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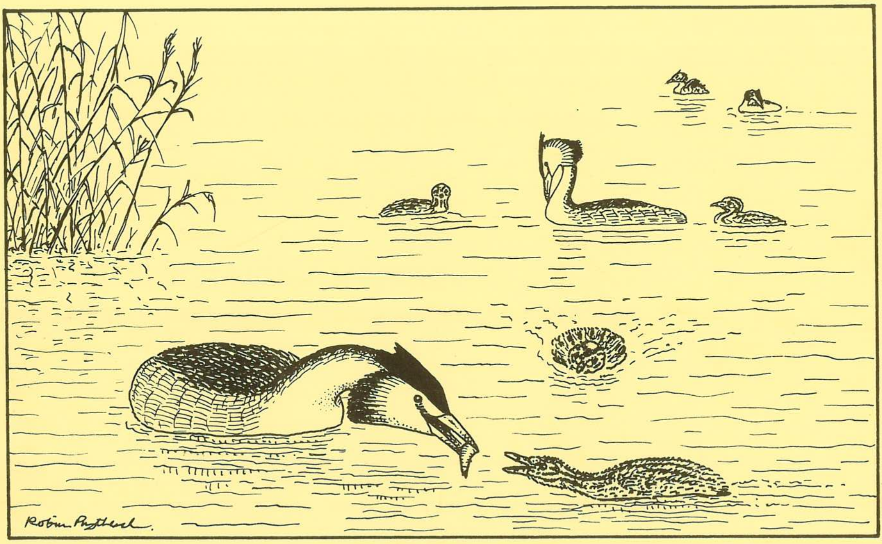

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Brood-division, Parental Favouritism and Parental Desertion in the Great Crested Grebe

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29 May 1970, after the main period of my research was over, but this was reduced to three chicks by 1 June towards the end of the carrying-phase, Chicks 4 and 5 being the ones to perish. Nor were any broods of five to come under observation during the third stage of my work in 1975-86, the single pairs nesting each year on Welham Pond, Leicestershire, rearing the following number of surviving chicks in eleven broods, of which all but the first two were followed through to independence: one (1975), three (1977), two (1979), one and two (1980), one and one (1982), four (1983), three (1984), two (1985), and four (1986), the birds being double-brooded in 1980 and 1982 but wholly unsuccessful in 1981 (there were no records for the years 1976 and 1978).

Of 31 broods recorded by me and other members of the Reading Ornithological Club at Old Theale in the period 1948-65, five had been of a single chick, 15 of two chicks, eight of three, and three of four. 47% of 124 broods at all the Berkshire sites (including Old Theale) were of two young, 25% of one, 22% of three, and 6% of four. A smaller sample of 34 broods at Chew was similar: 44% of two, 29% of one, 18% of three, and 9% of four. In the Great Crested Grebe Enquiry of 1931, out of a total of 431 broods recorded in England, Wales, and Scotland, only three were of five young (Harrisson & Hollom, 1932), a further brood of five having been noted for 1930 (see also Tucker, 1934).

Thus all the available evidence suggests that the Great Crested Grebe rarely succeeds in raising broods of more than four young in Great Britain, where it is on the northwestern edge of its Palearctic range, most consisting of one, two, or three young although viable clutches of up to six eggs are laid at times (see also Cramp & Simmons, 1977). The extra large brood at Old Theale in 1975 was of considerable interest, therefore, providing me with a rare opportunity to study the social organization of such a group, especially how the care of the young would be shared between the parents in a species which is known to practise a system of chick favouritism and brood-division, the latter resulting in the establishment of two family sub-groups in the case of broods of two or more young (see also Simmons, 1970a, 1989).

Although Burghfield GP near Reading had been my main study water in Berkshire, I visited Old Theale some 200 times in 1948-61 to check the grebes living there, especially in 1957 when the fortunes of three broods on the east pool were followed throughout the summer (Simmons, 1968, 1970b). Consisting originally of two main waters, each of some 20 acres (8.1ha), the pit was gradually being filled in during this period, the west pool finally disappearing by 1956 and the east pool reduced to about 18 acres (7.8ha) by 1957. During 1948-1958, there were always five or six breeding pairs but only one or two from 1959 onwards. None were recorded in the national census year of 1965 (Prestt & Mills, 1966) but my wife and I located two pairs on the remaining seven acres (2.8ha) of the pit during our visit there in March 1968. The discovery of a breeding pair in 1975 on the last five acres (2.2ha) of the

***Table 1** Time-table of observations on a family of Great Crested Grebes, Old Theale Gravel Pit, Berkshire, 1975.*

	Number of		Week	Estimated age of young (days)		
Date	adults	young	(see text)	youngest	eldest	observers
15/7	2	5	3	12	20	(a), (b)
2/8	2	5	6	30	38	(c)
3/8	2	5	6	31	39	(d)
9/8	1	5	7	37	45	(c)
12/8	1	5	7	40	48	(a), (e)
29/8	1	5	10	57	65	(e)
31/8	1	5	10	59	67	(c)
8/9	1	5	11	67	75	(c)
12/9	1	3	12	71	79	(c)
18/9	1	1	13	77	85	(c)
22/9	1	0	13	81	89	(c)

Observers: (a) author; (b) Marion Simmons; (c) Peter Gipson; (d) Peter Standley; (e) Robert Gillmor.

west pool came as a surprise, however, as most of this remnant area had been the least suitable for nesting grebes in 1948-61 and was now maintained and stocked as a busy angling water, the birds probably having managed to hatch their eggs there only because incubation had taken place during the fishing closed season.

Observations on a brood of five young (1975)

On 15 July, during our stay of just an hour, it was clear that both parent grebes were attending the five small young and that the brood was as yet undivided, which is the usual situation (although preferences, between adults and certain chicks and vice versa, sometimes start to form as early as this or soon afterwards). The adults were very wary, however, and no feeds occurred. The two oldest chicks were almost too large to be carried but the parents still allowed them, together with the younger ones, to climb up on their backs - usually three chicks on one adult and two on the other, but four of the five were once seen aboard the same adult. (At Villice Bay in 1970, during a watch of just under an hour, all five young had been carried by the female but, at change-over, the male prevented the two smallest chicks from boarding him and showed mild hostility towards them, this perhaps being a factor in their subsequent loss.)

As I now lived far away, I enlisted the help of members of the ROC to monitor the subsequent history of the Old Theale family for me, planning to

Table 2 *Log of time spent by a lone parent Great Created Grebe with five young in hunting (spells) and loafing (breaks), with number of feeds, Old Theale Gravel Pit, Berkshire, 12 August 1975, 10.55-17.55 GMT.*

Spell	Duration (mins)	Number of feeds (fish)	Break	Duration (mins)
1	(5)	(1)	1	25
2	38	4	2	15
3	14	6	3	14
4	29	2	4	19
5	30	5	5	9
6	38	6	6	20
7	8	1	7	22
8	14	2	8	71
9	35	7	9	8
10	(6)	(1)		
Totals:	3 hours 37 mins	35		3 hours 23 mins

Note: the first and last hunting spells were incompletely observed.

return and watch it myself on a later day. This I did on 12 August (with Robert Gillmor) - my main concern being that, like the one at Chew in 1970, the brood would be reduced to four young or fewer before I could come back. The reduction in the family that did occur was quite different however, for between 3 and 9 August, during Week 6 or 7, it was one of the adult grebes which disappeared (see Table 1), this new situation shifting the emphasis from the roles taken by two parents in caring for the five young to that of a single adult in rearing all or some of them unaided.

The observations on 12 August and subsequent visits by members of the ROC showed that the single bird did manage to rear all five young successfully, to the time of fledging at least (see Table 1), this usually occurring in Week 11 (Simmons, 1970b, 1974). Whether it was the male or female which remained was difficult to tell without the presence of the second bird for comparison but, from the size of fish caught, it must have been the male (see Table 3 which also gives data on feeds brought to the study broods in 1957 by both sexes). During the seven hours of a continuous watch on 12 August, the male divided his time almost equally between loafing (taking breaks lasting between eight and 71 minutes, mean 25 mins) and in searching for food (in spells lasting between eight and 38 minutes, mean also 25 mins), feeding the young 35 times (see Tables 2 & 3). These data indicate that the male was not finding the task of rearing five chicks difficult, almost certainly because the pool was generously stocked by the anglers with the coarse fish that comprised the staple diet of the species (especially Roach *Rutilus rutilus* and Perch *Perca fluviatilis*) and of a size which allowed for efficient parental feeding. Remembering that the weight

Table 3 *Size of 35 fish brought to its brood of five young by a lone parent Great Crested Grebe, Old Theale Gravel Pit, Berkshire, 12 August 1975, 10.55-1755 GMT, compared with size of 512 fish brought to the young of five broods (of all ages) there by parents of both sexes in 1957.*

Year:	Size category of fish:									
sex	1	2	3	4	5	6	7	8	9	10
1975: male	0	0	0	0	2	6	13	7	3	4
1957: male	1	17	3	66	31	27	42	57	7	0
1957: female	67	59	40	55	13	13	8	6	0	0

Notes. Fish size-categories (from Simmons, 1970b, 1977): 1, 'minute' (0.25in/0.7cm); 2, 'minute/tiny' (0.5in/1.2cm); 3, 'tiny' (1.0in/2.5cm); 4, 'tiny/small' (1.5in/3.8cm); 5, 'small' (2.0in/5.0cm); 6, 'small/medium' (2.5in/6.2cm); 7, 'medium' (3.0in/7.5cm); 8, 'medium/large' (4.0in/10.0cm); 9, 'large' (5.0in/12.5cm) and 10, 'very large' (6.0in/15cm).

As no females were ever seen to catch fish larger than category 9 during the first two phases of my studies, the 1975 adult is assumed to have been a male from the size of the fish it caught. It also ate at least three fish itself (of categories 7, 7 and 10) and also caught and abandoned a category 11 fish ('huge', 7.0in/17.5cm). The chicks were seen to catch two fish for themselves, one in category 4 and one in category 6.

In 48 additional feeds in 1957 (all in categories 1-8), the sex of the adult was not established.

of a fish increases as the cube of its length, most of the prey caught on this day (chiefly Roach and some Tench *Tinca tinca*) was amongst the higher categories in the prey-size range (Table 3), and represented a pretty respectable biomass of food (see Simmons, 1970b, 1977). It was clear too that, whatever the degree of brood-division which had been reached before the death or departure of the female, it did not prevent all the chicks obtaining sufficient food from the remaining adult to survive - subsequent checks showing that they did so to at least the age when they could start catching some food effectively themselves, something that most grebe chicks do by Week 8 or 9, two or three weeks before their first flight in Week 11 (when some become independent).

On the 12th, however, most of the young spent part of the time diving persistently for food, one (at least) with occasional success, suggesting that the special circumstances had caused these chicks to start hunting seriously sooner than is usual (in Week 7). In a single day's watching, it was not possible for me to differentiate consistently between the five young or to determine the distribution of food between them; nevertheless it was clear that all of them were fed by the male to a greater or lesser extent, suggesting that an inflexible system of brood-division had not yet been established by the time that the female went missing. In a brood of this large size, one would anticipate that the two adults might have taken charge of three and two chicks each, to a greater or lesser degree of exclusiveness, and that eventually each sub-brood would have operated independently of the other. Nevertheless, it was also quite clear that a degree of brood-division must have been established; not all of the young enjoyed an equal status in the family and some were favoured more than others by the remaining parent.

When starting a new loafing break, the male would be joined by one or more of the chicks, sometimes by all five if they were not off hunting by themselves. One chick would then keep at a greater distance from the adult than the others, just as it did when accompanying him while he was hunting (see below). While loafing, it often hung well off the rest, usually hiding both its bill and the facial characters which identify it to the adult by adopting the 'pork-pie' resting posture with its bare crown-patch engorged and showing bright red. Such behaviour is typical of the passive submissive behaviour of the least favoured chick in a family - which I have termed the 'odd-chick-out' (Simmons, 1970b) - suggesting that the brood had, in fact, been divided mainly two and two when both adults were still present. The behaviour of this bird contrasted to that of the other four chicks, all of which came nearer to the male though again not uniformly, only one of them coming and being allowed to remain really close to him. This latter chick obviously belonged to that class of young which I have termed the 'in-chick' - the adult's privileged chick, which alone of the brood forms a really firm and intimate bond with it, receiving preferential care (especially in feeding) and not usually eliciting its aggression.

Today, only this chick came into friendly contact with the male, the two of them loafing alone together during some of the latter's breaks, resting with bodies nearly touching at times. It frequently pestered the male, 'cadging feathers' from him, endlessly uttering the 'wheedling' call, sometimes right into his ear, and occasionally poking and prodding him with its bill, pointing and gaping at him, and even biting at his mandibles. It was the sole recipient of all seven of the 'feather-feeds' provided, and once it even pulled out and ate one of the male's feathers for itself. It would also lay its head on its parent's back (behaviour I have termed 'mock-boarding') and, more than the other chicks, it tended to 'copy-preen', i.e. attend to its plumage in the same sequence as the adult did.

None of the other young behaved in the same confident and intimate manner, showing that there was only this one in-chick; and only one of the rest habitually came near to the male and the in-chick when some or all the members of the family were loafing together - this individual, presumably, being what I have termed the male's 'out-chick' (the less favoured one in a sub-brood of two which, nevertheless, is treated better than the 'mate's young' in a divided brood). Thus, four units could be detected at times, especially when all the birds were inactive: the male and his in-chick, keeping together; the male's out-chick, lying slightly off them; the two 'female's chicks' (presumably), somewhat further off still; and the odd-chick-out, furthest off of all, though the latter would join the rest of the 'other chicks' when the male was absent. This suggests (as I have observed in other families) that it was afraid, not only of aggression from the male himself, but also of aggression from the other young induced by the presence of the male, due to inter-sibling rivalry. The male showed hostility at times to the other chicks, especially when one of them approached too close to him (e.g. was the first to join him when he took a break). The presence of the male - especially if he was particularly active (e.g. preening or bathing intensely) - sometimes induced a marked outbreak of demonstrative behaviour ('foot-splashing', 'sinking', 'gaping', etc.) from the chicks, such behaviour evidently serving to inhibit his antagonism (Simmons, 1970b).

Differential treatment of the young by the male was also much in evidence during feeding. He would feed the nearest chick on some occasions but by-pass it on others and give the fish to another chick, a plain indication of selective feeding. At least eight feeds (usually characterized as with 'no fuss' in the field-notes) occurred without incident - i.e. the fish was offered and taken with no sign of hostility from the parent or fear from the chick, the former watching and waiting passively until the food was swallowed before going on his way. The in-chick must have been the recipient of most or all of such feeds and it was also seen to refuse a few other fish offered to it. A further three feeds 'with no fuss', however, were definitely not given to the in-chick and may well have gone to the male's out-chick, as also a further four made with only a 'little fuss' (the chick in these cases sometimes turning-away from the male to eat the fish, a sure sign of unease), though a few of these latter feeds may have gone to the in-chick too.

The out-chick may sometimes have also been the one involved in cases where the chick demonstrated, by sinking and foot-splashing, while approaching the male to be fed, but most of such feeds probably involved the female's chicks and the odd-chick-out. Many similar feeds were made with obvious reluctance by the male and were followed by aggression, the adult rushing after the fed chick which would turn away and speed off immediately it secured the fish. The odd-chick-out was probably always the one which seemed loath to approach the male at all when other chicks were present - lying off and 'cringing' with head lowered and turned away while remaining stock still. It did, however, adopt the same ploy as certain chicks I was later to study at Welham Pond, i.e. follow the adult when all the other chicks were elsewhere and thus be the almost certain recipient of any fish caught when the two of them were thus isolated - taking advantage of the fact that, when parent Great Crested Grebes are carrying fish in the bill, they always appear to be inhibited against attacking the young and will then allow chicks of lowly status (including the mate's young) to take fish from them in such circumstances, though they attack them afterwards. It is probably largely by such 'begrudged' (involuntary or unintended) feeding that unfavoured young manage to obtain enough food to remain alive in circumstances such as those operating at Old Theale in 1975. Such a ploy is most successful when the rest of the brood is replete and, indeed, it was evident today that most of the chicks had become well fed by early afternoon, four of them loafing together (resting and preening) for a while even though the male was still hunting.

The observations at Old Theale in 1975, interesting as they are in their own right, become more significant when assessed against the knowledge acquired during the three main stages of my studies on the Great Crested Grebe coming before and after them, allowing useful discussion to be centred on three important topics: (1) brood-division, (2) parental favouritism, and (3) parental desertion.

