Parent-offspring aggression in moorhens

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Summary. The purpose of this study was to explain parental aggression to offspring in the moorhen (*Gallinula chloropus*). Males and females did not feed different subsets of chicks. In addition, there was a positive correlation between feeding rates of each parent to a particular chick and the number of attacks (tousles) directed to that chick, contrary to what was expected if aggression served to divide the brood. In moorhens, large chicks outcompeted small chicks for parental feedings. However, adults were more aggressive to large chicks and as a result small chicks spent significantly more time closer to parents and received more feedings than large chicks. In 84% of broods every chick was attacked at least once, although large chicks were attacked more often than small chicks. The behaviour of chicks changed immediately after an attack (Table 2). Before an attack chicks were <1 m from the parents while after an attack they were >1 m. The apparent effect of parental aggression in moorhens is to reduce demands by chicks for feedings. Aggression appears to reduce sibling competition and to encourage chick independence.

Introduction

Parents and offspring are expected to disagree about the timing of independence (Trivers 1974) and they may also disagree about the loss of siblings in species that practise brood reduction (O'Connor 1978). Aggressive interactions between parents and offspring are often taken as indicators that conflict exists. Aggression is particularly obvious during weaning in mammals (Hinde and Spencer-Booth 1971; Nash 1978; Berger 1979), but overt aggression of this nature is not usually observed in birds (for exceptions see Schaller 1964;

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Brown and Urban 1969; Elliot 1969; Rowe 1947). The prevalence of parental aggression in the Rallidae is therefore of special interest. Parents have been observed to attack young in white-throated rails (*Dryolimnas cuvieri*; Wilkinson and Huxley 1978), European coots (*Fulica atra*: Horsfall 1984), moorhens (*Gallinula chloropus*; Gibbons 1985), pukekos (*Porphyrio porphyrio*; Jamieson, personal communication) and American coots (Lyon personal communication). Several hypotheses may explain the function of aggression in rails:

1. Brood division hypothesis

In some species the brood is divided between the parents, so that each parent will care for particular chicks (Horsfall 1984). Aggression may serve to divide the brood. That is, parents may feed "in" chicks and attack "out" chicks, presumably to discourage them from begging and following that parent.

2. Sibling competition hypothesis

In some species there is a size hierarchy among the chicks (Horsfall 1984; Gibbons 1985). This hierarchy is often the result of hatching asynchrony, but may also exist because of sexual differences. If large chicks could outcompete small chicks for parental feedings then parents may use aggression to ensure that smaller chicks receive sufficient food. This hypothesis assumes that parents and larger/older chicks may be in conflict about how much food smaller chicks should receive and whether smaller chicks should survive (O'Connor 1978).

3. "Weaning" hypothesis

Rail chicks depend on their parents for food and shelter after hatching. Parents may use aggression

to force chicks to independence. This hypothesis suggests that parents and offspring may be in conflict about the timing of independence (Trivers 1974).

These hypotheses make the following predictions:
1. If parents are aggressive to divide the brood then: a) each parent should feed only certain chicks and b) each parent should be aggressive to the chicks that they do not feed.

2. If parents are aggressive to reduce sibling competition then: a) in the absence of aggression large chicks should have a competitive advantage over small chicks, b) parents should be relatively more aggressive to large chicks, and c) aggression should discourage large chicks from begging and thus increase feedings to small chicks.

3. If parents are aggressive to force chicks to independence then: a) all chicks, regardless of size, should be attacked, although the timing of attacks may be size dependent, b) parental feeding rates to chicks should decrease as aggression increases over the season and after each attack, and c) females may be more aggressive than males. This last prediction should hold if females need to wean chicks earlier than males to gather resources for the production of a second clutch.

The purpose of this study was to determine which hypothesis best explains parental aggression in the moorhen. Moorhens attack ("tousle", Horsfall 1984) their young by grabbing them about the neck and shaking them vigourously (Gibbons 1985). They are ideal for such a study because they are thought to divide their broods (Wood 1974), their eggs hatch asynchronously (Gibbons 1985), thus producing a size hierarchy, and their chicks are precocial with an extended period of dependence. In addition, they produce two broods per season on average (Gibbons 1985).

