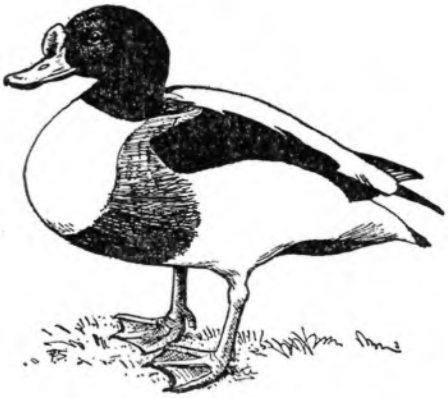

Social and population studies in the Shelduck

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Introduction

This paper describes breeding season studies of an estuarine population of Shelduck *Tadorna tadorna* on the Isle of Sheppey, north Kent, England. The population is part of the summer population of the Thames marshes, and although not strictly closed, there seems to be little movement, during the breeding season, between it and groups which centre on the adjacent Medway estuary and the Cliffe peninsula. The location and relevant topography of the island are shown in Figure 1; details of the habitat have been described previously (Hori 1964a).

Intensive field studies were carried out during the breeding seasons of 1964, 1965 and 1966, limited data from the years 1967 and 1968 are also included. These are combined with data from previous intensive field studies in 1960—63 to illustrate longer term trends. Methods were identical to those employed in the earlier study (1960-1963), except that colour marking of ducklings by injection of dye into eggs before hatching was used in 1966. This proved to be completely safe as far as ducklings were concerned and, in general, easy to execute. Difficulties of carrying out the work twenty feet up in a tree may however be imagined. The technique was that developed by Evans (1951) and others in the U.S.A. and information on it was supplied by the Delta Waterfowl Research Station and the University of Aberdeen. Eggs were injected with water - soluble food dyes, diluted with saline, shortly before hatching. A dosage of 0.3—0.4 ml. per egg, 3-4 days before hatching was used in most cases. Satisfactory results were also obtained with injections down to 24 hours before hatching with doses of 1.0 ml.

Injections were carried out with a 1 ml. hypodermic, a cork mounted on the needle limiting the depth of injection to just through the shell membrane. The dye was injected slowly and the hole closed with cigarette paper stuck down with nail varnish. Two trial clutches of captive birds, and eight clutches of wild birds were injected, and 100% hatching success was achieved. Purple, red, yellow, turquoise green and black were found to be particularly good colours in the field.

PART I: SOCIAL ORGANISATION IN THE BREEDING SEASON.

Territorial behaviour

This behaviour in Shelduck is of extreme interest because although vigorous inter- and intra-specific defence of a specific

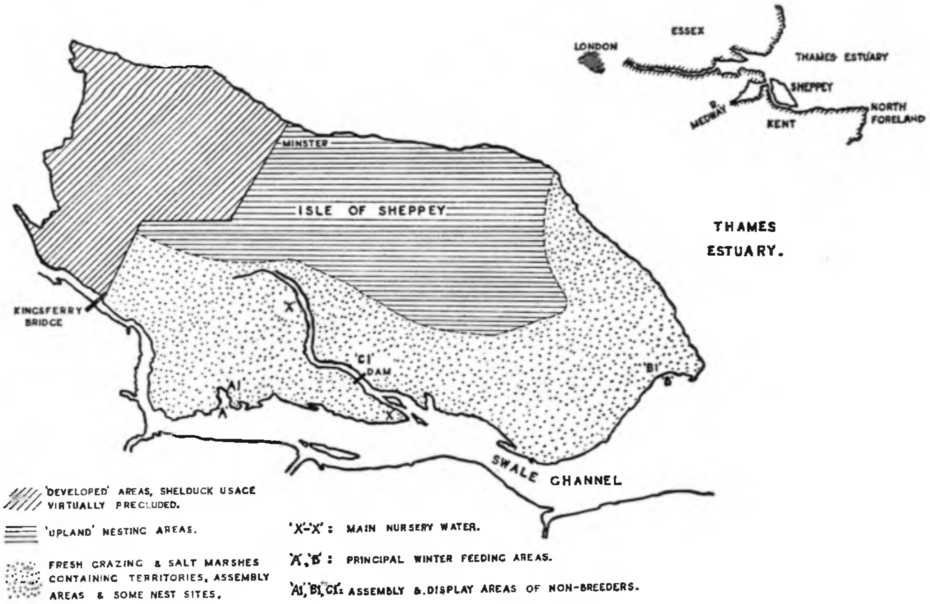

Figure 1. Shelduck habitat on the Isle of Sheppey. (Inset — location of the island.)

territorial location occurs, no nest was ever found within a territory. In a few cases nest sites were near territories, but in the great majority they were in distinctly different localities, up to 3 miles distant.