Brood-division in grebes and other birds

Brood-division, whereby male and female each take charge of part of their family of dependent young, has long been established as a parental option of certain grebes. Reviewing the subject of brood-division and the other breeding strategies in this group (Simmons, unpublished MS 1986), I gave evidence for the existence of brood-division in six species, namely (listed in order of discovery): Little Grebe *Tachybaptus ruficollis* (Selous, 1905, 1915; Finn, 1907; Ahlén, 1966; Cramp & Simmons, 1977), Great Crested Grebe (Pycraft, 1911; Turner, 1924; Boase, 1925; Harrisson & Hollom, 1932; Witherby, 1940; Simmons, 1955, 1959, etc.; Ahlén, 1966; Cramp & Simmons, 1977), Black-necked Grebe *Podiceps nigricollis* (Oldham, 1919; Pike, 1919; van IJzendoorn, 1944; Prinzinger, 1974, Cramp & Simmons, 1977), Red-necked Grebe *Podiceps grisegena* (Munro, 1941; Wobus, 1964; Ahlén, 1966), Slavonian Grebe *P. auritus* (Fjeldså, 1973; Cramp & Simmons, 1977; Ferguson & Sealy, 1983), and Giant Pied-billed (or Atitlán) Grebe *Podilymbus gigas* (LaBastille, 1974). However, in only four of a sudden spate of seven papers dealing with brood-division in individual species which appeared in the early 1980s (Dean, 1980; Smith & Merkt, 1980; Horsfall, 1984; Moreno, 1984; Edwards, 1985; Harper, 1985; McLaughlin & Montgomerie, 1985) were grebes mentioned at all in the discussions. Indeed, most of the grebe records were allocated by McLaughlin & Montgomerie to their lowest category of reliability ("qualitative evidence involving vague reference to the splitting of the brood"). Neither did I find an independent discussion of brood-division in any major review of breeding biology and parental care in birds (e.g. Kendeigh, 1952; Armstrong, 1964; Lack, 1968; Wilson, 1975; Skutch, 1976; Maynard Smith, 1977; Drent & Daan, 1980; Krebs & Davies, 1981, 1984; Perrins & Birkhead, 1983; O'Connor, 1984, 1985; and Trivers, 1985) - nor have I since (e.g. Clutton-Brock, 1991). Thus it is evident that the concept of brood-division in birds, even in the classic case of the grebes, has still to penetrate deeply into the consciousness of ornithologists and behavioural ecologists generally, and this in spite of a wealth of new cases that have come to light in recent years and which have been conveniently summarized for passerines by my colleagues in the concluding volumes of *The Birds of the Western Palearctic* (Cramp, 1988, 1992; Cramp & Perrins, 1993, 1994a,b).

In the grebes, it must be admitted, the quality of the information available on brood-division is variable, even for the Great Crested Grebe (earlier observations on which are reviewed in the first section of Part Two). Although it is quite clear from my own studies that this species does at times practise full brood-division (type-l, see below) in England, some observers on the continent of Europe have not detected the strategy at all or seen it operating to only a lesser degree. Whereas Ahlén (1966, working in southern Sweden on Little Grebes) found clear indication of brood-division, with separation of the family sub-groups, not only in that species but in the Red-necked and Great Crested Grebes breeding on the same water, Hanzák (1952, working in central Bohemia) was adamant that it did not occur amongst the Great Crested Grebes he had studied. In Holland, too, the general opinion in 1986 was that the Great Crested Grebes there only divide the brood loosely if at all (A.M. van der Poel and J.J. Vlug, *in litt.*). At that time, however, no one seemed yet to have watched the behaviour of parents and young in sufficient detail, nor had there been any special studies on brood-division in that country or elsewhere on continental Europe - perhaps suggesting that this phenomenon gets overlooked when observers are not primarily focused on the intimate ethology of their subjects (as opposed to the collection of breeding data).

It was clear from my discussions with the Dutch and other ornithologists in 1986 that the types of brood-division, in birds generally, needed to be more clearly defined and I offered the following provisional classification accordingly:

TYPE-1. The brood is divided permanently between the parents, each tending only its 'own young' and not the 'other young', each family sub-brood going its own way (total discrimination and total disassociation). The sub-broods themselves may also be divided, the parent having a favourite chick, which is given priority at feeding, and, one or more less-favoured chicks (Type-la) or there may be no further discrimination (Type-lb). In the Great Crested Grebe, as noted, the two categories of young (Type 1a) have been termed 'in-chick' and 'out-chick' respectively and the strategy itself 'the in-chick/out-chick situation' (e.g. Simmons, 1970a,b).

TYPE-2. The brood is divided permanently between the parents as in Type-l, with each adult tending only certain young, but the family sub-broods remain in contact to some extent (total discrimination and partial disassociation). (Types-2a and -2b as above.)

TYPE-3. The brood is divided permanently between the parents, each parent feeding mainly its own young though food may be sometimes be given to the other young (partial discrimination and partial disassociation). (Types-3a and -3b as above.)

TYPE-4. The brood is not strictly divided but each adult tends to favour certain young.

TYPE-5. The brood is only loosely divided, i.e. the composition of the two sub-broods is not consistent.

TYPE-6. The brood is only temporarily divided, e.g. for odd periods within a single day when the adults separate.

Type-6 should not, perhaps, be counted as true brood-division at all but, in any case, I would exclude from it, and from any other category of brood-division, cases of temporary care of the fledged section of the brood by one parent while the other still attends the rest in the nest - as in the House Sparrow *Passer domesticus* (O'Connor, 1984) - and of discriminatory feeding while the whole brood is still together in the nest before fledging. In both cases, of course, this may lead to true brood-division later (as may well happen frequently in the case of the House Sparrow, though this has still to be conceded by those who have studied this species). Neither would I classify cases of double- or multiple-clutching under true brood-division (see Smith, 1978).

Part One: Brood-division and Related Behaviour in the Great Crested Grebe

Brood-division

In the Great Crested Grebe, it is the cases of type-l brood-division, with its associated parental hostility to the 'other young', which have been stressed in general statements on the subject in the literature, including some of my own. In the 16 broods that I studied in detail at Theale, Chew (on Herriott's Pool and the inlet off Heron's Green Bay which I termed the 'Arm') and Welham Pond (a tiny 'borrow pit' beside a disused railway about 4 km north-east of Market Harborough) the situation was more varied (see Table 4), indicating a less inflexible system than has been fully realized before. Nevertheless, in no case

Table 4 *Data on 16 families of Great Crested Grebes studied in detail at Old Theale Gravel Pit, Berkshire, Chew Valley Lake, Somerset, and Welham Pond, Leicestershire*

Year: pair	Brood-size	Chick	Date of Hatch	Date of Departure	Chick's Status	Length of PC/Stage (weeks)	Date of Departure Male	Date of Departure Female
Old Theale								
1957: A	2	1	2/6	18/8	FIC/MOC	16	(W)*	(W)*
		2	3/6	22/8	MIC/FOC			
1957: B	1	B	30/6	13/9	MIC/FOC	15	5/11*	8/9
1957: D	3	1	2/7	(Died in Week 11)	FOC/OCO	22	5/11*	25/9
		2	3/7	25/9	FIC			
		3	8/7	5/11	MIC			
Chew								
1967: Pool	3	1	20/6	17/10	MIC	21	?/12*	17/10*
		2	21/6	3/9	MOC/OCO			
		3	23/6	13/9	FIC			
1968: Pool	1	W	30/6	(25/7)	MIC/FIC	?	(25/7)	(25/7)
1968: Arm	4	1	16/8	15/12	MIC	28	15/12*	(W)*
		2	17/8	11/11	FIC/FOC			
		3	19/8	11/11	MOC			
		4	21/8	21/1/69	FOC/FIC			
1969: Pool	2	1	26/5	(19/7)	FIC/MOC	*c.*18	28/11*	(21/7)
		2	28/5	25/8	MIC/FOC			
Welham								
1979	2	1	2/6	by 29/8	MIC/FOC/OCO	21+	(Died by 19/8)	29/8
		2	4/6	23/8	FIC/MOC			
1980	1	X	10/5	21/7	MIC	15		

***Table 4** (continued)*

						Length of	Date of	
Year:	Brood-			Date of	Chick's	PC/Stage	Departure	
pair	size	Chick	Hatch	Departure	Status	(weeks)	Male	Female
				Welham (cont.)				
1980	2	1	4/7	20/9	FIC/MOC	16	14/8	7/10*
		2	6/7	20/9	MIC/FOC			
1982	1	Y	30/4	1/7	MIC/FOC	14		
1982	1	Z	23/6	9/9	MIC/FOC	16	?/10*	8/8
1983	4	1	25/5	15/8	FOC/OCO	17	by 2/9	by 27/7
		2	27/5	by 29/8	MIC			
		3	29/5	by 29/8	MOC			
		4	3/6	by 29/8	FIC			
1984	3	1	6/5	19/7	FIC/OCO	15	by 7/8	18/6
		2	8/5	22/7	MIC			
		3	10/5	29/7	MOC			
1985	2	1	14/5	by 10/8	MIC/FOC/ MOC	15+	by 10/8	14/7
		2	16/5	by 10/8	FIC/MOC/ MIC			
1986	4	1	17/5	by 29/7	FIC/FOC	15+	by 29/7	15/7
		2	18/5	by 29/7	FOC/FIC			
		3	20/5	by 29/7	MIC			
		4	24/5	4/8	MOC			

Notes. Column 2 (brood-size): excludes chicks dying before the end of the carrying-phase, i.e. those less than three weeks old (most mortality occurs during the hatching and carrying phases). Column 3 (identity of chicks): in broods of more than one, the chicks are numbered by the age of those surviving the hatching phase as it was not always certain which chicks had died in the case of reduced broods. Columns 5 and 8 (dates of departure): estimated in some cases when visits were close; some individuals may, of course, have died rather than departed (known deaths are indicated) - see further in main text. In the case of the Pool family at Chew in 1968, the whole family left prematurely when the single chick (then only in its fourth week) went down the overflow into the main lake where contact with the birds was lost in Week six; the same mishap occurred with Chick 1 (the female's in-chick) in 1969 but only the female followed in this case. Column 6 (chick's status), key to code: MIC = male's in-chick, MOC = male's out-chick, FIC = female's in-chick, FOC = female's out-chick, OCO = odd-chick-out (see main text). Note the change of status in the female's chicks at Chew in 1968 (Arm pair) and at Welham in 1986 and of the male's at Welham in 1985. Additional records, Welham: the single six-week-old chick in 1975 was MIC/FOC and the three 10-week-old chicks in 1977 were MIC, MOC and FIC in a clearly divided brood. Column 7 (length of 'PC/stage'): 'P/C Stage' = Parent-chick Stage of the breeding cycle (calculated from the laying of first egg to the departure of the last chick). Column 8 (dates of departure, adults): an asterisk indicates that the bird completed its wing-moult in the breeding territory (i.e. before departing in the case of any which did not winter, or attempt to winter, there) and a '(W)' that the bird did winter there (until January at least).

with broods of two or more young was there any question that brood-division was not operating, the discriminatory arrangements starting in Week 3 or 4 (towards the end of the carrying phase or, more usually, soon after) and stabilizing between then and Week 6 - though there might be occasional changes later, especially if one parent departed before the other (see Table 4, and below). The situation may now be examined according to family size, starting with broods of one chick.

Broods of one young Five of the 16 study families were composed of just one chick, plus a sixth one at Welham in 1975. There was no question of true brood-division here, of course, but clear indication of discrimination in most cases. At Old Theale in 1957, both parents tended the chick equally at first - it was, effectively, the in-chick of both parents - but later it associated more closely with the male who then did most of the feeding and all of it after the female had left. At Chew in 1968, the Pool chick was cared for equally and solicitously by the two adults, both on the Pool itself and later on the main lake (where they had followed it after it left accidentally), until Week 6 at least (see Table 4). At Welham in 1975, however, the single chick, though fed by both parents, was clearly the in-chick of the male only. This was the case, too, in 1980 when the male took sole charge of the chick while helping to incubate the second-brood clutch, in which the female took the larger share. Again, in 1982, the single chicks of the first and second broods were each, in turn, the in-chick of the male, the female treating both as out-chicks and playing the lesser role in feeding.

These records indicate, therefore, that the care of broods of one devolves mainly on the male and such was the finding of the 1931 inquiry (Harrisson and Hollom, 1932; see further in the first section of Part Two). In a case at Burghfield GP in 1953, however, it was the female who eventually took sole charge of the single chick, leading it away to open water and leaving the male on his own in the territory.

Broods of two young There were five such broods in the study families and in all cases the chicks were clearly divided between the parents, at least at first, the existence of two family sub-broods being always evident though there was no permanent sub-brood separation. In all cases, however, what may be termed a 'double in-chick/out-chick situation' operated, i.e. the in-chick of the male was the out-chick of the female and vice versa, each parent supplying some feeds for its 'mate's young', albeit often begrudgingly (see Introduction). In 1957 at Old Theale, however, both chicks of A-family eventually came under the sole care of the male after incubation of the second-brood clutch (in which the female took the larger share) was in progress, although the majority of the small sample of 'identified' feeds (17:8) still went to the male's in-chick. The 1979 Welham family also provided an interesting variation in that the female's commitment to the young decreased for a while so that, though she continued to feed 'her chick', it effectively became the odd-chick-out of the family by Week 9. However, when the male became incapacitated in Week 9 (with a length of nylon fishing-line lashed around his bill), she took over the feeding of both young, continuing after his death in Week 11 and spending much time hunting, she and her chick departing together a few days after the male's chick had left.

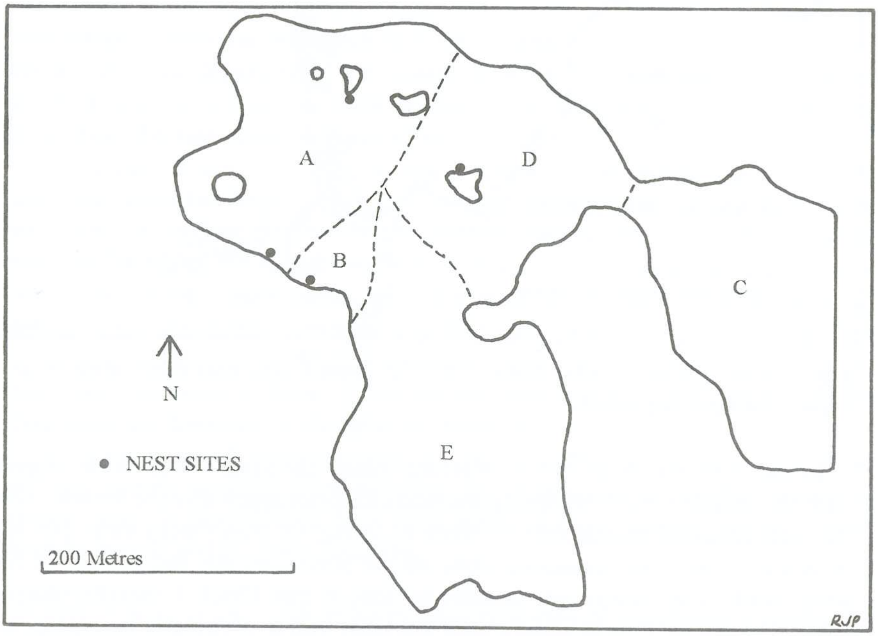


Fig. 1 Map of Old Theale Gravel Pit, 1957: territories and nest-sites.

