Territoriality and time budget of breeding Coots

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Introduction

The way which animals divide their time to meet the requirements of maintenance, growth and reproduction indicates much about their ecological niche (Pianka 1983:270). The breeding season may be the most crucial time for an animal successfully to resolve these conflicting demands. This paper seeks to show how the Coot *Fulica atra*, a predominantly herbivorous bird of freshwater marshes, allocates its time during the breeding season. Although a detailed time budget of an allospecies *Fulica americana* is available (Ryan and Dinsmore 1979), published data on the behaviour of *F.atra* are qualitative (Kornowski 1957; Wagner 1962; Glutz von Blotzheim *et al.* 1973; Cramp *et al.* 1980). Data have been collected quantitatively on Coot behaviour in order to determine the reproductive roles of the two sexes, and changes in behaviour throughout the breeding cycle. Marshes form very variable environments for breeding birds (Orians 1980), because the distribution and availability of resources, such as food or nesting vegetation, may change quickly. Dependence on these resources is probably greatest during the breeding season, and one strategy to ensure access to them is to defend a territory. Coots use this strategy and are well known for their impressive territorial disputes during the breeding season (Huxley 1934; Cramp 1947; Kornowski 1957; Wagner 1962; Fjeldså 1977). Therefore the cost of being territorial was analysed in terms of the amount of time spent in territorial behaviour during the breeding cycle.

Study area and methods

Pairs of Coots were observed (from a car or hide) on two marshes (La Capelière, 8.2 ha, and Baisse basse, 2.5 ha, on Tour du Valat) in the Camargue (44°N, 5°E), a wetland region at the mouth of the river Rhône on the Mediterranean coast of France. Both marshes had extensive areas of open water (providing submerged food) surrounded by reedbeds of *Phragmites australis* (providing nest sites). Their water level being maintained, they provided all the attributes of good nesting habitats for Coots (Salathé 1986). Yet, probably due to food depletion, Coots left these marshes during winter to recolonise them at the beginning of the breeding season in early March.

During 1983 and 1984 7 pairs were observed for a total of 280 bird-hours through 10 x 40 binoculars at distances of 5–50 m. Behaviour was recorded by instantaneous, focal-animal sampling (Altmann 1974) every 30 s for periods of one hour distributed equally throughout the day (06.00–21.00h local daylight saving time). All observations were diurnal, as Coots rested or slept hidden in dense vegetation during the night.

Both members of one, sometimes two, pairs of Coots were watched simultaneously. Sex was determined using sex-specific calls (Wagner 1962) and size differences. Within a pair the larger bird and the bird with the larger frontal shield was considered to be the male. This technique has been shown to be reliable by comparison with sex-specific calls and behaviour (courtship). Pairs were easily identified because of their highly territorial nature.

We have divided the reproductive season into three parts: (i) the pre-laying period from the beginning of territorial defence to the laying of the first egg, 3rd–26th April, (ii) the laying-incubation period, from the laying to the hatching of the first egg, 10th April to 12th May, (iii) the young-rearing period, from the hatching of the first egg until we were no longer able to locate the brood, or the young became independent and gathered in large groups (about 60 days after hatching), 10th May to 27th June.

Twelve categories of behaviour were recognized. These were defined as follows:

Feeding – actively searching for or ingesting food.

Intraspecific aggression – territorial chases, stereotyped postures such as the "low-posture", "neck-ruff-posture" and "shield-showing" (Cramp *et al.* 1980), and actual fights.

Interspecific aggression – aggression directed at individuals of other species

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(mainly ducks and moorhens).
Defence against predators – defensive threats against raptors, gulls and herons (large species).
Locomotion – swimming (mostly) and walking; only recorded when not occurring simultaneously with other behaviour (e.g. feeding, aggression and carrying nest-material or food for young).
Loafing – standing or floating idly; not engaged in any other behaviour.
Maintenance – preening, bathing or comfort movements (if they occurred during incubation, they were scored as incubation and not as maintenance).
Incubation – incubating the clutch or brooding small chicks; both sometimes occurred together with preening or nest-building activities.
Courtship – courtship preening, precopulatory chases, mounting and copulation.
Nest-building – obtaining, carrying or manipulating material for construction of nests or brood platforms (if this occurred during incubation, it was scored as incubation and not as nest-building).
Feeding of young – carrying and searching for food and feeding chicks.
Miscellaneous – calling, aggression directed at young ("tousling" Horsfall 1984a) and vague behaviours.