Methods

This study was conducted at Peakirk Waterfowl Gardens in Cambridgeshire from April to August, 1987. Twenty-one pairs of birds were used in this study, 89% of which were individually colour marked. Nests were found by observing breeding pairs and by twice-weekly searches of breeding sites. First egg date and clutch size were recorded. Nestlings were colour-ringed, weighed, and measured (tarsus-toe) at hatch. Twenty-six chicks were trapped and measured between 40 and 45 days of age. They were then sexed according to size differences (see Gibbons 1985).

First broods were observed every four days beginning when the oldest chick was four days old and continuing for 40 days (i.e. for a total of 10 observation periods/brood). Each adult was observed for 30 min and the number of feeds and tousles

given, the identity and location of the chick involved, and the time spent at all activities (foraging, preening, territory defence, standing etc.) were recorded continuously. When possible we observed all chicks simultaneously for 30 min. However, if the brood was dispersed, each chick was observed individually for 10 min. The number of feedings received, the identity of the feeding parent, the number of tousles and time spent at the above behaviours were recorded continuously. A scan of the whole brood, including parents, was done every 5 min and the location of each chick relative to each parent was recorded. When possible the relative size of the chicks was recorded. In our analyses we compare only the largest and the smallest chicks in the brood because the sizes of intermediate chicks were often ambiguous. Tousle rate refers to the number of tousles per minute of observation time, while feeding rate refers to the number of chick feedings per minute of observation time. An alternative measure of tousling rate would be the number of tousles/time the chick was close to the parent (<1 m). This would give the intensity of tousling given the chick was close and therefore may reflect the chicks' decision of whether to approach the parent. However, we are mainly interested in tousling as a parental strategy. Gibbons (1985) has used the former method and his results are consistent with ours. All means are $\pm$SD and all tests are one-tailed unless noted otherwise. Statistical significance was set at 0.05.

Results

In this study adults tousled chicks by grabbing their head or neck in their bills and shaking the chick laterally. Tousles varied in severity from light to vigourous shakes and in the most aggressive cases the chicks were lifted from the ground.

Brood divison hypothesis

We considered brood division to occur if each parent only fed certain chicks. Moorhens did not show such direct asymmetries in parental feeding (Table 1). Apparent asymmetries (e.g. to chick 2 in brood

Table 1. Total feeds given to individual chicks by each parent over the dependent period. Five broods were chosen at random to represent the general trends. Statistics in text were based on the entire data set

Brood	Parent	Chicks			
		1.	2.	3.	4.
1.	Male	31	33		
	Female	5	37		
2.	Male	26	49	35	18
	Female	134	54	51	94
3.	Male	118	14		
	Female	63	64		
4.	Male	140	105		
	Female	52	15		
5.	Male	13	8	3	73
	Female	13	7	24	31

4, Table 1) arose because parents provisioned in long bouts to each chick. Because parents fed in bouts, individual feeds were not statistically independent, so we could not test for brood division using categorical analyses such as χ^2 or binomial tests.

However, if each parent fed a particular subsample of chicks then there should be a negative correlation between the total number of feedings to individual chicks over the season by the male and the female. However, males and females did not feed different chicks ($r_s = 0.144$, $n = 32$, $P > 0.25$, Table 1). Also, if this analysis is done per observation period (i.e. total feed of each parent to individual chicks during each observation period) there was no significant correlation between feedings by males and females in 10 of 10 observation periods.

A negative correlation would also be expected between feeding rates of each parent to a particular chick and the tousle rate (tousles/min) of that parent. However, chicks that were fed by a particular parent were tousled more often by that parent ($r_s = 0.252$, $n = 55$, $P < 0.05$), contrary to the above prediction.

Sibling competition hypothesis

Of 2124 feedings where the position of the chick was recorded, 2088 (98.3%) were to the chick closest to the adult when it found food.

