birds showed less standing and more pacing than caged birds. The increases before feeding in pacing (in pens and cages) and head out behaviour (some of which may represent forward movement blocked by the cage front) presumably reflect anticipation of food delivery.

The fact that object pecking and drinker activity were minimal before and maximal immediately after a regular meal, with both EF and LF birds (Figure 1), indicates that such stereotypies are stimulated by food consumption, regardless of time of day. This was also evident from similar findings in restricted-fed pigeons, when their daily meal was shifted by 12 h (Palya & Zacny, 1980), and restricted-fed sows given one meal a day or two (Jensen, 1988; Rushen, 1985; Terlouw et al., 1991, 1993). The oral stereotypies of pigs (mainly chain manipulation and excessive drinking) were elicited specifically by ingestion of food, and not by exposure to a loud novel sound (Terlouw et al., 1993). It has been suggested that they represent persistence of (unfulfilled) foraging behaviour after all food is eaten (Lawrence & Terlouw, 1993; Terlouw et al., 1993). Feeding activity is presumably reinforced by ingestion of food, and may continue in apparently inappropriate form in the absence of cues normally associated with satiety. This idea is based on a model proposed by Hughes & Duncan (1988), in which an animal's behaviour gets into a "closed loop" when it does not have appropriate functional consequences, or does not have them soon enough.

Oral stereotypies of broiler breeders may be similarly explained. Object pecking was most commonly directed at the inside of the empty feeder, and presumably arose through birds continuing to peck at food particles remaining after they had eaten their ration. It can therefore be regarded as an extension of normal feeding, and its development into a stereotypy may be due at least partly to continued presence of visible particles too small to grasp. Drinker activity could also be an integral part of extended feeding behaviour, because, in unrestricted fowls, food and water consumption are correlated (Savory, 1978) and most drinking occurs immediately before, during or after spontaneous meals (Yeomans, 1987). While some of the drinking after the daily meal (Figure 1) presumably reflects normal food-related thirst (Toates, 1978), each bird's consumption of most of its daily 1 litre water supply (reflected by very wet faecal droppings) greatly exceeded the 114 ml that would be expected with (unrestricted) daily food intake of 58 g (Savory, 1978). Such excessive drinking may induce oropharyngeal and gastric stimulation additional to that provided by consumption of the meal (Terlouw et al., 1993). Mean hourly levels of object pecking and drinker activity declined in parallel after feeding (Figure 1), and were correlated ($P<0.01$) in both EF and LF birds. This indicates further that they are closely linked, that they may have common cause and function (Savory & Maros, 1993), and hence that it was justifiable to sum them here for assessment of individual variation.

Stereotypies and adjunctive behaviours have been assumed by some to reflect increased arousal (as defined by Delius, 1970) associated with frustration of specific motivational state(s), or with non-specific arousing stimuli (Berkson & Mason, 1964; Dantzer, 1986; Fentress, 1973; Killeen et al., 1978; Odberg, 1978). This assumption remains contentious (Lawrence & Terlouw, 1993) because of a lack of conclusive physiological evidence to support it. Nevertheless, it is possible that activities (mainly locomotor) that increase before anticipated mealtimes (Evans, 1971; Kostal et al., 1992; Mason, 1994; Mistlberger & Rusak, 1987; Figure 1 this paper), and those (mainly oral) that commence after feeding and then decline (Kostal et al., 1992; Jensen, 1988; Palya & Zacny, 1980; Rushen, 1985; Terlouw et al., 1991, 1993; Figure 1 this paper), reflect increasing and decreasing arousal, respectively.

Increasing arousal before a regular meal would presumably reflect anticipation, but decreasing arousal afterwards could be due to several factors. First, anticipation has ceased; second, an assumed increase in arousal caused by delivery of food may decay after feeding has ended (Killeen et al., 1978; Van der Kooy & Hogan, 1978); third, stereotypies themselves may have de-arousing consequences (Brett & Levine, 1979; Dantzer & Mormede, 1983; Dantzer et al., 1988; Hutt & Hutt, 1970). Stereotypies could thus be related to arousal in a homeostatic way (Delius, 1970; Odberg, 1993), being both stimulated by it and reducing it, just as feeding is related to hunger in unrestricted animals.

Two findings in Experiment 1 may support the notion of homeostatic control. First, individual birds' mean levels of the oral stereotypies (over all hours after feeding) were consistent on two observation days, whereas their hourly patterns were less so (Table 3). Similar consistency in stereotyped pecking over (four) days has also been found with laying hens (Blokhuis et al., 1993). Second, the secondary increases in stereotypies of some birds (e.g. EF6, EF12, LF3, LF9, Figures 2, 3) showed no evidence of extraneous causation, and might instead have been compensatory (the data from EF12 suggest different levels of compensation on the two days).

In Experiment 2, intended to test this homeostasis hypothesis, feeder and drinker removal in the first half of the 6-h test caused the overall mean proportion of time spent then in both oral stereotypies together to fall from 29% to 8% (from values in Figure 4). This reduction was balanced by corresponding increases in sitting (1% to 6%), head out (16% to 25%) and preening (17% to 23%), which were similar in magnitude. After return of the feeders and drinkers, the only significant effects of the removal treatments were with preening, which decreased in the third period, and the two oral stereotypies, which increased in the third period. The increase then in the mean proportion of time spent in both stereotypies together, from 29% to 43%, was greater than the corresponding decrease in preening (16% to 10%). There were no differences between effects of the 1.5 and 3 h removal treatments in the last two periods.

Preening was thus the only activity which showed significant changes, both during and after feeder and drinker removal, that were opposite to those shown by object pecking and drinker activity. This concurs with previous evidence indicating that preening can substitute with oral stereotypies in the post-feeding context (Kostal et al., 1992; Savory et al., 1992), although the results here show that this substitution may only be partial. The results also appear to demonstrate post-inhibitory rebounds in both object pecking and drinker activity, which may be the first such evidence with any stereotyped behaviour. It could be argued that some of the rebound in drinker activity may reflect physiological thirst due to water deprivation. This seems unlikely because, at moderate ambient temperatures, physiological thirst depends mainly on food intake (Savory, 1978, 1986; Toates, 1978), most drinking is closely associated with mealtimes (Yeomans, 1987), and testing here started 2.8 h after feeding had ended. Also, the commercial practice of removing the water supply from broiler breeders a few hours after feeding, to prevent soiling of floor litter, was found to have no effect on physiological indices of stress (Hocking et al., 1993).

The problem for the homeostasis hypothesis is that the size of the rebounds here did not reflect the duration of feeder and drinker removal, as predicted in the Introduction. This may not be serious, however, if preening, object pecking and drinker activity are substitutable in terms of their internal consequences (Savory & Maros, 1993). Thus, although drinker activity was reduced over the whole 6-h test with 1.5 and 3 h removal of feeders and drinkers, compared with 0 h, there were no significant differences between the three treatments with preening or object pecking, or with total oral activity (Table 4). It can therefore be argued that, instead of demonstrating homeostatic compensation in the two stereotypies after the return of feeders and drinkers, these results may demonstrate homeostasis in total (substitutable) oral activity over the whole test. Hence, they could be consistent with a working hypothesis that homeostasis of arousal underlies changes in broiler breeder behaviour before and after feeding time.

ACKNOWLEDGEMENTS

This work was carried out while L.K. was supported at the Roslin Institute (Edinburgh) by a Wellcome Trust Fellowship. It was part of a commission from the UK Ministry of Agriculture, Fisheries and Food. We wish to thank David Waddington for help with statistical analysis and Jacqui Mann for technical assistance.

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