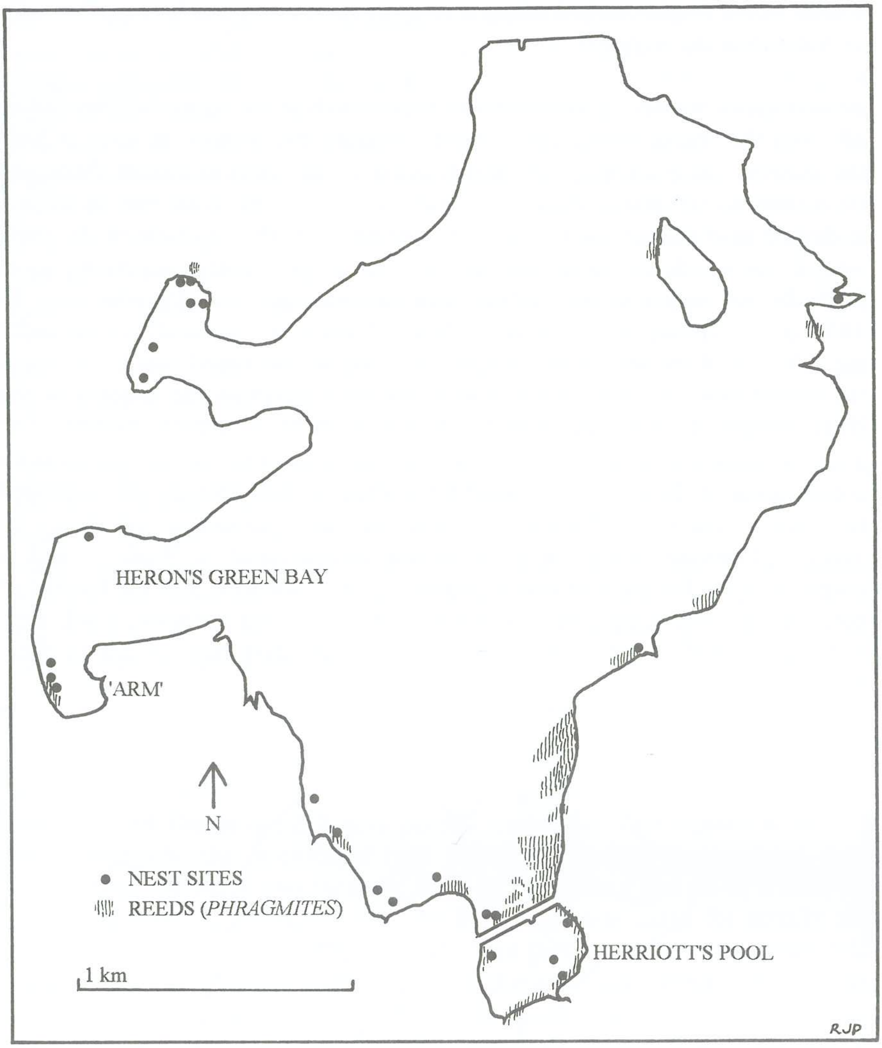


Fig. 2 Map of Chew Valley Lake, 1967-70: known nest-sites (excluding those within the main reed-beds).

In the 1980 family of two at Welham, much the same situation developed, with the female's chick becoming the odd-chick-out again and the female, after the male departed prematurely in Week 8, caring for both chicks until they left in Week 12 and then remaining alone on the pond until she had completed her wing-moult. This family was interesting, too, in that Chick 1 initially (during Week 3) associated most closely with the male before eventually becoming the in-chick of the female. With the 1985 Welham family, the basic arrangement

Table 5 *Distribution of 'identified' feeds between in-chicks and out-chicks by parent Great Crested Grebes at Chew Valley Lake, Somerset, and Welham Pond, Leicestershire.*

Year:	Number of identified feeds by Male		Female		Both		Brood-
pair	ICs	OCs	ICs	OCs	ICs	OCs	size
				Chew			
1967:							
Pool	129	31	230	31	359	62	3
1968:							
Arm	151	58	666	301	817	359	4
1969:							
Pool	791	44	707	16	1498	60	2
				Welham			
1977-86	38	18	23	10	61	28	3-4
1979-85	35	23	28	16	63	39	2

Notes. See main text and Table 4 for further details. ICs = in-chicks, OCs = out-chicks. Broods of one chick excluded. At Chew, a further 527 and 370 feeds were recorded for the in-chicks of the 1968 Arm female and the 1969 Pool male respectively after the departure of all other chicks.

was simpler (with no odd-chick-out) but unusual in that the male 'changed chicks' after the departure of the female in Week 10, her chick becoming his in-chick and his original in-chick becoming his out-chick, all three departing at or about the same time in Week 12 or 13.

In the case of the 1969 Pool family at Chew, the brood-division was more straightforward but began very early (during Weeks 3 and 4) and was linked with obvious feeding difficulties, the parents maintaining the highest feeding rates but bringing the lowest biomass of food of all the study pairs (details in Simmons, 1970b). Both adults gave the majority of their feeds to their in-chicks while the family remained together (see Table 5) the sub-broods then separating fortuitously in Week 9 when the female followed her chick on to the main lake (see notes to Table 4), leaving the male and his chick together on the Pool until the departure of the latter in Week 14.

All these cases of brood-division are best allocated to types-3b and -4 (as defined above), none of them fulfilling the criteria for the higher categories (types-l and -2) though these have been observed more casually in other cases, both by myself and by other observers.

Broods of three young There were three examples of brood-threes among the study broods plus a further one at Welham in 1977. In the latter case, all that can be said is that the ten-week-old brood was seen to be divided in a clear-cut manner, two with the male and one with the female, and that the male's chicks were an obvious in-chick and out-chick. The much better documented 1967 Pool family at Chew, in which the male again looked after the larger group, provided an excellent case of classic type-la brood-division. There were signs of preference as early as Week 3 but both adults favoured Chick 3 at first; by Week 6, however, it had become the female's in-chick, the male settling on Chick 1 with Chick 2 (very much an odd-chick-out in the earlier stages) as his out-chick. There were indications of food difficulties in this family: the adults left the chicks unguarded at times in the immediate post-carrying phase and from Week 6 onwards the two sub-groups operated independently as if they were unrelated families, the chicks avoiding the 'other parent' and the adults themselves showing mutual hostility when in each other's vicinity - though they 'made up' from Week 14, loafing and even displaying together at times, and both underwent their wing-moult on the Pool.

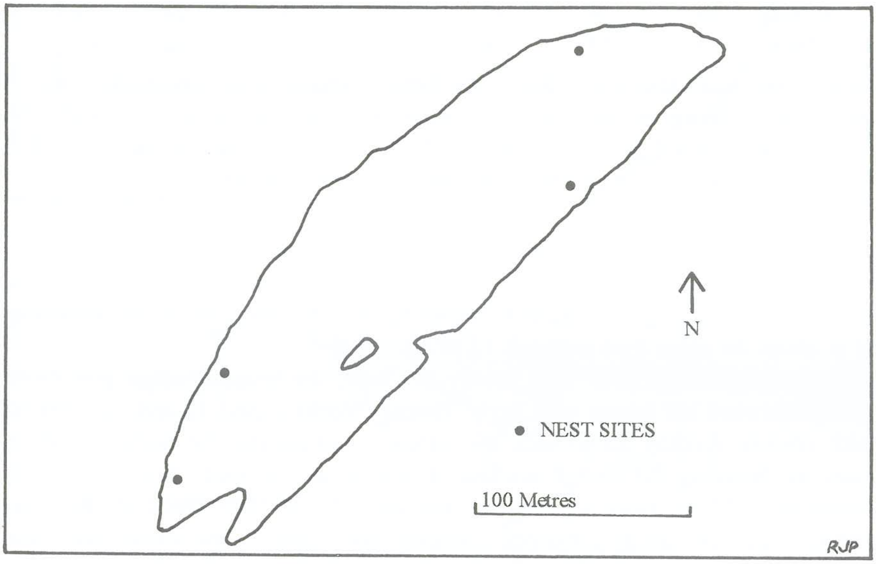


Fig. 3 *Map of Welham Pond, 1979-86: nest-sites.*

At Welham in 1984, the male again took charge of two chicks and the female one, the brood-division in this case being of type-3a however. The parental preferences were obvious soon after carrying was over though there was never total disassociation, the male feeding the female's chick at times, if begrudgingly, both before and after the female's premature departure in Week 7. This chick then became the odd-chick-out of the combined sub-broods and adopted the intermittently successful tactic (referred to earlier in the Introduction) of tagging the male when he was isolated in the hope of intercepting some of the feeds intended for its more privileged siblings, even though this provoked the adult's hostility afterwards. It was the first chick to depart, the male's out-chick and then his in-chick following later, leaving the male alone on the pond for a while until he left to undergo the wing-moult elsewhere.

I have left D-family at Old Theale in 1957 until last as this case is particularly interesting and instructive. Here, unlike in the other three broods of three, it was the female who took on two chicks and the male one. Again, brood-division started early (by Week 4) and, unlike in the two other study families in 1957, the young were left mainly unguarded once carrying was over so that both parents could work at bringing food at the same time. Parental hostility was particularly marked in this family from Week 6 onwards, especially by the male who, though he directed his attacks mainly at the female's chicks, also made some against his own chick. Nevertheless, in spite of the indications of food difficulty, there was some casual feeding of the 'other chicks' by both parents until the dramatic incapacity of the female early in Week 7 when an angler's fish-hook became embedded in her mouth.

The female abruptly stopped feeding her two chicks but the male made no effort voluntarily to feed them as well as his own and they remained with the female at first. From the next day, however, the female's out-chick (Chick 1) started tagging the male and his chick (Chick 3) and managed to obtain a few feeds, either when Chick 3 was replete or by intercepting feeds intended for it, and then only by snatching fish from the male and making off rapidly with them; it thus became the odd-chick-out of the family.

The female's in-chick (Chick 2), meanwhile, remained mostly with the female though receiving no food from her. It loosely tagged the male at times, taking up a position even rearward of Chick 1, but usually returned to the female before too long. It did receive an occasional feed from the male, however, usually when the latter deliberately came into the vicinity of the female as if he wanted to feed her, though he never followed this through while I was watching. In a sample of 31 'identified' feeds by the male during Weeks 7-9, 22 went to his in-chick, six to Chick 2, and only three to Chick 1 (thereafter, all 16 observed feeds went to Chick 3). Thus Chick 2 survived on the odd feed from the male for a period of about ten days, after which the female started to hunt again and to feed 'her' chick, continuing to do so to some extent, at least, into Week 10. By this time it was obtaining most of its food for itself by persistent hunting - both of them then departing on the same day in Week 12. The male and Chick 3 also continued to associate, remaining together during the former's wing-moult, and departed together afterwards in early November during Week 19.

The female did not associate with Chick 1 after her recovery and it received no further food from her - all 13 of her observed feeds going to Chick 2. Nor did Chick 1 manage to obtain anything further from the male after Week 9. It tried to feed itself but it was not successful enough and died of starvation early in Week 11 after crawling ashore on one of the islets.

This case throws considerable light on the adaptive significance of the brood-division strategy of the Great Crested Grebe, leading me to make the preliminary suggestion (Simmons, 1959) that brood-division in this species was "an insurance in larger families that, in the event of sickness or death, or even neglect by one parent, only those young dependent on that parent suffer and not the whole brood". I also pointed out that if a single working parent had to feed all the chicks in such circumstances, then all of them might be lost. In the light of other case-histories, particularly the 1975 one at Old Theale, this is obviously an over-simplification, there being much more to it than that, as I subsequently realized (Simmons, 1970b, etc.).

It must also be said that this case does not sit comfortably in my proposed classification of 1986. Though one of extreme brood-division that led to the death of one of the young through parental neglect, it has (once again) to be allocated to type-3a only as it does not satisfy the criteria of total discrimination and total disassociation that would permit it to be allocated to one of the higher categories. This suggests that the classification may need revision, at least so far as the grebes are concerned (see further, below).

Broods of four young Three such large broods occurred among my study families, one at Chew in 1968 and two at Welham in 1983 and 1986, the young being divided two and two between the parents in every case. In all three families, too, the first signs of brood-division occurred in Week 4 after carrying was over, each adult then being accompanied by its two chicks when loafing, and the in-chick/out-chick situation was firmly established a week or so later.

In the Arm family at Chew in 1968, everything was in place by Week 5 but later there was a change in the female's sub-brood when the status of her two chicks was reversed - Chick 4 (which had been the out-chick) becoming the in-chick and Chick 2 (which had been the in-chick) becoming the out-chick. It is interesting to note here that Chick 4 had attached itself to the female very early on, which reinforces my suggestion (Simmons, 1970b) that the relationship which develops between adult and chick involves a process of mutual selection to a greater or lesser extent, though the final word (as it were) lies with the adult.

The brood-division was clear-cut in this family but the adults were still giving some feeds to the 'other young' in Week 5 although strongly favouring their own - to the tune of 114 out of 145 'identified' feeds in the case of the male and 177 out of 196 in the case of the female. Thereafter, however - although the occasional fish continued to be given to the 'other young' (up to Week 11 by the male, up to Week 13 by the female) - the selective feeding was even more strongly marked: of 856 'identified' feeds by the male, only 76 went to the female's chicks, and of 1061 such feeds by the female, only 43 went to the male's. The two sub-broods tended to operate independently from Week 8 onwards, with obvious hostility between the adults, but the latter started to establish their bonds again during Week 10, even offering fish to one another. Both the in-chicks of this family remained long after the two out-chicks had finally departed, the bond between the female and her in-chick being particularly strong and persisting even after the departure of the male (see further, below).

My observations on the brood of four chicks at Welham in 1983 were limited in the earlier stages so I had not established all the details when the female left prematurely in Week 7. She had, however, certainly been giving the odd feed to the 'other young' in Weeks 4 and 6 and I suspect the same was true of the male. After the female's disappearance, her in-chick (Chick 4) soon associated fairly closely with the male and his two chicks but the female's out-chick (Chick 1) kept its distance. The male, though favouring his own chicks, would feed the nearest chick to it at times so both the female's young received some food from him; both would often join the male's chicks in following him when he made his hunting trips around the pond - one of them also employing the 'lone tagging' tactic mentioned earlier.

Chick 4 continued to associate with the male and his young, receiving some feeds into Week 10 at least. When the four birds were loafing together, it took up a position on the periphery of the group and persistently adopted the submissive pork-pie posture. As usual, only the in-chick (Chick 2) remained close to the male, his out-chick (Chick 3) then positioning itself next. All three chicks departed in Week 12, the male leaving a week later to moult elsewhere.

Chick 1, meanwhile, had become the odd-chick-out by Week 8. It still tagged the male but was evidently afraid of him and reluctant to approach when he came with a fish. By Week 9, although it continued to follow the male distantly at times, it remained mostly on its own away from the rest of the family; if it did loaf in the vicinity of the others, it lay well away from them (too far, in fact, for it to have to adopt the submissive posture). By Week 10, when it was last seen on the pond, it spent much of its time diving independently. Whether it then left or died was uncertain but no corpse was found.

The last family of four - at Welham in 1986 - was also the last family of Great Crested Grebes to date that I have watched intimately. There was a prolonged hatching period in this case, four chicks surviving from the five eggs laid; it must have been the fourth egg which failed to produce a chick judging from the timing and the appearance of the smallest chick (called 'Chick 4' but really Chick 5). In Week 4, when brood-division and the in-chick/out-chick situation had already been established, there was still some feeding of the 'other young' at first, by the male especially, but the adults were soon concentrating their efforts on their 'own young' and showing hostility towards the rest. Chick 4 (the male's out-chick) was, however, already adept at intercepting some of the fish being carried by both parents, e.g. two by the male (out of six) and four by the female (out of 13) on 13 June at the end of Week 4. There were strong signs too at this time of sub-brood disassociation though this did not last long and all members of the family were loafing together again in Week 5 and continued to do so subsequently, with occasional feeding of the 'other young' by both adults.

In Week 7, there was another of those occasional changes in status in the female's sub-brood, her previous out-chick (Chick 2) becoming her new in-chick and her previous in-chick (Chick 1) becoming her new out-chick. By Week 8, all the chicks were spending much of their time hunting even though the adults seemed to be coping well, the young were well fed, and relationships peaceful; it is in circumstances like this, incidentally, that brood-division could be overlooked by the casual observer even though still operating fully. Once again, however, the family was depleted by the sudden departure of the female in Week 9, leaving all four young in the care of the male. The latter, though giving most food to his own young, fed the female's too - with only slight aggression - and continued to do so into Week 10 at least. It was noticeable, however, that only his in-chick (Chick 3) was allowed anywhere close to him by then - i.e. Chick 4 (his out-chick) was treated much as the female's chicks were. The male, Chick 3, and the female's two chicks departed in Week 11, leaving Chick 4 alone on the pond into Week 12.

In two of these families of four the brood-division was of type-1 but only for a while, being best allocated to type-3 for most of the time, as with the third family. Two of these case-histories show once again that a single parent can cope with the burden of the whole brood after the desertion of its mate - which puts the 1975 business at Old Theale in clearer perspective - though the survival of the less favoured young must depend as much on their own efforts, in self-feeding and in 'conning' food from a reluctant parent, as on provisioning by the latter.

Re-classification and comment In the light of the information given, I am inclined to simplify the classification of brood-division that I circulated in 1986 - insomuch as it refers to grebes, that is - using letters not numbers for reference this time so as to avoid confusion between the two classifications and omitting the in-chick/out-chick situation, which is best treated separately (see below).

TYPE-A. The brood is divided between the parents, each feeding its 'own young' only and not the 'other young', the two family sub-broods separating and operating independently (total discrimination and total disassociation).

TYPE-B. The brood is divided between the parents as in Type-A, with each adult mainly feeding its 'own young', but the family sub-broods remain in contact to a greater or lesser extent and there is some feeding of the 'other young' (partial discrimination and partial disassociation).