Chicks were sometimes observed in direct competition for food (i.e. two chicks were at the same distance from the parent when it found food). If large chicks outcompete small chicks for food, then large chicks should get significantly more feedings than small chicks when in direct competition. Under these circumstances large chicks were fed significantly more often than small chicks (64/87, Binomial test, $P < 0.005$). Large chicks usually moved ahead of small chicks as the parent approached.

Adults tousled larger chicks more often than smaller chicks (tousles/min/chick, large: 0.025 ± 0.03; small: 0.012 ± 0.05, $n = 19$; Wilcoxon paired t-test, $T = 44$, $P < 0.025$). During the dependent period parents fed small chicks at a significantly higher rate than large chicks (feedings/min/chick, large: 0.20 ± 0.16; small: 0.40 ± 0.31, $n = 17$; $T = 24$, $P < 0.01$). This is presumably because small chicks were closer to parents more often than large chicks (number of total scans in which closer, large: 2.11 ± 2.08, small: 5.17 ± 2.62, $n = 18$; $T = 25$, $P < 0.005$). The proportion of time chicks spent foraging did not differ between the groups (large:
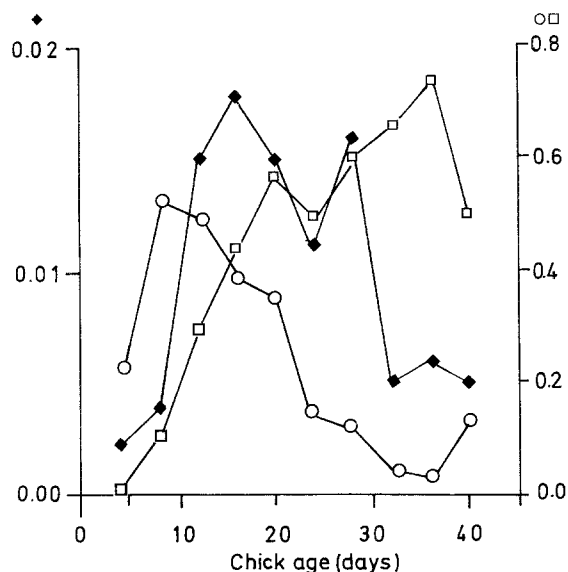

Fig. 1. Mean tousle rate, feeding rate of parents to chicks and the proportion of time that chicks spent foraging on their own for each age group (♦Tousles/chick/min; o Feeds/chick/min; □ Proportion time foraging)

0.63 ± 0.28; small: 0.56 ± 0.26, $n = 13$, $T = 42$, $P > 0.05$). In addition, the chick next fed after the tousling of a middle sized chick was smaller than the tousled chick more often than expected by chance (26/35, Binomial test, $P < 0.005$).

The difference in tousling rate with size was not related to sexual differences. Male and female chicks were tousled at similar rates throughout the season (tousles/min/chick, male: 0.01 ± 0.01, $n = 18$; female: 0.02 ± 0.01, $n = 5$; Mann-Whitney U-test, $U = 67.5$, $P > 0.10$ (two-tailed)).

"Weaning" hypothesis

If parents were aggressive to force chicks to independence then all chicks should be tousled. In 84% of broods every chick was tousled at least once, although larger chicks were tousled more often than smaller chicks. The timing of tousling also did not differ between large and small chicks. That is, the age at which the tousling rate was highest was not significantly different between the two groups (large: 21.84 ± 8.64 days, $n = 15$; small: 24.56 ± 10.12 days, $n = 14$; $U = 122.5$, $P > 0.10$). The peak of parental feeding, tousling and independent foraging occurred in that sequence (Fig. 1; Pages L-test, $L = 196.5$, $n = 15$, $P < 0.005$).