Time budget data were expressed as percentages. The sample unit for statistical analysis was 1 bird-hour, made up of a maximum of 120 spot observations. As Coots were not always visible, all percentages were calculated from the amount of time birds were visible. Only sample hours in which birds were visible for at least 30 spot observations were used in this analysis. Examination of coefficients of variation showed that this did not effect the result. Percentage data were arcsine transformed. If variances were homogeneous, comparisons were made using 1-way ANOVA. If the ANOVA was significant, Student-Newman Keuls procedure was used to detect which differences were significant. If the variances were heterogeneous, an approximate t-test was used for further calculations (Sokal and Rohlf 1981). We chose the 0.05 level of significance.

Results

Coots were visible on average 84.2% of the time. Visibility did not differ between the sexes (males mean = 85.0%, females mean = 83.4%, $F_{(1;278)}=0.49$) nor between different periods of the day (06.00–10.00h: 85.0%, 10.00–14.00h: 81.4%, 14.00–17.00h: 84.8%, 17.00–21.00h: 86.5%, $F_{(3;276)}=1.08$) but visibility did differ between the periods of the reproductive cycle (pre-laying: 77.4%, laying-incubation: 93.3%, young-rearing: 82.5%, $F_{(2;277)}=20.89$, $P<<0.001$). Visibility was greatest during the laying-incubation period, because at least one member of a pair could be watched continuously while incubating. In other periods, both partners

Table 1. Significance levels resulting from tests comparing time budgets during four diurnal periods. Time periods are 06.00–10.00, 10.00–14.00, 14.00–17.00 and 17.00–21.00h local daylight saving time[a]), 0 = the respective behaviour did not occur; 1 (2) = only one (two) diurnal periods in which the respective behaviour occurred; * = $P<0.05$, ** = $P<0.01$.

Behaviour	Pre-laying		Laying-incubation		Young-rearing	
	male	female	male	female	male	female
Feeding			*	*		
Feeding of young	0	0	0	0		*
Intraspecific aggression				**	*	2
Interspecific aggression	**	2		*	*	
Defence against predators	1		1	1		
Locomotion				*		
Loafing						
Incubation (Brooding)	0	0	*	*		
Maintenance					*	
Courtship			**	*		
Nest-building						

a) respective sample sizes of bird-hours for the four diurnal periods are: pre-laying: n=4,15,9,9; laying-incubation: n=7,13,13,12; young-rearing: n=10,15,10,14 for each sex.

often simultaneously disappeared in dense vegetation. This was most obvious later in the season, while rearing chicks.

Most behavioural categories were equally distributed throughout the day (Table 1). However, during the laying-incubation period males incubated more and fed less as the day progressed, while females did the opposite (Figure 1, Horsfall 1984b). The other significant differences in Table 1 were probably either a consequence of this (e.g. increased aggression by females late in the day was because they incubated early in the day) or were due to high variability in categories that occurred infrequently (e.g. interspecific aggression and courtship). Because of this, all further analyses were made on data pooled over the whole day.