TYPE-C. The brood is only loosely divided but each adult associates more closely with one or more chicks.

The former categories 2, 5 and 6 are perhaps best abandoned, the last two because they appear not to apply to the Great Crested Grebe, though they may possibly do so to other grebes (such as the Pied-billed *Podilymbus podiceps*, see the second section of Part Two), and category 2 because I am now convinced that there will always be some feeding of the 'other young' - of the unintentional sort at least - if the sub-broods do not separate totally (which they are much more likely to do on large waters like the main lake at Chew, where most broods hatch in one reed-bed and then disperse elsewhere, than on small ones like Welham Pond).

On the evidence given here, it is likely that type-B brood-division is the rule in most Great Crested Grebe families with a minority showing type-A or type-C, at least for a time. All three categories also represent the stages through which individual families may go sequentially (C to A) during the period of parent-chick association, or may adopt temporarily, depending on the nature of the food situation operating at any one time and its effect on parental feeding efficiency. Type-A brood-division will develop when the parents encounter difficulties (lack of the larger categories of fish, general shortage of food, etc.), this being exacerbated when broods are of three or more young. Conversely, when feeding conditions were favourable, the brood-division would tend to slacken, as Harper (1985) found with the Robin *Erithacus rubecula*, and this may explain why some continental workers have failed to detect it in the Great Crested Grebe. Nevertheless, I remain convinced that a degree of brood-division must always occur in this species, as an evolutionary stable ('obligate') strategy, even when circumstances are particularly favourable (see further, below).

I hope that the information and classification presented here will stimulate further studies on brood-division in grebes (including the Great Crested) and other birds. In the best studies one would hope that: (1) the parent birds would be identified individually - visually (through marking if necessary) and/or by behaviour; (2) the young would be identified individually in the same way; and (3), in species with food-dependent young (such as the grebes), counts were made of the distribution of food by each parent between individual members of the brood.

In the case of the Great Crested Grebe, it is usually possible to distinguish between the sexes even though the species (like other grebes) is isomorphic - the male being the obviously somewhat larger and brighter bird in most pairs. Because of asynchronous hatching, the individual young can be distinguished by size (especially in the earlier weeks of dependency) though, as incubation may start just before the laying of the second egg, or with it, Chicks 1 and 2 are often closely similar. The young, however, also differ individually in the pattern - and often the density - of the markings (stripes and spots) on the head, this being the main character by which I, like the parent grebes, have distinguished between them, backing this up by noting any obvious differences in their behaviour, including their attitude to the adults and to one another.

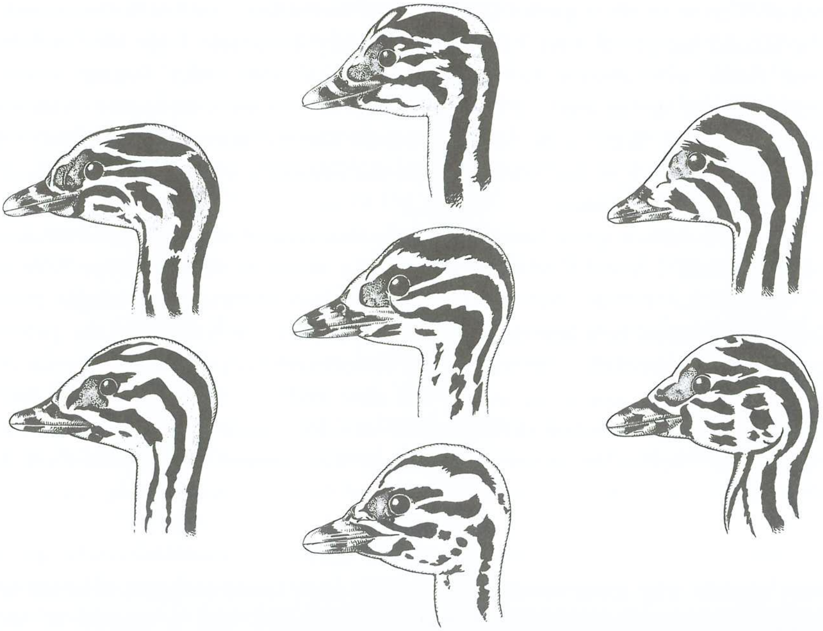


Fig. 4 *Examples of the variation in head markings of Great Crested Grebe chicks. Drawn by Pierre Déom from photographs (see* La Hulotte *72:18, 1995).*

The above criteria apply to other Podicipedidae, to a greater or lesser extent, but there may well be difficulty with the smaller and more secretive species, especially those with less boldly marked young. It should be remembered that, in cases when observations on the association between a single adult and one or more chicks are brief (as often happens, for example, during general census work or brood counts), it could be difficult to know at times what was involved: real brood-division, with a permanent or temporary separation of mates and sub-broods, or permanent desertion by (or the death of) the mate.

If the Great Crested Grebe can be taken as the optimum type, then grebes that (1) specialize on particular organisms for food (especially fish), (2) inhabit unstable habitats, (3) face food unpredictability when breeding and run the risk of food shortage, (4) have to provide parental care over several weeks, and (5) usually attempt to rear only one brood in a season should, perhaps, be the best candidates as practitioners of brood-division. As yet, only seven other grebes (the five species listed earlier plus the Pied-billed Grebe and the Western Grebe *Aechmophorus occidentalis*) are known to be likely brood-dividers. The available information is given in the second section of Part Two, and an assessment of the situation in the remaining species of grebes in the third.

The function (adaptive significance, survival value) of brood-division in birds generally is disputed but, before this is discussed further in the Great Crested Grebe, two remaining topics - parental favouritism and parental desertion - need to be examined first.

Parental Favouritism

The selection by a parent Great Crested Grebe of one particular chick for preferential feeding and other parental care out of a family of up to five young is a striking instance of parental investment which has not previously been fully assessed, I believe. Its significance has been masked by treating it merely as an aspect of brood-division but I now realize that such favouritism precedes brood-division and is the basis of it, rather than vice versa. In other words, it is the establishment of a privileged in-chick - one each for male and female in families of more than one young - that is paramount, brood-division following on from it to a greater or lesser degree, depending on brood-size and the current food situation. A strong bond is thus formed between the adult and in-chick which, in fact, is much firmer than that between the parents themselves during this phase of the breeding cycle.

As well as bringing enhanced protection to the in-chick through its close association with its adult, such favouritism results in its having priority in feeding when there are two chicks in the sub-brood or when the mate's chick is treated as an out-chick - as in the case of brood-twos (though then, of course, each out-chick receives major provisioning from its adult as well). Thus the in-chick can receive a disproportionately high share of the food provided by the adult (see Table 5 tor the main supporting figures, given separately for each family at Chew but lumped for brood-threes and -fours and for brood-twos at Welham, where samples were smaller). In all cases, the strong bias towards the in-chick is quite clear. It seems likely, too, that the in-chick receives larger fish on average than does the out-chick (Table 6), especially when the greater biomass of the higher size-categories of fish is taken into account. As well as the larger share of caught food (mainly fish), the in-chick probably also receives most of the feathers given by its adult, these being an essential supplement to the diet of the young, aiding digestion and forming the basis of pellets (Simmons, 1956, 1973, 1989; Piersma & van Eerden, 1989). Out of a small sample of 36 'identified' feather-feeds at Welham, for instance, in-chicks received 28 and out-chicks and other categories of young only eight. It is likely,

Table 6 *Size of 188 feeds brought to in-chicks and out-chicks by male and female Great Crested Grebes, Welham Pond, Leicestershire, 1979-86.*

	Size category of fish									
Number of feeds by	1-2	3	4	5	6	7	8	9	10	Totals
					ICs					
Males	1	4	3	13	10	10	13	15	2	71
Females	2	1	5	15	5	5	13	5	0	51
Totals	3	5	8	28	15	15	26	20	2	122
%	2.5	4.1	6.6	22.9	12.3	12.3	21.3	16.4	1.6	
					OCs					
Males	1	4	5	3	11	8	5	3	0	40
Females	0	3	1	5	7	3	3	4	0	26
Totals	1	7	6	8	18	11	8	7	0	66
%	1.5	10.6	9.1	12.1	27.3	16.6	12.1	10.6	0.0	

Note: for further details and code, see main text and Table 3.

too, that the in-chick gets the majority of its parent's defaecated intestinal worms, these being relished as food by both adults and young and highly nutritious (Simmons, 1975).

I am not yet certain why particular chicks become in-chicks rather than others in the same brood or sub-brood. It seems not to be a question of age (Table 7), no clear pattern of selection emerging from the available figures; nor, however, is it likely to be arbitrary. That some 'quality' of the chick commends itself to the parent seems to be suggested by those cases in which an adult later exchanged one established in-chick for another - as if the former in-chick no longer met the requirement as well as the later one did. This may be a matter of fitness in the simplest form of the term, assessed by the adult during the progress of daily life, or of the sex of the in-chick. Perhaps males favour female young and females male young, as is likely with the Blackbird *Turdus merula* (Snow, 1958) and Robin (Harper, 1985)? Sexual imprinting may be particularly important in the case of species like the Great Crested Grebe which are isomorphic in behaviour as well as in appearance, making it the possible goal of in-chick selection while posing the difficult question of just how an adult grebe identifies the sex of its in-chick or reveals its own sex to it.

The problem remains open, therefore, though I would not rule out the sexual option. In this respect, the case referred to earlier, involving the 1968 Arm female at Chew and her second choice as in-chick, may be instructive (full details in Simmons, 1970b): the association between the two was renewed after the departure of the male in Week 11, an ambivalent relationship then

***Table** 7 Family status of young Great Crested Grebes in relation to age (all study families of more than one chick).*

	Number of times as					
Chick	MIC	FIC	MOC	FOC	OCO	Total records
1	4	5	4	5	4	22
2	6	5	3	5	1	20
3	2	1	3	0	0	6
4	0	2	1	1	0	4
Total records	12	13	11	11	5	52

Notes. Based on Table 4 (which see for code). In cases where the status of chicks changed (see Table 4 and main text), a score has been made in both categories.

developing, with parental feeding and chick demonstration on the one hand and a tendency towards male-female behaviour when mother and chick met on the other (in all, during Weeks 18-24, I observed 18 instances of tentative and usually short-lived courtship display between the two). Although such an extreme situation seems atypical, the association between an adult and its in-chick often lasts up to four weeks longer than that between an adult and its out-chick and can sometimes persist elsewhere after the simultaneous departure of the two from the natal water.

There remains the question of the out-chick in the sub-brood. I do not know whether it too is selected by the adult - or, if so, on what basis - but am inclined to think that, not having been chosen as an in-chick, it attaches itself to the adult which is the least intolerant of it, this being its best survival ploy in the face of a difficult situation. In the early part of the parent-young stage, independent of the adults, the young establish an age-hierarchy which gives the advantage to the oldest chicks in the family - especially to Chick 1 which, during the later carrying-period can be the first to station itself in the water and intercept food before the feeding adult can reach the younger chicks on the mate's back (Simmons, 1970b, 1974). Parental favouritism and brood-division often remove the age-advantage that the older chicks enjoy during the early weeks so that out-chicks and odd-chicks-out have later to do the best they can.

Parental desertion

At the time, I had assumed that the disappearance of the female parent at Old Theale in 1975 was due to her death (as, of course, it may have been). Because of the large size of the brood, it never occurred to me then that the bird may have deliberately deserted her mate and unfledged young, thus putting the latter at risk if the male could not cope. However, I later recalled that four of the five breeding females at Old Theale in 1957 had departed well ahead of their mates, leaving them behind in the territory to undergo the wing-moult alone (Simmons, 1970b). As these departures came late in the season, when chicks were near or had passed fledging, and as no real instances of chick desertion were involved - except in the case of D-family, in which the female had been unwell - I believed (probably correctly) that they were due largely to the strong tendency for female Great Crested Grebes to leave smaller waters ahead of their mates and seek bigger and safer moulting areas elsewhere. Similar departures by females were also recorded among the study pairs at Chew, though there it was a case of their leaving the breeding territory for the wide spaces of the open waters of the main lake where large assemblies of wing-moulting Great Crested Grebes are known to occur annually.

The later observations at Welham give a different perspective on the early departures of one parent, however, as most of these occurred well before the fledging of the young (see Table 4 and the brood accounts) and clearly involved parental desertion by one of the adults, leaving the mate 'holding the baby' as it were. In the five consecutive years, 1982-86, it was the female that left early, always some weeks before the departure of the young, three times in July, once in June, and once early in August - at least two individuals being involved. There was no desertion by the female in 1979, the year that the male died accidentally, and in 1980 it was the new male which departed early, over a month before his in-chick did. In 1981, the year in which no young were raised, the male again left first (after the failure of the third nest), a week or more before his mate.

Thus it is established that both male and female Great Crested Grebes are likely to desert the young dependent on them before they are fledged or even fully self-feeding. The Welham cases, however, like that at Old Theale in 1975, strongly indicate that it is the female which is more likely to desert than the male. The reason for the desertions remain largely unclear, especially at Welham where the birds were quite habituated to the close presence of fishermen and grebe watchers, though disturbance of some sort cannot always be discounted, evidently affecting females more than males.

As unilateral parental desertion is known to occur in other grebes (see the second and third sections of Part Two), I am inclined to believe that it can be a deliberate strategy at times in the Great Crested Grebe - a decision, as it were, by the departing adult to 'cheat' on its mate (in the sense of Trivers, e.g. 1985), not in order to find a better opportunity to breed with a new mate elsewhere in what remains of the season (pair formation being a prolonged process in this species) but for the sake of personal survival. This interpretation assumes that the hard work of rearing young brings with it an increased risk of mortality, especially when broods are large (as at Old Theale in 1975 and at Welham in 1983, 1984, and 1986) or feeding conditions unfavourable. Conversely, the deserter may go only after, in effect, 'assessing' that the situation is favourable enough for its mate to stand a good chance of raising the young unaided. By its departure, nevertheless, it must put the whole brood as well as its in-chick at risk, so there can be no possibility that parental desertion is part of a strategy for successful breeding rather than of one for self-survival, unless, of course, we take into account the bird's potential for raising future young through its survival. We may also wonder just what effect such desertion has on the strength of the pair-bond and the likelihood of the deserted partner's choosing the same mate again next year, having itself been put at greater risk, not least by being condemned at times to pass the flightless period of the wing-moult on an unsuitable water.

For birds leaving in August - as at Old Theale in 1975 and at Welham in 1982 - the imminent onset of the wing-moult could have been the trigger for departure (as it was at Old Theale in 1957) but this was an unlikely cause in the other cases. One last speculation: could desertion sometimes occur because the parent had found that it had, after all, selected the 'wrong' type of offspring - or an eventually inferior individual - as its in-chick?

As I was completing this paper, I received some interesting information from Dr A.M. van der Poel (*in litt.* November 1995). In answer to my further queries, and in the absence of any references in the continental literature to either brood-division or parental desertion by Great Crested Grebes, he had now analysed his data from 27 individually marked pairs studied on the ring of moats surrounding the old city of Leiden, Holland, in 1983-88 (see, e.g., van der Poel, 1985). Once again he confirmed that there was no clear evidence of brood-division in this population. However he did record that, in 27 "last cycles" - i.e. counting only the final cycle in those pairs that were not single brooded but raised two or, in one case only, three families in a season - there were ten cases of what I have termed parental desertion involving eight females and two males (a third male "deserter" was later found dead).

Thus, as with my birds, parental desertion in the Leiden population of Great Crested Grebes appears to be practised mainly by females. Such behaviour is as much a puzzle to Dr van der Poel as it is to me, especially when it seems clearly not to be linked with the onset of the wing-moult for, as he says, there then appears to be "no cost and no benefit" connected with it. His data reveals that the breeding success of deserters and non-deserters in the years mentioned was closely similar; indeed, the former even did a little better than the others, though the difference is not statistically significant (since the behaviour apparently has no negative consequences for the remaining members of the family, he suggests that the term 'early departure' may be better than 'desertion'). Nor did he detect that it was of any personal benefit to females to depart early, there being no apparent difference in the individual survival of 'deserting' and 'non-deserting' birds from one season to the next. He did, however, have one case of a female leaving her mate and family and then starting a new cycle with a new male. As this was the only case of "partner change" during the same season that he ever observed, such behaviour would seem to be exceptional.