The behaviour of chicks also changed immediately (the first behaviour recorded following a tousle) after a tousling event (Table 2). In general, before a tousle chicks were < 1 m from the parent (begging, fed by parent), while after a tousle they

Table 2. Percent of tousled chicks <1 m (standing, walking, fed or begging from the tousling parent) or >1 m from the tousling parent before and after a tousling event

	Before	After
<1 m from parent		
standing, walking	11.6 (39/334)	20.6 (69/334)
fed by parent	21.3 (71/334)	1.8 (6/334)
begging from parent	60.8 (203/334)	3.9 (13/334)
>1 m from parent[a]	1.8 (6/334)	65.3 (218/334)
Unknown	4.5 (15/334)	8.4 (28/334)

[a] Includes standing, walking, foraging

were usually >1 m (foraging on their own, walking, standing). The behaviours before and after a tousle differed significantly from the behaviours before and after a feeding (before: $\chi^2 = 143.0$, $df = 4$, $P < 0.001$; after: $\chi^2 = 369.6$, $df = 4$, $P < 0.001$). This suggests that the behaviours observed before and after tousling are associated with tousling itself rather than any interaction with a parent.

Tousling rate/chick is not correlated with the time between the hatch of the first clutch and the initiation of the second clutch ($r_s = 0.04$, $n = 13$, $P > 0.25$) as would be expected if tousling was important in allowing parents to begin a second clutch. The mean tousle rate/chick was also not correlated with the size of the second clutch ($r_s = 0.36$, $n = 13$, $P > 0.25$).

Because of the high cost of egg production females may be expected to tousle more often or earlier than males. However, female tousle rate over the season did not differ from males (female: 1.41 ± 1.55, male: 1.09 ± 1.34; $T = 74$, $n = 21$, $P > 0.10$) nor did the timing of the peak tousle rate (female: 22.7 ± 8.9 days, $n = 12$; male: 19.7 ± 5.52 days, $n = 14$; $U = 101$, $P > 0.20$). The overall provisioning rate (total number of feedings/min, female: 0.47 ± 0.49, male: 0.35 ± 0.36) and the proportion of time spent foraging (female: 0.48 ± 0.17, male: 0.45 ± 0.13) did not differ between the sexes ($T = 72$, $n = 21$, $P > 0.20$ and $T = 72.5$, $n = 19$, $P > 0.25$, respectively).

Discussion

Tousling in moorhens appears to reduce demands by chicks for feedings. Thus tousling could serve both to reduce sibling competition and encourage chick independence. We have presented evidence for both functions. Larger chicks can monopolize

feedings by reaching parents ahead of smaller chicks. They are preferentially tousled, and after tousles small chicks are fed more often. Thus tousling apparently counteracts sibling competition. During the period of chick dependence, tousling rate increases as parental feedings decline, and as tousling increases, chicks spend more time feeding themselves. The absolute number of tousles then declines, although the probability of a chick being tousled when close to the parent increases (Gibbons 1985). After each tousling event, tousled chicks move away from their parents and beg less than they did before being tousled. Thus tousling also apparently encourages chick independence.

This study is one of few in which parent birds have been shown to interfere aggressively with sibling competition or offspring dependence. Horsfall (1984) documented similar behaviors in coots, but attributed different functions to them. Three questions are therefore especially relevant to our results: 1) do the functions of tousling actually differ in coots and moorhens, and if so, how, 2) how does the nature of sibling competition or weaning in moorhens differ from other birds, and, most importantly, 3) why is parental interference accomplished through aggression?

Brood division: contrasts with coots

In coots, tousling also serves to restrict access to feeds from the tousling parent. However, unlike moorhens, coots divide their broods, and tousle the chicks that they do not feed ("minor" chicks). Horsfall (1984) found no evidence for sibling competition after chicks left the nest. He concluded this by studying the few cases in which parents did not feed the closest chick, but did feed the next chick along. He predicted that larger chicks would be fed in such situations, because they would inhibit acceptance of food by closer, smaller chicks. Instead, he found that smaller chicks were fed. However, if his initial assumption of intimidation by large chicks were false, he could get this result even if there were sibling competition. In fact, in similar circumstances, moorhens also feed smaller chicks more often (unpublished data), even though the evidence for sibling competition in this species is strong.