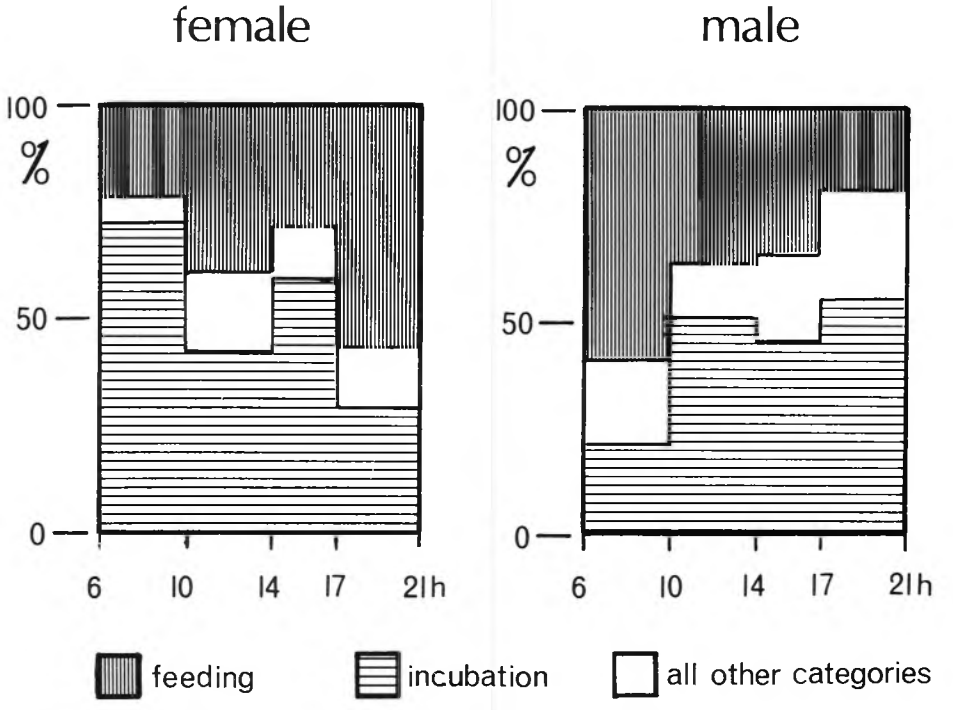

Figure 1. Allocation of time by breeding Coots during the laying-incubation period. Mean percentages are shown.

Allocation of time through the breeding season

(i) Pre-laying period

The pre-laying period was characterised by the establishment of territories, so intraspecific aggression was highest in this period for both sexes (Table 2). Most of the locomotion category was due to birds involved in territorial defence by swimming about the territory seeking out any intruders that may have entered (see also Ryan and Dinsmore 1979). Actual fights with neighbouring Coots were seen about every second day of observation and interspecific aggression was regularly directed at Moorhens *Gallinula chloropus*, ducks *Anas platyrhynchos*, *A. querquedula*, *Aythya ferina*, Herons *Ardea cinerea* and Coypus *Myocastor coypu*, if these entered the Coots' territory. The commonest activities during this period were, however, foraging and, to a lesser extent, maintenance and loafing. A surprisingly small percentage of time was needed to construct nests and platforms during this period, and even less in the later periods when nest-building consisted simply of repairing existing nests or building brood platforms for small chicks.

Table 2. The allocation of time by breeding coots. Mean (± S.D.) percentages and results of statistical comparisons are shown: A = pre-laying vs. laying-incubation period, B = laying-incubation vs. young-rearing period, C = pre-laying vs. young-rearing period, and D = comparison of males vs. females. * = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$.