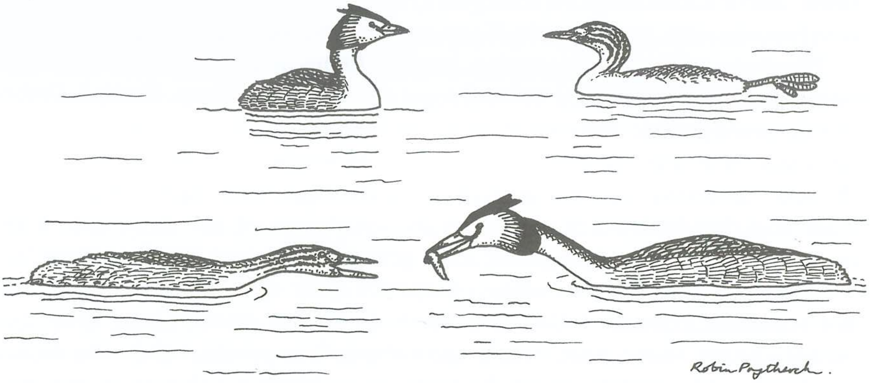
Assessment

After examining the available information, I see no reason to change my earlier view that in-chick favouritism and brood-division belong to a series of sustaining breeding 'co-adaptations' (strategies) which give Great Crested Grebes the chance of raising young under environmental conditions that are unpredictable and often difficult (Simmons, 1970a,b; 1974). The lakes and ponds they frequent being such unstable habitats, nesting is often delayed, a reliable food-supply for the young cannot be guaranteed, and the risk of food shortage is a distinct possibility. Much the same may well be true of other grebes which divide the brood (see Ferguson & Sealy, 1983).

Although a brood of two seems to be the optimum number under average conditions, the Great Crested Grebe (like most birds) usually seeks to maximize its breeding output, i.e. raise as many young as it can. It will at times, therefore, lay a full clutch of five or even six eggs - in part, of course, to cover the mortality of chicks during the hatching- and carrying-phases, when they are at their most vulnerable from bad weather (especially cold and rain) and from predation. If feeding conditions are good, up to five young can be raised (as we have seen) though the usual brood-size is lower due to losses from causes other than food. At other times, however, a policy of brood reduction may well operate: not only can smaller clutches be laid (right down to two eggs) but the last egg or two of larger clutches, though still viable, may be abandoned before the end of the hatching period. This will apply in both cases, probably, after the current food situation has been assessed by the hunting adults, the female in particular; and, if feeding conditions are poor later in the cycle, the chosen in-chicks are favoured over all other young. As a constant supply of fish of the optimum size for the young at each stage of their development cannot be guaranteed, it seems likely that the setting-up of one or two in-chicks in the brood is an obligate strategy, the follow-up behaviour then depending on the food situation subsequently - the out-chicks and, especially, the odd-chicks-out being expendable and sacrificed, if necessary, but reared otherwise.

Brood-division also facilitates the preferential feeding of the in-chick, reduces competition between the chicks (especially when the chick-established system of size-dominance goes against the grain of adult in-chick selection), and reduces food-competition between the adults, particularly when the sub-broods separate, not only for long periods (permanently or temporarily for days or weeks) but also for shorter spells during the ebb and flow of the daily routine. Brood-division also increases parental feeding efficiency, the young in each sub-brood being fed at a greater rate and on a larger biomass of food than when the brood was combined, as established at Chew in 1966-70 (details in Simmons, 1970b).

The strictness with which brood-division is applied, especially in the matter of the feeding of the 'other young', must depend on current feeding conditions, for it cannot be in the parents' interest to reduce the chances of survival of even the 'other young' unnecessarily, as remarked also by Snow (1958) and Harper (1985) for the species they studied. There may well be a draw-back to brood-division, however, in that it may provide a 'cheat's charter' which gives one of the adults an inducement to desert when its own survival - immediate or long-term - is in question. That it is usually the female suggests that she takes advantage, as it were, of the evidently stronger parental instincts of the male.



Part Two: Review

Early observations on the Great Crested Grebe

The famous ornithologist W.P. Pycraft may have been the first to observe divided Great Crested Grebe families, on the Norfolk Broads during August and September 1911 (Pycraft, 1911). Having encountered "numerous broods" consisting mostly of two chicks and never of more than three in the care of a single adult, he believed that although the male takes an equal share of parental care until the young are at least half-grown, it is the female alone that tends the brood subsequently.

The chicks which Pycraft encountered were all of post-carrying age, mostly "about half grown" though some were smaller, and followed the parent for food or had the fish brought to them. He recorded no parental hostility but did describe how the chicks uttered quick, shrill calls incessantly on approaching the adult for food and how "often when forging full speed ahead they throw out on either side a curious crescentric stream of water in perfect rhythm" as they "strike outwards and backwards just under the surface of the water" with the feet. According to Pycraft, the chicks were fed alternately though he also stated that food was given to the first chick to reach the adult, swimming in the manner described, this being the first record of the foot-splashing behaviour of the young Great Crested Grebe known to me.

The most likely interpretation of Pycraft's observations is that he was really observing family sub-units in charge of single adults of either sex as well as whole families in charge of one. Why he identified the parent as a female in all cases is far from clear but this was probably a reflection of the widely held, often subconscious, view in those days that parental care in birds invariably devolves upon the mother, as in *Homo sapiens* and most other mammals.

The same Victorian assumption is to be found also in the writings of the bird-photographer Emma Louise Turner who studied Great Crested Grebes during photographic sessions at nests on Hickling Broad, Norfolk, and from her house-boat there (Turner, 1907, 1924). Although she clearly distinguished the sexes at times - realising, correctly, that the larger and brighter bird was the male and that both sexes shared in the incubation of the eggs and in the carrying and feeding of the young - she generally assumed that the sitting bird was always the female and often interpreted other events accordingly. Thus, her statement (Turner, 1924) that the male of one pair in June 1906 took "entire charge of the little ones", aged about three weeks, while the female incubated a new clutch, cannot be taken as authoritative though it may well have been true (see the case-histories in Part One of the present paper), as also her generalisation that "if the female nests a second time, the first brood remains with the male till the needs of a second family claim his attention". While noting, correctly, that parental feeding can continue after the chicks are full-grown, she then asserted that it was done by the males "especially" - this in spite of claims that, in August, "the males sometimes vanish mysteriously, and the female alone feeds and tends the young", and that males appear occasionally to "move away from their territory before the female". In spite of such inconsistencies, however, Miss Turner was evidently grappling with the same phenomena of sub-brood separation and parental desertion that I was to encounter many years later.

In 1922, Miss Turner observed that the female of a grebe family living near her boat always went about with two chicks and the male with one; the female "took an intense dislike" to the single chick, refused to feed it, and sometimes pursued it and pushed its head under the water. Thus, she appears to be the first ornithologist definitely to observe a case of brood-division and parental hostility in the Great Crested Grebe. It is interesting also to note that, during the early 1920s, she detected a shortage of food on Hickling Broad, where the water-level was dropping and the nesting population of grebes declining, and thought the parent grebes had difficulty in finding enough suitable food for the young.

From about 1918, the indefatigable Scottish naturalist Henry Boase kept records of the Great Crested Grebes present on the estuary of the River Tay and breeding on three small hill lochs lying at a height of nearly 700 ft above sea-level on the border of the then counties of Perthshire and Forfarshire. Some of his notes on parents and young (Boase, 1925) are confusing. He claimed that, in the cases he watched, "the care of the young in the early stages devolved on the male, on whose back they were carried while the female sought food" although it is clear from his account that the female also carried the young at times at some "later stage". He also stated that "During the next period", when the chicks were still small but now "diving freely with the adult", "the female seemed to be in sole charge ... the male paying little heed". Later, however, in the case of a brood of two, "the adults each took charge of a juvenile and continued to feed their particular charge until full grown", a clear indication of brood-division.

Neither Pycraft, Turner, nor Boase followed the fortune of any Great Crested Grebe family from hatching through to fledging and independence. This was first done by the team of bird-photographers Oswald J. Wilkinson and Charles R. Brown who, in June and July 1915, took photographs at a nest on Pettypool, Cheshire, at which three chicks hatched though only one was to survive the carrying period (Wilkinson, 1915; Brown, 1915-16). The notes made during incubation and hatching are detailed but those subsequently are sketchy and open to some doubt as observation was far from continuous. Allowing for the disturbance caused by bird-photography - of which (as is often the case) they were blissfully unaware though the unease of the sitting birds is evident in the published photographs - Wilkinson and Brown established that both male and female share the duties of incubation, of carrying (back-brooding) and feeding the young in the nest, and of tending them later. In this case, the surviving chick was left in charge of a single parent, said to be the female, after the departure of the mate in Week 10, the lone adult continuing to care for the chick until shortly before departing four weeks later, one week ahead of the juvenile.

The most important advance in our knowledge came with the report on the Great Crested Grebe Enquiry of 1931 (Harrisson & Hollom, 1932) which included, besides the main census data, information on breeding habits based on the observations of the organisers themselves and many other bird-watchers. Information on parental behaviour, though not quantified, contained the following important statement about brood-division, the first clear-cut one in the literature.

> Both sexes assist in all the nesting processes, but the male is undoubtedly the harder worker. There is a definite division of labour in feeding the young. At first the young are mostly carried by one sex (the male according to C.J. Patten and T.A. Coward, the female in our Surrey observations) and fed by the other, but after about a week the male and female tend to feed different young. All the young may go about together, they may all attempt to take food from the same adult; careful observation shows, however, that nearly always each parent deliberately feeds one or two young and no more, so that there is a definite distinction between "male's young" and "female's young". If there is only one chick the male tends to do most of the feeding ... Julian Huxley has stated that the female attends to all the young when they are well grown, but this is certainly incorrect of all cases observed during 1931. Indeed, we have seen the male attack and drive away "the female's young" and *vice versa*.

The claim that carrying is a function of one sex only has not been borne out by later, more detailed, observation. In my own studies, for example, there was no significant difference in the time spent carrying and guarding the young by the two adults, males being thus engaged for 48% of the nearly 200 hours observation-time, females for 52% (Simmons, 1970b). The reference to J.S. Huxley by Harrisson and Hollom was to his famous paper of 1914 on the courtship of the Great Crested Grebe in which he stated, referring to Pycraft (1911), that care of the older young falls to a single bird "probably the hen"; Huxley also suggested that the female does the larger share of incubating the eggs. He made no observations of his own on these topics, however.

The observations on brood-division were made by Phil Hollom, mainly in 1930 at various waters in Surrey, while conducting the ecological survey of aquatic birds in that county which gave rise to the national enquiry of 1931 itself (P.A.D. Hollom, *in litt.* 1986 and 1995, supplementing Harrisson & Hollom, 1932). In his field-notes for 16 August 1930, for instance, Hollom (then a 17-year-old schoolboy) identified the two chicks of one divided family at Virginia Water Lake as "the male's young" and "the female's young" respectively. He perceptively noted, however, that "the male on this date once or twice fed the female's chick so the brood-division was not absolute, not stupidly rigid! - e.g. when the male caught a fish and found his chick sated, having been fed four times in the previous eight minutes, he gave the fish to the hungry, pestering female's chick" even though he had refused it immediately before and avoided it "in a rather fox-and-goose chase manner". That same day, Hollom also saw the female threaten the male's chick and observed that her chick "sometimes put its beak onto her back (? remnant of climbing on back)", behaviour which I was later to term 'mock-boarding' (see Introduction).

The pre-war British findings on the parental behaviour of the Great Crested Grebe were summarised in Vol. IV of the Witherby *Handbook* (1940). According to F.C.R. Jourdain, incubation is performed by both sexes, in spells of three to three-and-a-half hours - this statement seemingly being based on the observations of Wilkinson (1915) and Brown (1915-16) though neither was mentioned by name - and the chicks "tended and fed by both parents", the "male assiduous at first, but not so in later stages, the young becoming independent of the parents at 9-10 weeks". According to B.W. Tucker, young chicks "are habitually carried on [the] back of one parent, while the other brings them food ... Later the brood tends to become divided, one or more [young] in charge of each parent".

This then was essentially the state of play when I commenced my studies in 1948. Though there were already clear references to brood-division in my notes, it was not until 1952 that I fully realized that it occurred in my study population, having overlooked or forgotten the earlier records in the literature, and it was also rediscovered independently in the same year by Derek Goodwin and John F. Burton, both of whom drew my attention to it at the time (Simmons, 1955).

Brood-division in other grebes

LITTLE GREBE *Tachybaptus ruficollis* The situation here remains uncertain because no modern studies have confirmed brood-division in this species; Bandorf (1970), for instance, did not mention it in his monograph. Nevertheless, the observations of Edmund Selous on a family in west Suffolk (made in 1901, published 1905) had indicated a tendency for the parents to separate after the nursery-platform had been abandoned for good and to "divide the care of the [three] young between them". His later study, in west Suffolk again (1914, published 1915), produced clearer evidence of the division of a brood of three as well as giving details of parental hostility (which he linked, not only with brood-division but also with brood-reduction).

Frank Finn's observations on a tank in Calcutta (1900-02, published 1907) were outlined in general terms only but revealed how the parents had once "divided the [two] young between them" after carrying was over. One of the adults then departed, leaving its partner alone with the brood; this bird then fed only one of the chicks, however, the other eventually crawling ashore where it was found in an emaciated condition by Finn and died next day (the first case of extreme parental neglect in the grebe literature). Finn also noted that parental hostility was directed against the neglected chick and that there seemed always to be a "favoured Benjamin" in broods of this species - this being the first published indication of the in-chick/out-chick situation in grebes.

Apart from these cases, we only have the statement by Ahlén, based on studies in southern Sweden (1954-65, published 1966), that he had several times noted that, if only two young remained in the brood, the parents would take care of one chick each and separate to different parts of the same lake.

My own brief observations on a family at Chew (August and September 1969, unpublished), when the three young were well-grown, revealed no obvious sign of brood-division at first, all the chicks appearing to follow both parents freely for food with no sign of parental hostility. Some ten days later, however, when just a single parent was feeding the chicks, all 17 of the fish I saw it bring were given to only two of the chicks - the first six to one (A), the next nine to the other (B). The third chick (C), though calling, was not fed; nor did it approach the adult like the other two did (all three loafed on the family nursery-platform, Chick-A and then Chick-B leaving it each time to meet the adult when it came with a fish). Chick-C had all the characteristics to me of an odd-chick-out and was probably the in-chick of the departed parent, the other two chicks being the in-chick (A) and out-chick (B) of the remaining one.

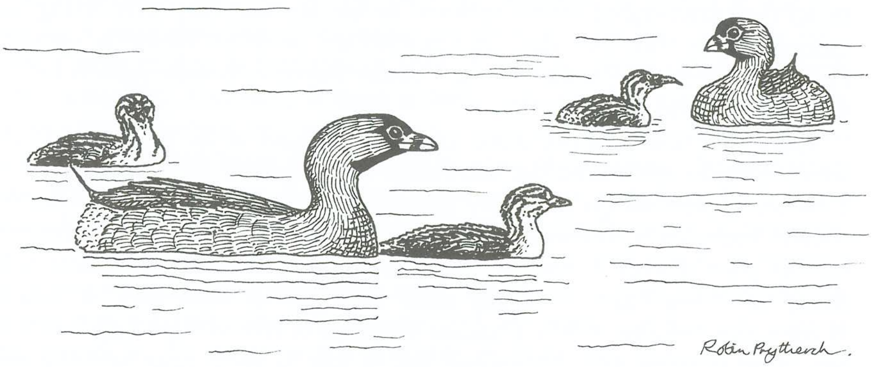
Chick-A, indeed, showed no fear of the adult and did not demonstrate to it whereas Chick-B, which had waited until Chick-A was replete before approaching the adult for food, did so intensely after each feed, turning-away, sinking, foot-splashing, and calling then sometimes swimming off with head low and once diving when at a safe distance. Once also, after surfacing within three feet of the loafing parent, it adopted a prone appeasing posture: while sunk and splashing, with its body three-quarters turned away, it swayed its neck from side-to-side in a peculiar fashion while keeping its bill in a fixed position, pointing away throughout.

These observations suggest to me that a system of brood-division and chick-favouring was operating and had been established earlier in this family after all (as in the case of the 1986 Great Crested Grebe family at Welham during Week 8).

It appears, therefore, that brood-division of some kind certainly does occur in the Little Grebe at times, its exact nature probably depending on the number of young and whether first, second, or third broods are involved. Unlike the larger grebes (including the Great Crested) - of which the majority are single-brooded - the Little Grebe and most other small grebes regularly raise two or more families during the one breeding season.