In coots, larger chicks are fed by females, which feed chicks at a higher rate than males (Horsfall 1984). A combination of differential feeding rates by males and females, combined with sibling competition, might therefore create brood division in coots. In oystercatchers (*Haematopus ostralegus*),

for example, larger chicks, when hungry, monopolize access to the parent that is feeding the young. Because the parents take turns feeding the brood, however, brood division does not occur (Safriel 1981). In skuas (*Catharacta maccormicki*), brood division arises out of direct parental intervention in chick fights; the dominant chick is aggressively discouraged from feeding from the same parent as the subordinate chick (Young 1963). Unlike coots, male and female moorhens feed young at the same rate, so larger chicks would not gain any advantage by monopolizing a particular parent. This may explain why coots divide their brood but moorhens do not.

Sibling competition

Selective pressures favoring sibling competition include size asymmetries among siblings, low genetic relatedness among siblings (O'Connor 1978), food monopolizability (Mock 1984), and variability in food abundance (Lack 1947). In moorhens, size asymmetries are initially produced by hatching asynchrony, and later by sexual dimorphism. Prey items offered by parents are small and hence monopolizable, although we have no data on food abundance. Thus the existence of sibling competition in this species is not surprising.

The costs of pursuing smaller siblings may account for the lack of direct sibling aggression in moorhens. The young of other semi-precocial species show aggression only when confined. Young western grebes (*Aechmophorus occidentalis*) peck each other when riding on one parent's back (Neuchterlein 1981). Young oystercatchers show sibling aggression when they are confined to hiding places. Confinement in artificial enclosures increases the frequency and seasonal duration of sibling fights (Safriel 1981). Such initial confinement is lacking in moorhens, and sibling aggression, and the hierarchies that result, are not observed.

Under certain conditions, parents and their more vigourous offspring may be in a genetic conflict over whether less vigorous chicks should survive (O'Connor 1978). Evidence for such a conflict in birds is scant, partly because parents rarely interfere with competition between siblings (for possible exceptions see Ferguson and Sealy 1983; Forbes and Ankney 1987). Parent egrets, eagles, and oystercatchers have never been seen to interfere with siblicide or chases among siblings, either during or between sibling interactions. Parents in altricial species may in some cases counteract sibling competition by preferentially feeding smaller offspring (Stamps et al. 1985). Presumably bypass-

ing larger chicks to feed smaller ones is too costly for moorhen parents because their young are not confined (see also Horsfall 1984).

Weaning

Weaning conflict is expected if there is a period of mixed offspring dependence and independence (Trivers 1974). Moorhens are among the few precocial species in which chicks are intially dependent on parental feedings (Ricklefs 1983). In other precocial species in which this is the case, parent-offspring aggression has not been reported (Norton-Griffiths 1969; Simmons 1974; Neuchterlein 1981). In altricial and semi-precocial birds, weaning occurs after young leave the nest, but is accomplished without parental aggression (Davies 1976). Why should aggression occur in rallids, but not in other species in which the opportunity for weaning conflict exists?

Davies (1976; 1978) has shown that young passerines become independent as their foraging efficiency increases and begging profitability decreases. Presumably moorhens also become more efficient foragers with age (see Desrochers and Ankney 1986 for evidence for coots). However, the profitability of begging might not decrease as rapidly in moorhens, because the costs of following parents are small. Because moorhens get most of their food by gleaning and pecking, following the parent does not interrupt self-feeding substantially. Also, because offspring remain on the parents' territory and territories are relatively small, keeping near the parents should be energetically inexpensive. The resultant reluctance of chicks to feed on their own might force parents to "artificially" increase the costs of dependence through tousling.