Behaviour	Pre-laying male n=47 hrs female n=47 hrs	Laying-incubation male n=45 hrs female n=45 hrs	Young-rearing male n=49 hrs female n=47 hrs	Statistical		
Feeding						
male	54.6±17.7	34.8±27.1	17.4±14.0	A***	B**	C***
female	74.4±17.4 D***	37.8±29.4	17.4±18.8	A***	B***	C***
Feeding of young						
male			50.1±29.2			
female			56.0±32.9			
Intraspecific aggression						
male	2.5± 3.2	2.0± 3.9	1.0± 2.8			C**
female	1.2± 2.3 D***	0.5± 1.0 D*	0.7± 2.6			C*
Interspecific aggression						
male	0.8± 1.3	0.3± 0.6	0.3± 0.7	A*		C*
female	0.4± 1.4 D**	0.4± 0.9	0.2± 0.5			
Defence against predators						
male	0.4± 2.5	0.0± 0.1	0.6± 1.6		B**	
female	0.5± 2.5	0.0± 0.1	0.5± 1.4		B**	
Locomotion						
male	12.7± 8.3	4.5± 5.6	3.0± 3.8	A***		C***
female	7.7± 6.6 D***	3.1± 3.4	2.7± 3.8	A**		C**
Loafing						
male	7.5± 8.7	0.3± 1.0	2.4± 5.9	A***	B*	C***
female	5.4± 9.3 D*	0.7± 2.9	3.0± 8.6	A**		C*
Incubation (Brooding)						
male		48.4±35.3	11.1±25.0			
female		50.1±36.6	10.4±26.1			
Maintenance						
male	9.9± 7.3	5.5± 6.3	11.7±14.5	A**	B*	
female	6.1± 6.4 D***	3.6± 5.5	7.6±10.8	A*		
Courtship						
sexes combined	1.8± 2.0	0.4± 0.7	0.3± 1.3	A***		C***
Nest-building						
male	8.5± 9.9	3.7± 6.1	1.4± 5.3	A**	B**	C***
female	1.1± 3.8 D***	3.2± 6.5	0.8± 2.9	A*	B**	
Miscellaneous						
male	0.8± 1.3	0.2± 0.5	0.8± 1.5	A*	B*	
female	1.1± 2.0	0.3± 0.6	0.6± 1.4	A**		

(ii) Laying-incubation period

The main occupation of the Coots in this period was incubation (Table 2). After three to five eggs had been laid, the clutch was continuously incubated. Thus only half of this period was available for other activities. Two thirds of the remaining time were used for feeding. The decline of maintenance preening and loafing between the pre-laying and laying-incubation periods may be due to the fact that they were not scored if they occurred during incubation. Similarly the decline in nest-building activities was because the nest was generally repaired during incubation. Towards the

end of the incubation period, however, pairs generally built at least one brood platform. Territorial behaviour (intra-and interspecific aggression) was reduced to only the most urgent disputes with intruders, and swimming about the territory (locomotion) was reduced by more than half. Courtship decreased markedly once all the eggs had been laid. During the pre-laying period one copulation was observed on average every 5.8 hours, but this declined to one every 7.5 hours in the laying periods.

(iii) Young-rearing period

During this period Coots spent up to half of their time feeding young. This resulted in significant changes in many behavioural categories (Table 2). Small chicks attracted predators such as Marsh Harrier *Circus aeruginosus*, Black Kite *Milvus migrans*, Yellow-legged Herring Gull *Larus cachinnans* and Carrion Crow *Corvus corone*, so parental defensive behaviour increased. Nest building behaviour decreased further, as the construction of brood platforms did not take long. Maintenance behaviour increased up to the values of the pre-laying period. Brooding only occurred at night and when the chicks were small, so it was seen infrequently. Finally intraspecific aggression was lowest during this period, as neighbouring pairs were fully occupied feeding their young.

The role of the sexes

The differences between the time budgets of males and females were extremely marked during the pre-laying period, but practically non-existent during the laying-incubation and young-rearing periods (Table 2, rows D). Males were responsible for most aggressive (intra- and interspecific) and territorial (locomotion) behaviour and constructed most of the nests. Females spent significantly more time feeding than males during the pre-laying period. This extra feeding may be necessary for clutch formation (Alisauskas and Ankney 1985). Because of this females spent less time in maintenance and loafing than did males. Incubation was shared equally by the sexes. Males spent more time in intraspecific aggressive encounters during the laying-incubation period. They frequently displacement preened after aggressive encounters, which caused the difference in the amount of maintenance behaviour between the sexes during this period. The situation was similar in the young-rearing period. Males spent more time in maintenance and slightly more in aggressive behaviour, while females fed the young more, however, differences were barely significant.

Discussion

The allocation of time by breeding Coot in this study showed close adaptations to the environment in which they bred. Being largely herbivorous, they spent a large amount of time in search of, and ingesting, submerged macrophytes and algae. The amount of time spent foraging changed in relation to the demands of reproduction was greatest in the pre-laying period but decreased during the laying-incubation and young-rearing periods when half of the day was spent incubating or feeding young.