PIED-BILLED GREBE *Podilymbus podiceps* Of the two *Podilymbus* grebes, only the Giant Pied-billed Grebe *P. gigas* of Lake Atitlán in Guatemala was known definitely to have practised brood-division when I first drafted this paper (see under that species, below). No comprehensive studies of its closely related, smaller, and commoner congener had yet been published, a surprising situation seeing how well-distributed it is in North America, though its skulking habits make it particularly difficult to watch intimately, which is essential in order to establish the existence of brood-division. Highly vocal, the Pied-billed is strongly territorial and extremely pugnacious towards other grebes and waterbirds as well as towards its own species, actively defending its young at times - even against Man (e.g. Wetmore, 1920). Like the Giant Pied-billed Grebe, it has a stout and powerful bill adapted for breaking crustaceans but Fjeldså (1981b) characterised it as an opportunistic feeder, taking "a wide spectrum of smaller aquatic insects and fish" as well as "frogs, heavy bodied and even armoured and spined fish, shrimps, crayfish and crabs".

The only published observations on the nesting habits of the Pied-billed Grebe known to me in 1986 were those of Deusing (1939) in Wisconsin though its nesting ecology was studied by Glover (1953) in Iowa and by Chabreck (1963) in Louisiana and its territorial behaviour by Faaborg (1976) in North Dakota. In all cases, however, observations did not proceed past the nesting stage, mostly ceasing soon after the young hatched, a situation typical for many grebe studies in North America. Yet, in view of the situation in the Giant Pied-billed Grebe, I decided that the common Pied-billed Grebe remained a strong possibility as a brood-divider, especially as there were indications of the related co-strategy of egg-abandonment (see Palmer, 1962).



The relevant information to be gathered from these and other earlier studies was meagre and rather confusing. According to Chabreck (1963), the clutch - which, in his study, consisted of five to nine eggs - hatched over a period of "about two weeks", having been completed in a similar period, laying being "somewhat irregular" (i.e. with gaps of more than a day between eggs in many cases), so that individual broods often consisted of young of "several sizes". At a nest studied by Glover, however, the hatching period for a typical clutch of six eggs was spread over only two days, each chick taking from thirty minutes to two-and-a-half hours from the first sign of pipping, depending upon climatic conditions. While the speed of hatching must be typical for this species, as for other grebes, one might suspect - especially in view of Chabreck's findings - that the short spread of hatching was due to disturbance during laying which delayed the start of incubation. All the other indications (see, e.g., Fugle & Rothstein, 1977) were that eggs of the Pied-billed Grebe are usually laid at one-day intervals as in other smaller grebes; because incubation would appear usually to start with the laying of the first egg or soon after, the hatching period of a clutch of six eggs (say) should, theoretically, be spread over 5-6 days not just two (see also Palmer, 1962), causing age- and size-differentials among the young.

Whether the Pied-billed Grebe is typically double-brooded also remained to be definitely established. Though this did not seem unlikely, in view of the apparently short period that the young are dependent (see below) and of the definite second broods that have been reported (e.g. Miller, 1943), this species obviously does not attempt to raise multiple broods in the manner of the Least Grebe *Lymnodytes dominicus* (see the last section of this review, below) even in the tropics where the breeding season is long. When it does attempt a second brood, however, it may overlap broods in the manner of that species (Miller) and others, including the Great Crested Grebe. There was also uncertainty about the age at which the young become independent of parental care; this is possibly under three weeks according to Palmer (1962), and McAllister (1963) found that hand-reared chicks matured so quickly that they were flying and independent by their 28th day. On Lake Atitlán, however, where the common Pied-billed Grebe is a winter breeder, chicks stayed with their parents for 3-6 weeks (LaBastille, 1974).

There have now been two more recent field-studies of the Pied-billed Grebe which considerably extend our knowledge of the species' breeding biology: in 1984 on a (presumably) migratory population breeding in the prairie pothole country southeast of Minnedosa, Manitoba, where pairs were usually dispersed one per pond (Forbes & Ankney, 1987), and during 1988-92 on resident pairs living on Green Lake, an urban water in a heavily used park in Seattle, Washington, (Muller, 1995). Clutches consisted of five to eight eggs hatching over three to seven days (Manitoba), and of four to seven eggs hatching over one to four days (Washington). The eggs were laid at one-day intervals but with one or more gaps (usually of one day) later in the clutch in most cases. Even though incubation usually started on the day the first egg was laid, or very soon after, the number of eggs hatching on the first day varied between one and four. Nevertheless, there was usually a noticeable size difference between siblings and an obvious age-hierarchy which put the younger chicks at a disadvantage (Forbes & Ankney).

There was no indication in either study of double-brooding, though replacement clutches were laid, or of egg or brood desertions. In Manitoba in 1984, most of the young became independent of parental care about 35 days after "mid-hatch" (the date on which half the brood had hatched) but on Green Lake parental care usually continued well past day-35 though one chick became independent on day-33 and another on day-34. In 1988, most of the young did not become independent until day-58 and one chick was still being fed at 62 days of age; in 1989, the first chick in one brood became independent at 47 days but two others from the same brood were still being fed on day-57, though also actively seeking food for themselves. Other records from Green Lake were of independence on day-46, day-53 (two siblings) and day-57.

The Green Lake study is particularly interesting in that the Pied-billed Grebes there have become "habituated to human presence" so that they can be watched at close range without disturbing them. However, Muller said nothing about brood-division, which is nowhere mentioned in the text, although he did draw my attention (*in litt.*, 1995) to a possible case in which the adults in charge of a brood of three separated some time during the first three weeks after hatching, one parent with the smallest chick and the other with the two older ones (see Muller, 1995: 55, for further details). At the time, this evidence did not seem strong enough for me to include the Pied-billed Grebe as a brood-divider. Indeed, I began to think that it probably was not: surely, under such favourable conditions of observation, brood-division would have been evident if it were really occurring?

Brood-division, however, is described and discussed by Forbes & Ankney, making it quite clear that it was being practised in some form by those Pied-billed Grebes studied in Manitoba in 1984, though its precise nature still needs to be established. According to these authors - who used the term descriptively for incidents in which the two parents occupied separate regions of the pond simultaneously, each being accompanied by some of the young - brood-division was largely a temporary if frequent event and may well have been just a facultative arrangement not an obligatory strategy (in the sense of Simmons, 1974), the brood being periodically amalgamated again and contact maintained by calling when the sub-groups were apart. Yet the impression remains that the authors may not have come fully to grips with the problem of brood-division in this species in the single season available to them and, considering all the evidence (including that from Green Lake), it remains a strong possibility that the Pied-billed Grebe practises typical brood-division of at least type-C and probably of type-B and also shows parental favouritism towards particular chicks.

Forbes & Ankney did not say whether the family sub-groups they observed were of constant composition or not, so these may well have been. The "amalgamation" of the sub-broods from time to time does not mean that there was no real brood-division, merely that there was no full disassociation. Further, the authors showed that the distribution of food by the parents was often "non-random" - i.e. certain chicks were selected to be fed - and that the parents would determine which chicks were allowed to maintain positions near them, such "parental intervention" overriding the sibling hierarchies "in terms of food distribution within ... broods", this being observed in broods 15 days or more past the mid-hatch date. To me, these facts indicate not only the existence of true brood-division but also the likely presence of in-chicks in the sub-broods.

There is too much other detail in both these later publications for me to summarize them fully here. Forbes & Ankney make a particularly important contribution to the literature of brood-division and parental investment, and their paper should be read by all those interested in these topics. As these authors see it, brood-division in the Pied-billed Grebe, backed up by aggression directed at the chicks, is a form of parental regulation which, in the long run, is more effective than size-hierarchies among the chicks in determining the allocation of food and may well be the chief means of enabling the adults to raise as many young as possible, especially when food is short. They thus imply that brood-division is more important a reproductive strategy than they were at first prepared to admit.

GIANT PIED-BILLED GREBE (ATITLÁN GREBE) *Podilymbus gigas* Our knowledge of this peculiar flightless grebe is due almost entirely to the studies of Ann LaBastille (LaBastille Bowes & Bowes, 1962; LaBastille Bowes, 1965; LaBastille, 1974). Now extinct, it was confined to Lake Atitlán in Guatemala and extremely difficult to watch, yet until quite recently rather more was known about some aspects of its biology and behaviour than that of its congener the common Pied-billed Grebe with which it shared many characters (see under that species, above). It was largely a fish-eater, however, though freshwater crabs and snails were included in its diet and may once have been of more importance before their depletion in modern times following the disastrous introduction of exotic fish into the lake. Its dependence on fish while rearing young - except in the immediate post-hatching stage, when aquatic insects (especially hellgrammites) also figured - may explain the prolonged period of association (10-12 weeks) between parents and their offspring, the latter not becoming self-sufficient for food until they were 9-10 weeks old, which is much longer than in the common Pied-billed Grebe (as we have seen).

Although nesting by Giant Pied-bills were reported in several months, it would appear to have been usually a strictly seasonal breeder and single-brooded. The first indication of brood-division in this species was published in 1965, when a case of two chicks in the care of a single adult was noted, fuller but essentially qualitative details being given in 1975 (references above).

Broods were divided one and one, two and one, two and two, three and one, and four and one, starting (I judge, for the facts are not entirely clear) when the young were 3-5 weeks old and accompanying the parents on feeding trips - i.e. when carrying was over and the adults had escorted them away from the cover of the littoral vegetation out into open water. The chicks were by then wearing their second generation of down in which the new configuration of stripes on the head and neck was particularly striking, this probably helping the adults to recognize them individually (as in the Great Crested Grebe). Although the young were not thus identified by the observer, each adult did seem to care for the same young throughout the remaining period of dependence, each favouring the chicks in its care more than the others.

The female was thought to remain longer with the surviving young than did the male. Parental hostility, especially by the male, was shown as the chicks grew larger, the adults also decreasing the amount of food they gave the young and spending less time in feeding them. Chicks from the age of 9-10 weeks evinced fear of any adult (especially males) that passed by, immediately retreating to the nearest vegetation cover. Giant Pied-bills, the males in particular, were strongly territorial and parental hostility in this species may have been due to this factor as well as being linked with brood-division (a correlation not made by LaBastille, however) and the weakening of parent-young bonds at the time of decreasing dependence - due to a 'clash of interests' between offspring and adults.

Thus it is evident that the Giant Pied-billed Grebe did practise a well-defined kind of brood-division (type-B). In view of the evident harshness of the lake environment, it seems likely that even stricter division may have occurred at times (type-A) but now, of course, we shall never know.

SLAVONIAN GREBE (HORNED GREBE) *Podiceps auritus* In Europe, only Jon Fjeldså appears to have made any observations on brood-division in this species which he studied for 13 years during the 1960s and 1970s at numerous localities, mainly northern Norway and Iceland (Lake Mývatn and area) where the birds are typically single-brooded (Fjeldså 1973). He found that it was customary for the young to be divided between the parents when the former were some two weeks old, the members of each sub-brood then swimming close to one adult which fed them but without any obvious signs, in the course of general observation, of further discrimination between the chicks (Fjeldså, 1973; *in litt.*, 1986). Chicks started catching some of their own food during Week 2 and were sometimes avoided or pecked by the feeding adult in Week 3 when they begged. Except in the case of some late-season broods, most family groups remained together for about six weeks with both parents in attendance. Mates then left the nesting area simultaneously or one might depart before the other.

At least in the Lake Mývatn area, however, about one-third of the young were found to associate with a single adult. This may have been because of the separation of sub-broods but was thought more likely to have been due to the death, desertion, or temporary absence (on a feeding excursion to the main lake in the case of birds breeding on the smaller ponds and tarns) of the mate. Quite often, parental desertion was definitely a factor, one adult (perhaps usually the female) disappearing between three and four weeks after hatching and leaving all the young in the charge of the other. Fjeldså (1973) also recorded that there was an average monthly disappearance of 4.1% amongst adults, affecting male and female more or less equally, which he attributed to accidental mortality. It seems likely, however, that some of this too may have been due to sub-brood separation and/or desertion by one member of the pair. Care of broods or sub-broods late in the season by single adults was noted by Mrs Cecilia Knowles on lakes in Inverness-shire, Scotland (see Bannerman, 1959), and this may be interpreted similarly.

The above observations - in Norway, Iceland, and Scotland - refer solely to the heavy billed race *P. auritus arcticus*. Unlike the finer billed forms found elsewhere in the Palearctic (nominate *auritus*) and in North America (*cornutus*), this bird is an unspecialized feeder, taking whatever food is available (though mainly small fish and nektonic arthropods) in a variety of lake types, whereas the other two specialize on arthropod food in mainly eutrophic or mixtrophic lake types (Fjeldså, 1973). There are as yet no records of brood-division in nominate *auritus* but it has been well-documented in the North American race by Ferguson & Sealy (1983) who studied it in 1974 and 1975 on pothole marshes in Manitoba, Canada, an unpredictable but highly productive habitat which supports high densities of nesting Horned Grebes - perhaps the highest in North America - though the birds are usually single-brooded, as elsewhere.

As elsewhere too, the chicks (which usually fledged when between 45 and 50 days old) were found to develop feeding skills quickly; although the smallest young in the brood were fed for up to 24 days, the older chicks could be independent of parental care by the time they were 19-21 days and often departed from the natal pond before their younger siblings. Brood-division, said to be similar to that described for the Great Crested Grebe by Simmons (1974), occurred in six out of the seven families with four or more chicks but was recorded in only one family of three chicks and only one family of two. On the basis of size difference between the young, there was no indication that they were divided according to age. However, in families of five or more young, in which the age difference between the first- and last-hatched chicks was often as great as eight or nine days, the division did not involve the whole brood: the oldest one or two chicks, being nearly independent when the family carrying stage was over, foraged alone or with other independent siblings, leaving only the younger chicks to be divided between the parents. Older chicks, aged 16-18 days, approaching the adults for food were frequently chased away, such parental aggression - which only occurred, however, when the family or sub-brood consisted of two or more young - being particularly pronounced when the adult was feeding a smaller chick.

Parental desertion occurred in six out of eight study families with three or fewer young, one adult departing within a week of the end of the carrying period, leaving the mate to care for "its young" as well as for the rest of the brood; in four families in which the adults were individually marked, this twice involved the female and twice the male. Munro (1941) had earlier recorded that, although both parents remained with the young for "the first few weeks", one of the pair, "presumably the male", usually left the nesting pond while the other remained with the young until they were "nearly full grown" (see also Palmer, 1962).

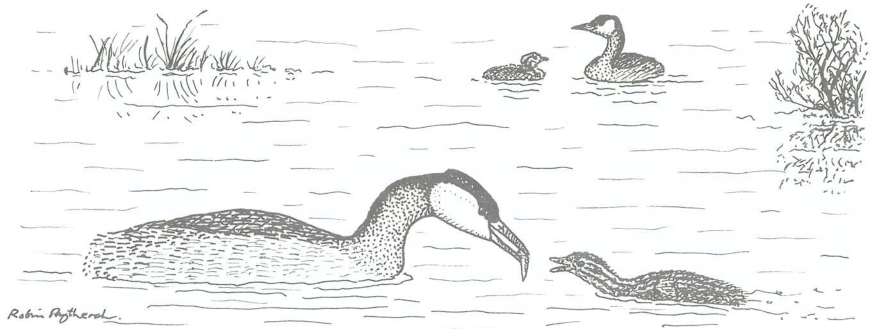
Brood-division and unilateral parental desertion are clearly important factors in the breeding biology of at least some populations of the Slavonian Grebe though the exact type of brood-division still remains to be established. To date, the information provided by Ferguson & Sealy (1983) is the most detailed that has been published on brood-division in any species of grebe other than the Great Crested and gives a number of pointers to some of the factors involved. As yet, however, we lack detailed case-histories and quantitative data on parental feeding; neither has the possibility of an in-chick/out-chick situation, as found in the Great Crested Grebe, been properly investigated through the identification of individual young.

RED-NECKED GREBE *Podiceps grisegena* The information on brood-division in this species is limited and largely overlooked - receiving no mention, for example, in regional handbooks (e.g. Cramp & Simmons, 1977) - even though the topic was covered by Ulrich Wobus in his 1964 monograph.

Wobus (1964) found, from his own studies in Germany during the early 1960s, that in some but by no means all pairs of Red-necked Grebes there would be a "sharing out" of the young between male and female after a brief period in which both sexes cared for them jointly. As most broods consisted of two chicks, the adults would each take over the care of one of them and then often separate completely, each unit occupying different areas of the same water. The division was such that the male would attack the female's chick and the female the male's (as recorded in the Great Crested Grebe) though the two family units would sometimes rest close together without any sign of friction. Brood-division was rare on small ponds occupied only by a single pair but common on larger and well populated waters with a long unbroken border of aquatic vegetation. In only one case, however, was Wobus able to make detailed observations on the first stage of the process which started four days after the hatching of the last chick of three - by which time it had died - the smallest surviving chick staying with the female and the larger with the male, though the female was seen to feed the male's chick and the male to carry both chicks. Three days later, the division was much more clear-cut, there being no "exchange" of young or feeding of the other young, but observations ended next day when both chicks succumbed during a spell of inclement weather.