In summary, moorhens may tousle their offspring to counteract sibling competition and to encourage chick independence. We suggest that parental aggression, which is rare in most birds, is characteristic of moorhens mainly because of their unusual combination of nidifugy and the partial dependence of offspring on parents for food. We are currently studying whether the behavioural conflicts we observed are underlain by a genetic conflict over the reproductive success of parents and offspring. We are also interested in whether tousling chicks affects the likelihood that they will help raise subsequent broods, thus suggesting a primitive "socializing" function (Trivers 1974) for parental aggression.

References

Berger JC (1979) Weaning conflict in desert and mountain bighorn sheep (*Ovis canadensis*): An ecological interpretation. Z Tierpsychol 50:188–200

Brown LH, Urban K (1969) The breeding biology of the Great White Pelican (*Pelecanus onocrotalus roseus*) at Lake Shala, Ethopia. Ibis 111:199–237

Davies NB (1976) Parental care and the transition to independent feeding in the young spotted flycatcher (*Muscicapa striata*). Behaviour 59:280–295

Davies NB (1978) Parental meaness and offspring independence an experiment with hand-reared great tits *Parus major*. Ibis 120:509–514

Desrochers BA, Ankney CD (1986) Effect of brood size and age on the feeding behaviour of adult and juvenile American Coots (*Fulica americana*). Can J Zool 64:1400–1406

Elliot BC (1969) Life history of the Red Warbler. Wilson Bull 81:184–195

Ferguson R, Sealy SG (1983) Breeding ecology of the Horned Grebe, *Podiceps auritus*, in Southwestern Manitoba. Can Field Nat 97:401–408

Forbes MRL, Ankney CD (1987) Hatching asynchrony and food allocation within broods of Pied-billed Grebes, *Podilymbus podiceps*. Can J Zool 65:2872–2877

Gibbons DW (1985) Cooperation, conflict and manipulation in the moorhen, *Gallinula chloropus*. Unpubl PhD thesis, University of Cambridge, Cambridge

Hinde RA, Spencer-Booth Y (1971) Effects of brief separation from mother on rhesus monkeys. Science 173:111–118

Horsfall JA (1984) Brood reduction and brood divison in coots. Anim Behav 32:216–225

Lack D (1947) The significance of brood size. Ibis 89:302–352

Mock DW (1984) Sibling aggression and resource monopolization in birds. Science 225:731–733

Nash L (1978) The development of mother-infant relationship in wild baboons. Anim Behav 26:746–759

Norton Griffiths M (1969) The organization, control and development of parental feeding behaviour of the Oystercatcher (*Haematopus ostralegus*). Behaviour 34:55–114

Nuechterlein G (1981) Asynchronous hatching and sibling competition in western grebes. Can J Zool 59:994–998

O'Connor RJ (1978) Brood reduction in birds: selection for fratricide, infanticide and suicide. Anim Behav 26:79–96

Ricklefs RE (1983) Avian postnatal development. In: Farner DS, King JR, Parker KC (eds) Avian Biology vol III. Academic Press, New York, pp 1–82

Rowe EG (1947) The breeding ecology of *Aquila verreauxi*. Ibis 89:576–606

Safriel UN (1981) Social hierarchy among siblings in broods of the oystercatcher, *Haematopus ostralegus*. Behav Ecol Sociobiol 9:59–63

Schaller GB (1964) Breeding behaviour of the White Pelican at Yellowstone Lake, Wyoming. Condor 66:3–23

Simmons KEL (1974) Adaptations in the reproductive biology of the Great Grested Grebe. Br Birds 67:413–437

Stamps J, Clark A, Arrowood P, Kus B (1985) Parent-offspring conflict in budgerigars. Behaviour 94:1–40

Trivers RL (1974) Parent-offspring conflict. Am Zool 14:249–264

Wilkinson R, Huxley CR (1978) Vocalizations of chicks and juveniles and the development of adult calls in the Aldabra White-throated rail *Dryolimnas cuvieri aldabranus* (Aves: Rallidae). J Zool Lond 186:487–505

Wood NA (1974) Breeding behaviour and biology of the moorhen. Br Birds 67:104–157

Young EC (1963) The breeding behaviour of the South Polar Skua. Ibis 105:203–233