Several pairs of Coot occupied the study marshes at the beginning of each breeding season (4/5 pairs in 1983–84 at La Capeliere and 3 pairs in 1984 at Baisse basse). By establishing exclusive territories (average size = 0.7 ha), they ensured access to nesting and brooding sites and to an area of open water (average = 0.5 ha) providing submerged vegetation and emergent insects as food. To establish and defend the territory during the pre-laying period, they spent up to a sixth of their time in territorial activities. This included much swimming about the territory which was an integral part of territorial vigilance. Time budget data showed that males spent more time swimming about the territory and repelling intruders than did females. Furthermore, males did not incubate much during the morning, when territorial disputes were commonest (Horsfall 1984b). In general, and within each pair, males are larger than females (Glutz von Blotzheim 1959; Glutz *et al.* 1973; Cramp *et al.* 1980). This is probably a consequence of female selection for larger and heavier males which are better suited to territorial disputes. During the laying-incubation and young-rearing periods, the territories having been established, territorial (locomotion) and aggressive (intra- and interspecific) behaviour was significantly reduced, but still occupied 4 to 7% of the time. Interspecific aggression occurred in all periods, but was highest in

the pre-laying period. Similarly males attacked more intruders than females. Some (ducks, Moorhen) were potential competitors for food, others (raptors, Heron) were a potential threat to small chicks.

Another striking difference between the time budget of males and females was that females spent much more time feeding in the pre-laying period than did males. Production of eggs obviously requires a great deal more energy than the production of spermatozoa. This major energy demand occurs during the pre-laying period as rapid synthesis of yolk begins seven days before ovulation. Rapid acquisition of protein reserves for clutch formation may play an important role in the timing of laying (Alisauskas and Ankney 1985). Later, during the laying-incubation and young-rearing periods, both sexes took an approximately equal share in incubation and feeding young. Both these categories were important and took half of the time available. Territorial Coot need to spend much time and energy in establishing the territory in the pre-laying period. But this enabled them to devote most of their time to urgent needs, such as incubation, feeding and feeding of young, during the laying-incubation and young-rearing periods, avoiding disputes and fights over food patches.

A very similar study was undertaken in Iowa on the allospecies *Fulica americana* by Ryan and Dinsmore (1979). In general, the time budget of the American Coot was quite similar to our data on *F. atra*. These behavioural adaptations to their habitat seem to be the same in the Nearctic as in the Palearctic. American Coot spent most of their time feeding, in territorial advertisement and defence (locomotion and intraspecific aggression), and in maintenance. There was a similar decline in aggressiveness and locomotion between the pre-laying and the laying-incubation periods, and marked differences between the sexes (males devoted more time to territorial behaviour while females fed more). Interestingly they found differences between the sexes in nearly all the categories during the young-rearing period. Males fed themselves and the young less, while females devoted less time to aggression, locomotion, loafing, maintenance, and nest-building. These authors mentioned difficulty in distinguishing between self-feeding and feeding young, and this may well explain the differences from our study, where the respective percentages are reversed. In both species, adults spent 60–80% of their time self-feeding and feeding the young. The proportions of intra- and interspecific aggression obviously depend on the presence of territorial intruders, and may vary from one site to another and through the breeding season. Furthermore the American study did not separate defence against predators from interspecific aggression and excluded all observations of incubating birds. Therefore, comparisons should not be pushed too far. In general, however, both Coot species are very similar.

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Summary

The time budget of breeding Coot *Fulica atra* was studied in the Camargue, southern France. The amount of time Coot spent feeding was highest during the pre-laying period, and declined after egg-laying. Females spent about half as much time again feeding during the pre-laying period as did males, and this was probably related to clutch formation. During the same period males spent more time in territorial advertisement and territorial defence. Incubation and feeding of young was shared equally by the sexes. Variability in resources in the marsh habitat probably forced Coot to compete for good territories. Thus territorial behaviour during the pre-laying period occupied up to 16% of the time budget. The allocation of time by Coots was very similar to that of its American allospecies *Fulica americana*.

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