If typical, this case suggests that brood-division in the Red-necked Grebe starts earlier in the cycle than it does in the Great Crested Grebe - about 7-8 days after the hatching of the first egg. This is born out by the recent studies in Poland of Janusz Kloskowski who, however, found that brood-division was rare in his study population - occurring in just one family out of some ten watched for about 100 hours each and starting as soon as carrying was over, the parents soon separating to different parts of the same lake (Kloskowski, *in litt.* 1995). It should be noted that carrying apparently lasts only between one and two weeks in this species (Wobus) and that, like the Great Crested Grebe, no use is made of the nest or other platform as a nursery for the young. Brood-division was also implicit in the earlier studies of Munro (1941) in British Columbia, Canada. He observed that broods of Red-necked Grebes which were accompanied by both parents tended to be larger (1.9 young, sample 35) than those accompanied by one (1.3 young, sample 9) even though the range in brood-size was the same (1-4).

Monro also found that the relative number of the single-parent units did not increase as the season advanced and attributed them mainly to desertion by one of the pair as a seemingly "individual reaction". Unilateral parental desertion in the Red-necked Grebe has now been confirmed by J.J. Vlug and by J. Kloskowski (both *in litt.*, 1995). The former has found it to be relatively common in the population he studies in Schleswig-Holstein, Germany (see, e.g., Vlug, 1993), usually occurring when only a single unfledged chick remains in the brood, the deserting adult probably departing early in order to moult its wings elsewhere. And in nine cases documented by Kloskowski, it was the male which departed first in six and the female in three.



When it does occur, brood-division in this species is evidently often of type-A, as also indicated by the statement by Ahlén (1966; see Part One). In the light of our knowledge of the Great Crested Grebe, the Red-necked Grebe would appear to be a likely candidate as a practitioner of brood-division. Over much of its Palearctic range, where the nominate race (*grisegena*) is in competition with the larger and dominant Great Crested Grebe, the diet of the Red-necked is more generalised - though with a tendency towards taking aquatic worms, gleaned from underwater plants and picked up from the bottom (Fjeldså, 1982b). In the northernmost parts of the western Palearctic, in Finland and Russia, it has evolved a longer and more slender bill and appears to specialise in catching fish and squid (race *"schioleri"*); the same trend, together with an overall increase in size, is found in the birds (race *holboellii*) occupying east Siberia and western North America (Fjeldså, op. cit.). All these forms of the Red-necked Grebe, but especially those that take a good proportion of fish in their diets, are likely to divide the brood. Desertion of the nest at times before all the eggs have hatched (Palmer, 1962) may be a related strategy (see Part One).

BLACK-NECKED GREBE (EARED GREBE) *Podiceps nigricollis* The evidence for brood-division in this opportunistic colonial species, although convincing, is restricted (see summaries in Cramp & Simmons, 1977). The earliest observations, by Oliver Pike (the bird-photographer) and by Charles Oldham, were on two of the pairs breeding at Marsworth Reservoir, Tring, in June-August 1918. These have been mostly overlooked and are not mentioned in either Witherby (1940) or later handbooks, so I will give the details here (scanty as they are).

In the first family, according to Pike (1919), each adult took charge of a single chick in the brood of two immediately after hatching was completed, this arrangement continuing for at least the next 12 days. By about the 16th day, however, the young were catching fish capably for themselves "although each parent still had charge of one baby". In the second family, comprising three chicks, a further "division of labour" was observed by Oldham (1919) about two weeks after the adults had first been seen sharing carrying and feeding duties: now (the young being some 16-17 days old on my calculation) "one parent had sole charge of two and the other of one of the clamorous and apparently insatiable chicks, each party feeding independently of and at some distance from the other". By about the 34th day (again on my own calculation), the young were diving successfully for their own food though still being mostly fed by the adults; seven days later, however, they appeared to be quite independent.

Although the credit for the discovery of brood-division in the Black-necked Grebe belongs to Oldham and Pike, the brunt falls on van IZendoorn (1944) who watched a solitary pair nesting on a smallish pond at Shellinkhout, in the north-east Netherlands, in June-July 1943. After the hatching of the brood of three, the family remained for some days within or close to the cover of the reeds but moved into the open much more when the young were older. At about a week after hatching, each adult started "to look after part of the young ones" with an evident "loosening of the nuptial tie, caused by the offspring, as the partners always seem to shun one another, are even hostile when they meet ... On one occasion I saw an adult bird pecking at a young one". Van IZendoorn had no idea why such hostility occurred though he did note that, after the brood was divided, a chick might sometimes join the other parent. The parents continued to feed the young after the latter were able to feed themselves (at about two weeks) and they were said to have become fully independent after about three weeks. At feeding, a chick would approach the parent with its neck stretched forward while uttering "a rather loud chirping sound", take the food, and, almost invariably, swim away immediately from the adult for a distance of "three or more decimetres". The biological significance of this "instinctive flight" seemed clear to him: "the young bird secures the safety of its [share of food] by this action, especially when other young birds are in the neighbourhood"; although it was still performed whether or not there was any danger of the food being stolen, van IZendoorn did not link the behaviour with fear of the adult, neither did he see any comparable behaviour from young Little Grebes or young Great Crested Grebes being reared on the same pond.

Though van IZendoorn may well have underestimated the age of his young Black-necked Grebes, this species does appear to have a shorter period of dependence than most other sympatric grebes. The age of fledging is about the same as in the rather smaller Little Grebe though some populations of the rather larger Slavonian Grebe may fledge even earlier. The reduced period of parental care in the Black-necked Grebe is not linked with double-brooding (though this occurs in a minority of pairs) but with a strong tendency towards opportunistic colonial nesting on ephemeral waters, often in protective association with small *Larus* gulls or *Chlidonias* terns, and feeding on flushes of tiny aquatic invertebrates, taken on the surface, often by 'skimming' with the specially adapted bill (with its flattened gonys and wide base), as well as by diving.

Prinzinger (1974) - who studied a small colony of Black-necked Grebes on Guggenhauser Weiher, an 8 ha fish-pond, in Germany in 1965 and in 1970-73 - appears to be the only other grebe-watcher to record brood-division in this species, there being no American records so far as I know. In a brief account of the parent-chick stage, he said that the "family bond" begins to dissolve 10-12 days after hatching as each adult takes a section of the brood for itself and tends it separately from the mate, this segregation going so far at times that the adults attack each other's young if they approach.

Thus, although there have still been no detailed studies, brood-division certainly occurs at times in the Black-necked Grebe, both in colonial and solitarily nesting pairs, and can be of the highest type (A). However, there is some evidence that it may be replaced, partially or wholly, by a form of crèching not found in other Palearctic grebes (J. Fjeldså; see Cramp & Simmons, 1977 and Fjeldså, 1977). The details of this crèching still remain to be established - though it may be linked with a degree of parental desertion which leaves single adults tending whole broods at times.

WESTERN GREBE *Aechmophorus occidentalis* Like the Great Crested Grebe, of which it is in some ways the North American counterpart, this species is a specialist fish-eater and normally single-brooded. It is highly colonial, however, and the male's habit of providing substantial amounts of food for the female prior to nesting is one shared, among grebes, only by its sibling species Clark's Grebe *A. clarkii*. Its courtship behaviour has now been well-studied (Neuchterlein, 1980, 1981a,b; Neuchterlein & Storer, 1982, 1989) but little has yet been published about its breeding strategies and parental behaviour (but see Neuchterlein, 1981c, 1988).

The Western Grebe always seemed to me to be a likely candidate for brood-division but, in 1986 when I drafted my original review, I could find no evidence for it. Indeed, I had earlier been told by Virginia Scammell - who had undertaken pilot studies of Western Grebes at Eagle Lake and at Tule Lake, California, where it is resident and seems to maintain permanent pair-bonds - that it might well not do so (V.L Scammell, *in litt.* 1975; see also Scammell-Tinling, 1983). Considering this possibility, I suggested to her (*in litt.*, 1975) that, as brood-division seemed to be an adaptation against the chance of food failure during the chick-raising period, its possible absence in the Western Grebe might be correlated with a predictably plentiful and dependable food supply for, as I saw it, the birds could nest colonially in large numbers and 'invest' in courtship-feeding only because the food situation permitted them to do so. There would then be no need for brood-division and related strategies, and this might explain certain other features of the Western Grebe's breeding biology - e.g. the speeded-up laying schedule (an egg a day, thus reducing the age and size differentials between the young) - and the lack of conspicuous striping in the down-pattern on the head and neck of the chicks (because there was no requirement for the young to be individually recognizable).

In spite of such considerations, however, brood-division is now thought to occur in the Western Grebe (Storer & Neuchterlein, 1992; G.L. Neuchterlein, in litt, 1995), at least in the northern breeding populations studied by Neuchterlein and his associates at the Delta Marsh, Manitoba, where the species is migratory and forms seasonal pair-bonds only. Here, the parent birds appear to "split the brood" when the young are 3-4 weeks old (i.e. after the carrying period is over), the adults then "separating for long periods while foraging", perhaps permanently. Regular population surveys have revealed that chicks which are half or more the size of the adults tend to be accompanied by a single parent rather than by two and that full-grown young are rarely seen together with both parents. Further study of the chick-rearing phase of the cycle is planned, however, for at present it is difficult to follow individuals in an unmarked population of over 600 birds at Delta Marsh, especially as the adults head for large open bays with their young and are not easily watched from the fixed observation hides. Nevertheless, it certainly looks as if brood-division does occur regularly in the Western Grebe and can often be of type-A. The full story is awaited with keen anticipation.

Notes on the remaining species of grebes

Two further large New World grebes - Clark's Grebe (North America) and the Great Grebe *Podiceps major* (southern South America) - may also be likely brood-dividers, both being specialised fish-eaters and single-brooded. Relatively little is known about the biology of the Great Grebe, a solitary nester, but its behaviour has been studied by Storer (1963); though still classified as a *Podiceps*, its affinities clearly lie elsewhere, possibly with the *Poliocephalus* grebes (Fjeldså, 1981b). As for Clark's Grebe, it has been officially separated as a distinct species from the Western Grebe only relatively recently (AOU, 1985) so we have still to wait until all the important differences in their biology have been fully disentangled. Brood-division, however, remains a distinct possibility.

The last of the larger *Podiceps* grebe, the rare and distinctive Hooded Grebe *P. gallardoi* of southern Patagonia, was first described for science only quite recently (Rumboll, 1974). General accounts of its discovery, habits, and status are given by Conway (1980), Storer (1982), and Simmons (1983). Though clearly a 'good' *Podiceps* in many characters, including manner of courtship (see Storer, 1982; Fjeldså, 1982a), it is peculiar in some features, not least in that the chick, though having the typical bare face-patches of its congeners, lacks the bare tonsure and has in its place a small, triangular patch of white down (Neuchterlein & Johnson, 1982). The absence of the tonsure may be correlated in the Hooded Grebe with the unique breeding strategy of the species: it lays two eggs, like all the endemic Andean grebes, but invariably leads away but a single chick from the nest, soon abandoning the viable second egg if the first hatches successfully. The expendable second egg or chick, therefore, would appear to act as 'insurance' in case of loss or infertility of the first, as in certain boobies *Sula* for instance (see, e.g., Simmons, 1967, 1970a), though these have altricial young and the 'disposal' of the surplus nestling is effected by its sibling. As a result, the single Hooded Grebe chick suffers no competition from siblings and is not subjected to the stresses of brood-division - for, of course, there is no question of brood-division in this species, the one grebe in which that strategy certainly does not occur.

The importance of brood-reduction by deliberate egg-abandonment in the Hooded Grebe strengthens the likelihood that this particular parental breeding strategy may play a role at times in other grebes (see Part One), though none appear to have taken it to the same extreme. Clearly, like the boobies and many other tropical seabirds, the Hooded Grebe just cannot rear two chicks under the normal conditions in which it breeds and the full joint attention of both parents is essential for the survival of even a single chick. The factors involved have yet to be fully studied but must be related to a large extent to the type of food and the feeding frequency. The parent Hooded Grebes are able to provide only small invertebrates for the chick to eat and spend a huge proportion of their time each day diving for them and ferrying them singly to it (G.L. Nuechterlein, personal communication; J. Fjeldså, *in litt.* 1986).

The remaining species of *Podiceps* all belong to that closely related nexus of colonial-nesting 'eared' grebes which includes the Black-necked Grebe. Of these, the Colombian Grebe *P. andinus* - first described only in the late 1950s (Meyer de Schauensee, 1959) - was confined to Lake Toto where it has since been totally extirpated before anything could be discovered about its behaviour. Little detailed information is available either on the breeding and general biology of the two other Neotropical species, the closely related Silver Grebe *P. occipitalis* (the more widespread of the two) and the Junin Grebe *P. taczanowskii* (which is confined to the lake of that name in Peru). Both species, which feed and nest sociably but rear their young solitarily, lay two eggs so that broods consist of one or two young only. What is known of the Silver Grebe - which feeds on tiny items of invertebrate prey and can, therefore, breed only on highly productive waters - suggests that it is the one which more closely resembles the Black-necked Grebe in its reproductive biology (see especially Fjeldså, 1981a,b). It may, therefore, be expected to practise brood-division at times, at least as an occasional strategy, though observations on adults feeding both small and medium-sized young have so far given no obvious indication of it (J. Fjeldså, in litt. 1986).

The rather larger and flightless Junin Grebe seems to me even more likely to practise brood-division for, unlike the Silver Grebe, it feeds on small fish. Fjeldså (1981a), who studied both species on Lake Junin during field-trips in 1977 and 1978, found the Junin Grebe appeared to show a marked sexual dichotomy in parental care, of a type not reported from any other grebe: only the males were seen to carry the young, the females bringing all the food for them, though the males, which practically ceased diving during this period, did sometimes offer the chicks midges which they picked up from the surface of the water. One male shot when carrying young was found to have little subdermal fat and its stomach only contained 51 feathers, the remains of at least 173 midges and one small fly, and four fish otoliths. His mate, however, was well-nourished, her stomach containing mainly fish remains. Because of this division of labour, Fjeldså thought that brood-division was unlikely to occur.

The importance of brood-reduction by deliberate egg-abandonment in the Hooded Grebe strengthens the likelihood that this particular parental breeding strategy may play a role at times in other grebes (see Part One), though none appear to have taken it to the same extreme. Clearly, like the boobies and many other tropical seabirds, the Hooded Grebe just cannot rear two chicks under the normal conditions in which it breeds and the full joint attention of both parents is essential for the survival of even a single chick. The factors involved have yet to be fully studied but must be related to a large extent to the type of food and the feeding frequency. The parent Hooded Grebes are able to provide only small invertebrates for the chick to eat and spend a huge proportion of their time each day diving for them and ferrying them singly to it (G.L. Nuechterlein, personal communication; J. Fjeldså, *in litt.* 1986).

The remaining species of *Podiceps* all belong to that closely related nexus of colonial-nesting 'eared' grebes which includes the Black-necked Grebe. Of these, the Colombian Grebe *P. andinus* - first described only in the late 1950s (Meyer de Schauensee, 1959) - was confined to Lake Toto where it has since been totally extirpated before anything could be discovered about its behaviour. Little detailed information is available either on the breeding and general biology of the two other Neotropical species, the closely related Silver Grebe *P. occipitalis* (the more widespread of the two) and the Junin Grebe *P. taczanowskii* (which is confined to the lake of that name in Peru). Both species, which feed and nest sociably but rear their young solitarily, lay two eggs so that broods consist of one or two young only. What is known of the Silver Grebe - which feeds on tiny items of invertebrate prey and can, therefore, breed only on highly productive waters - suggests that it is the one which more closely resembles the Black-necked Grebe in its reproductive biology (see especially Fjeldså, 1981a,b). It may, therefore, be expected to practise brood-division at times, at least as an occasional strategy, though observations on adults feeding both small and medium-sized young have so far given no obvious indication of it (J. Fjeldså, in litt. 1986).

The rather larger and flightless Junin Grebe seems to me even more likely to practise brood-division for, unlike the Silver Grebe, it feeds on small fish. Fjeldså (1981a), who studied both species on Lake Junin during field-trips in 1977 and 1978, found the Junin Grebe appeared to show a marked sexual dichotomy in parental care, of a type not reported from any other grebe: only the males were seen to carry the young, the females bringing all the food for them, though the males, which practically ceased diving during this period, did sometimes offer the chicks midges which they picked up from the surface of the water. One male shot when carrying young was found to have little subdermal fat and its stomach only contained 51 feathers, the remains of at least 173 midges and one small fly, and four fish otoliths. His mate, however, was well-nourished, her stomach containing mainly fish remains. Because of this division of labour, Fjeldså thought that brood-division was unlikely to occur.

The situation obviously deserves further investigation; if really a stable strategy, and not due to ephemeral causes (e.g. disturbance), then one might expect it to be pushed to its logical conclusion, with the female providing food for the male as well as the chicks if current conditions permitted. (Carrying adult Great Crested Grebes will at times eat fish brought for the chicks by the mate, when the former are replete or the prey too large.) Whether carrying is confined to one sex or not has little if any bearing on the likelihood of brood-division, however, for (as we have seen) this is likely to occur only after the carrying phase is over.

The behaviour and biology of the two *Policephalus* grebes - the New Zealand Hoary-headed Grebe *P. rufopectus* and the Australian Hoary-headed Grebe *P. poliocephalus* - have been surprisingly neglected by local ornithologists, the best studies being by visiting grebe specialists; see Storer (1971) for the former species and Fjeldså (1983) for the other, though neither was able to make any significant observations on parents and young. Neither do I know of any substantial studies on the reproductive biology of either species, though it is clear that the New Zealand bird is a solitary, territorial breeder and the Australian one a highly colonial, opportunistic one. In fact, the latter's diet of tiny invertebrates and dependence on temporary waters for nesting parallels that of the majority of the eared-grebe group. It is probably single-brooded.

The New Zealand Hoary-headed Grebe, on the other hand, includes more fish in its diet. It has a prolonged breeding season and, though clutches are small and nest losses high, is probably often double-brooded. The only observations on parents and young that I know of are those of Buddle (1939) who gave a diary account of a pair with two chicks that he watched at Lake Rotoiti (North Island) in the period 8-23 February 1938.

At the beginning of the watch, the young had already hatched; though described as "small", their exact age was not known and they were probably older than Major Buddle thought. They were said to leave the nest immediately after hatching, following their parents long distances while the latter searched for small fish and often resting on the back of one or other of them. When an adult surfaced with a fish, there "ensued a wild race between the two young, the first to arrive snatching the fish from the mouth of the parent, which immediately dived again". The adults were seen copulating on 13 February and a new nest with one egg was found on the 14th. Though still quite small, the young were now fed only occasionally and hunted for themselves for much of the time. The nest had been washed out by the 16th, however; copulation continued and the one chick that appeared near the parents that day was driven off whenever it approached the mating place. By the 18th, the young appeared to be "almost as big as the parents and not easy to distinguish without the aid of field glasses". The female was seen to feed them on the 20th, though "apparently very unwillingly", and they were "savagely chased away" by the male. Another new nest was then under construction; the birds were busily building on the 21st, the chicks not being allowed within 20 feet of it, and an egg was laid there that day, though by next day it was in the water and the nest abandoned. The birds appeared to be building at a new site on the 23rd when the watch ceased.

Though these observations are equivocal, a strategy of overlapping broods and an early break-up of parent-young bonds is indicated. In this case, the parental hostility shown would seem to relate to such a strategy rather than to brood-division; the latter may also have been involved, of course, and overlooked or misinterpreted (as it is so easy to do). Parental hostility towards their single surviving offspring, then 4-5 weeks old and full-grown, was recorded from a pair of Australian Hoary-headed Grebes that nested in New Zealand in 1975-76 (Barlow, 1976). In this case, no second brood or clutch was involved. The juvenile remained in the same general area of the lagoon as its parents but was more often 50-80 metres away than close to them and fed independently. It frequently tried to approach the adults, however, but was "chivvied and chased, or rebuffed by a threat posture of lowered head" by one or both of them.

The 'conflict of interests' between parents and chicks at this stage of the cycle is particularly complex for in some grebes the young of earlier broods are tolerated, as in the Least Grebe *Lymnodytes dominicus* (see below), and may even help to feed their younger siblings (Fjeldså, 1977). This has been recorded, for instance, in the Little, Black-necked, Slavonian, Red-necked, and Great Crested Grebes (see Cramp and Simmons, 1977) though it remains to be properly documented and I myself have never recorded a single instance of such behaviour in 50 years of watching the Great Crested Grebe.

No hint of brood-division has been recorded for any of the *Tachybaptus* grebes other than the Little Grebe or for the apparently closely related Least Grebe. Unlike many of the species reviewed so far, these small grebes have a stable breeding strategy of attempting to raise more than one brood in a season, though detailed studies are lacking. The biology of the two *Tachybaptus* dabchicks on Madagascar is almost totally unknown and both are endangered species - the Aloatra Little Grebe *T. rufolavatus* because of interbreeding with the more recently arrived Little Grebe, and the Madagascar Grebe *T. pelzelnii* because of competition with it (Voous & Payne, 1965). They and the better known Black-throated Little Grebe *T. novaehollandiae* (Australia and Australasian islands) seem as likely to divide the brood as the Little Grebe itself, however.

Parental hostility has been noted in the Black-throated Little Grebe by Ashby (1933) but only that directed against young of the earlier brood after the hatching of the next. Similar behaviour was recorded by Gross (1949) in his classic study of a pair of Least Grebes that nested on a pond in Cuba during 1947-48, rearing a total of 24 young from eight attempts and six clutches during a period of continuous breeding activity over about a year. The broods were overlapped, the female laying a new clutch soon after the hatching of the last and male and female sharing the duties of incubation and feeding the young. While the fifth clutch was being incubated, for example, the chicks from the fourth were still being fed. The independent young from the two previous broods were also tolerated on the pond, and were fed occasionally by the male. When the next brood hatched, feeding of the previous one continued for a time, so the parents were, at first, performing the duties of incubation, carrying, and feeding two sets of young concurrently. For the first four nights after all the new chicks had hatched, "the female or the male spent the night on the nest with the four young on its back. The attitude of the adults to the brood of older young [then] changed. When the latter appeared too near the downy young they were chased away by the male and sometimes by the female. Nevertheless when a large crustacean much too large to serve as food for the downy young was caught it was fed to the older ones."

It is difficult to see how brood-division could be fitted into such a complex situation and, though a measure of competition between the dependent young for food was evident, there was no obvious indication of any hierarchical system among the siblings themselves or of any parental preferences for particular young, though Gross may have missed them, of course. Like the *Tachybaptus* grebes, the Least Grebe uses the nest as both a day- and a night-nursery well after hatching, for about 10-14 days in all according to Palmer (1962). Little has otherwise been published on its biology though a start has been made to study its behaviour (Storer, 1976; see also summary by Storer, 1992). Fjeldså (1981b) has suggested that its high reproductive powers and ability to take to flight easily may be adaptations for rapid population build-ups on new waters (see also Smithe & Paynter, 1963).

The reproductive biology of the remaining group - the Neotropical golden grebes *Rollandia* - is little known. The White-tufted Grebe *R. chilensis* is abundant and widespread in the non-tropical parts of South America where it occupies a great variety of habitats with abundant vegetation (Fjeldså, 1981b). The large race *morrisoni*, which occurs on Lake Junin in Peru (Simmons, 1962a), is a fish-eater but otherwise the species appears to be a generalized feeder over most of its range (Storer, 1967; Fjeldsa, 1981b). Though so-called breeding colonies have been reported, it seems to be typically a dispersed, highly territorial nester. In the Puna Zone at least, it usually lays a small clutch of eggs (1-3, usually two) and may well be single-brooded. Being shy and skulking when nesting, it is not easy to observe.

The closely similar but much larger form that occurs on the Falkland Islands - the Falkland Grebe *R. rolland*, which I prefer to treat as a distinct species (Simmons, 1962a,b) - appears to be mainly a fish-eater and a dispersed, territorial nester with a limited breeding season (see Cobb, 1933; Woods, 1975) and hence single-brooded; the clutch is small (1-3 eggs). What little is known of the biology of the still larger but flightless Titicaca Grebe *R. microptera*, a most distinctive species confined to the Lake Titicaca area of Peru and Bolivia, suggests that it may be a dispersed, seasonal breeder with a long reproductive cycle; it lays 1-4 eggs but most clutches are of two eggs. Large fish were found by Fjeldså (1981b) to provide the largest biomass in its diet.

All the *Rollandia* grebes, and especially the fish-eating forms, seem likely to be grebes which divide the brood. In the two mainland species, however, the available evidence is not supportive. Dr Fjeldså tells me (*in litt.*, 1986), the rule is for the adults and chicks to remain together in the territory and, although the young usually leave their parents before the next breeding season, he has single records for both *R. chilenis* and *R. microptera* of a juvenile from a winter nesting remaining after the hatching of the next brood and occasionally feeding its younger siblings. He also reports that parents will sometimes show intense aggression towards dependent chicks, or avoid them, but he has no direct evidence of any in-chick/out-chick or any other arrangement, the hostility also occurring when there is only one chick in the brood. The question remains open, however.

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Club Activities, 1995 & 1996

At the beginning of 1995 Club membership stood at 558, and by the end of 1996 it had reached 583. In January 1996 Jane Binstead became the two thousandth birdwatcher to enrol as a member since the Club formed in 1966.

Activities in **1995** started with the usual New Year visit to Slimbridge, followed by thirty-one field trips to a variety of locations including the Somerset Levels, Abbotsbury, Wentwood, Barrow Hill, St. Catherine's Valley, Arne, Highnam Woods, the Quantocks and Capel y Ffyn with evening trips to Frampton, Rowberrow and Marshfield. The morning of the Dawn Chorus meeting was beset by heavy rain and only one stalwart member plus the leader turned up, but despite the appalling weather it was reported that Song Thrushes were singing well. A Beginners' field trip was to the Frome Valley and a Tally Hunt/Summer Social was held in July. Three coach trips were organised to the Exe Estuary, Pagham Harbour and Durlston/Winspit, but the last was changed into a car trip owing to low support for the coach. Birds of note during the field meetings included Dartford Warbler at Sand Point, Firecrest at Stourton Woods, Melodious Warbler at Pagham Harbour and Spotted Crake at Chew Valley Lake.

The 1995 Club holiday was a week on the Isles of Scilly, and weekend trips were made to Norfolk (eight Hen Harriers at roost and Snow Buntings) and South Devon (with Cirl Buntings and many Little Egrets). The Dorset weekend was cancelled.

Indoor meetings during 1995 provided a variety of speakers with a wide range of interesting topics, all illustrated. The year opened with Robin Prytherch talking about birds and conservation problems at Ascension Island. The Members' Evening showed, yet again, that many members are very able speakers. Mike Reid showed us the stunning Greenland scenery as well as the birds, Graham Wren talked of the fortunes of our breeding seabirds, Mike Wilkes related his spring in Spain, Jeff Blincow his experiences of birding in Australia and Malcolm Sainsbury rounded off the indoor meetings with a talk about the birds of the Pacific North West at the AGM. This followed the business part of the meeting when the three officers agreed to continue to serve - Nick Ayers as Chairman, John Tully as Treasurer and Jean Lay as Secretary. Judy Copeland (Membership Secretary), Robin Prytherch and Margaret Searle were re-elected to the General Committee; Brian Lake and Clive Leyman joined as new members. Ken Hall and Gordon Youdale agreed to continue as co-opted members and Trevor Silcocks as Honorary Auditor to the Club. There were no nominations for the Stanley Crick Award.

During 1995 the Club donated £50 to Duncan James to help in his efforts to raise funds to work in Vietnam. Duncan later talked at the Members' Evening about his time in Vietnam. £30 was donated to the BTO Save our Skylark appeal and £50 to the Wildlife Trust Tree Planting Scheme at Folly Farm, where about 20 trees were planted by a group of (very wet) Committee Members early in 1996. The Club organised another open evening at Taunton Leisure. It acquired an excellent new notice board for use at indoor meetings and at other meetings in the area where the Committee felt it would be of interest. Club details were, as usual, included in the Bristol Central Library information leaflet.

The **1996** 1st January Slimbridge field meeting raised £74 sponsorship for the BTO Save our Skylark appeal. There were a further twenty-nine field trips during the year, including visits to the Gwent coast, Clevedon, Sand Point (two Ring Ouzels and Tree Sparrows), Lower Kilcott, the New Forest, the Forest of Dean, Haldon/Yarner Wood, Titchfield Haven, Portland, Kenfig (Sabine's Gull) and Berrow (male Snow Bunting and Jack Snipe), plus three evening meetings to Abbots Leigh, Inglestone Common and Marshfield, and a Beginners' meeting at Leigh Woods. Coach trips to the Exe, Durlston/Winspit and Portland were well supported as were weekend trips to Flamborough Head and Norfolk and two very successful holidays to the lakes in North-east France (Common Cranes and White-tailed Eagles) led by Ken Hall and to Holy Island (dramatic thrush passage on one day) led by Robin Prytherch.

Indoor meetings during 1996 again provided a variety of interesting and informative evenings with Julian Hector talking about birds and radio programmes, Robin Khan on the Nightjars at Haldon Forest, a Members' Evening which provided an interesting collection of topics, Derek Toomer gave us much information about the BTO Garden Birdwatch survey, Malcolm Sainsbury transported us to the Rift Valley, Michael Leach gave us a fascinating 'owl evening' and at the AGM Ken Hall shared with us his interest in France and its birdwatching potential. Joint meetings with the Bristol Naturalists' Society were held during 1995 and 1996 on a reciprocal basis.

The AGM marked the end of more than 20 years' service on the General Committee by Ken Hall. Steve Hale and Tony Scott also resigned; their places being filled by Michael Johnson and Gordon Youdale. Nick Ayers, John Tully and Jean Lay continued to serve as Chairman, Treasurer and Secretary respectively and Judy Copeland as Membership Secretary. Trevor Silcocks continued as Honorary Auditor to the Club. There were no nominations for the Stanley Crick Award.

During 1996 the Club donated £100 to the Gordano Valley Ringing Group and £30 to the Somerset Wildlife Trust for its Water Meadow appeal. The Club purchased a stand for the projector (which was overhauled) as well as a new lens and new carousels. A clip-on microphone was bought to help improve the sound system.

The Club Committee again took responsibility for arranging protection for the Avon Gorge Peregrine nest. In both 1995 and 1996 two young fledged. The nest site was on the Clifton side of the Gorge in 1995 and although this did not provide the excellent watching of previous years, the nest was comparatively safe. The pair nested on the Leigh Woods side of the Gorge in 1996. Mike Glover, with great success, took over the organisation of the watch from Andy Beattie in 1995. The BOC is grateful for the continued support from the public and particularly from its sponsors: Bristol Water, ICI Fertilizers, Rhone-Poulenc, Britannia Zinc and *BBC Wildlife*. The Club were given a Kowa telescope by Pyser SGI Ltd, a discount on the purchase of a tripod by Ace Optics and a carrying bag from Gyles Bros of Blackboy Hill, all for the use of those on duty, and the public, at the Peregrine watch. A hearty "thank you" to them all. Mike Glover was able to call on a large number of members (and other volunteers) for the Peregrine watch. Many members gave of their time to take part in the BTO Breeding Bird Survey and Common Bird Census as well as our own House Martin Survey and also the Over-wintering Warbler Survey. The Club appreciates the time and effort given by so many people.

In 1995 and 1996 the mid-week birding walks, which started in October 1994, established themselves as a regular part of the Club's weekly activities. Much effort was put into the organisation of the walks by David Tombs and Steve Kirk, and many other people have gradually become involved in planning and leading meetings. Statistical analyses of these walks have appeared in *Birds News*. The Committee continued to invite Club members to sit in on their meetings and appreciate the input from all those who attended.

Indoor Meetings

19. 1. 95	Robin Prytherch - Ascension, Island of Volcanoes and Boobies
16. 2. 95	Members' Evening
2. 3. 95	Beginners' Meeting
16. 3. 95	Mike Reid - Arctic Riviera (NE Greenland)
21. 9. 95	Graham Wren - Britain's Breeding Seabirds
19. 10. 95	Mike Wilkes - Spring in Spain
16. 11. 95	Jeff Blincow - Birdwatching in Australia
14. 12 95	Annual General Meeting
18. 1. 96	Julian Hector - Birds of the Air
15. 2. 96	Robin Khan - Nightjars
7. 3. 96	Beginners' Meeting
21. 3. 96	Members' Evening
19. 9. 96	Derek Toomer - Long Tails and Tall Stories: BTO's Garden Birdwatch
17. 10. 96	Malcolm Sainsbury - Return to the Rift Valley
21. 11. 96	Michael Leach - The Complete Owl
19. 12. 96	Annual General Meeting