While investigating the use of territory a change in feeding habits was discovered. This occurred in most of the Sheppey breeding population as soon as it returned to the home range. Olney (1965) has shown that Shelduck wintering in the Thames estuary have an extremely narrow feeding ecology. Their diet in the Swale and Medway consists overwhelmingly of the small estuarine snail *Hydrobia ulvae.* This animal has been shown to be important to them in other localities, for example, in the Heligoland Bight (Goethe 1961) and in North Uist (Campbell 1947). However, direct observation on Sheppey showed that during the laying and incubation periods the majority of breeding adult Shelduck feed in the freshwater grazing marshes, mostly in territories. This was confirmed by examination of faecal material from females caught during incubation (Hori, in prep.). The situation was complicated because during the laying and incubation periods, the non-breeding population and a small proportion of those breeding continued to feed on the inter-tidal zone in locations where *H. ulvae* were prolific. Faecal material from one incubating female caught in 1966, on the 22nd day of incubation, contained 584 *H. ulvae* shells. Young (1965), working on the Ythan estuary in Scotland, maintained that most of the breeding birds there fed on *H. ulvae* throughout the breeding season. Observations from the Ythan and the observed feeding behaviour of part of the summer population on Sheppey support the belief that there is no significant seasonal variation in the biomass of *H. ulvae* (Dr. R. Newell, pers. com.). Thus the majority of breeding adults on Sheppey move away from prolific feeding grounds, which a few months earlier supported a winter population at least four times as large as the summer numbers. Defence of territory consequently appears conventional (Wynne-Edwards 1962) as far as food supply is concerned because there is an abundance elsewhere in the breeding habitat which is completely ignored. Since *H. ulvae* are not eaten by ducklings, the change of adult diet cannot be an advantage to the species in this context.

Shelduck territories are also puzzling if considered as a dispersion mechanism, not only because they do not contain nests, but because most of the birds holding territory congregate and act gregariously at nesting sites during the same period. The most likely explanations for Shelduck territorial organisation appear to be either that it provides isolation for pairs, or acts in a density dependent manner to achieve dispersion, or that it provides meeting places for the pair during incubation. Hochbaum (1944) suggested that the primary function of territorial behaviour in ducks is to limit interference during copulation. This view has been criticised by McKinney (1965) who observed that Eiders *Somateria mollissima* successfully accomplished copulation in crowded colonies. However, isolation would appear to be advantageous because the sight of copulating or diving birds causes extreme excitement in other Shelduck with consequent interference. This is most evident in bathing parties seen in winter flocks, where a diving bird will release similar activity in many others so that twenty or thirty birds begin diving wildly. These displays are notable for their intensity and on two occasions males have been seen to mount another male, after the latter had dived, and remain in a typical copulatory position, hanging on to the nape feathers.

Territory usage was well illustrated by a pair studied intensively in 1966. These were of special interest because they also adopted a sub-territory; the major part of their home range is shown in Figure 2. The pair occupied a primary territory on a main fleet in April and initially used this regularly. This was the territory which the female had used each year since 1963. Use of the sub-territory appeared to develop because of frequent disturbance on the primary territory, by fishermen or farm workers. Although the water of the sub-territory obviously contained sufficient food it was probably of insufficient depth for coition, being no more than 8″ deep. It was unusual in being small, approximately 2 yards × 30 yards total length, and in its position on the slope of a hill, and was more like the loafing places used by Shovelers *Anas clypeata*.

Both birds spent extensive periods feeding in the pool, which, being floodwater, gradually dried out. After incubation started, the female's range was restricted to the nest and sub-territory. The behaviour of the male in calling the female off the nest, her waning response, her greeting call when she flew down to the sub-territory and her return to the nest accorded with behaviour described by Hori (1964a). The female's feeding visits averaged two a day and when caught at the nest on several occasions her faecal discharge confirmed that she was not feeding at all on the inter-tidal zone. On the sub-territory she fed, preened and slept. The male left the sub-territory at irregular times, presumably to visit the inter-tidal zone; mainly in the evenings and possibly at night. During late May and the whole of June the male spent approximately 80% of the daylight hours on the sub-territory and he was seldom absent when the female arrived.

Territory in Shelduck may thus function to maintain the pair bond as it does weakly in other ducks. Mallard *Anas platyrhynchos* were often seen to rendezvous at feeding places in a similar manner during early incubation. The females leave nests as dusk gathers and fly low over the marsh to escape the attentions of other males. Their own males, who have been loafing in the vicinity, follow them to the feeding place or may already be waiting there. But this behaviour lapses quickly when the males desert incubating

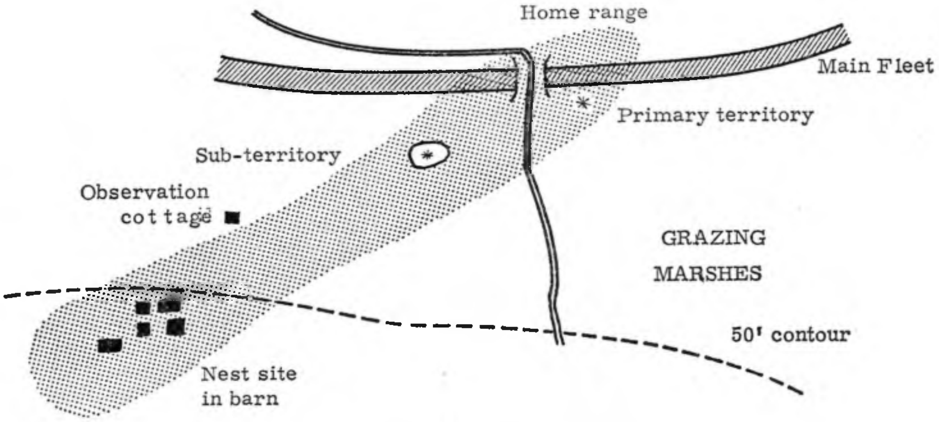

Figure 2. Home range of Shelduck pair in 1966 (stippled area). Included in it are the primary territory on the Main Fleet, the sub-territory on a small pond and the nest site in a barn (left-hand of group of buildings).

females and I have not been able to determine whether females continue to use the same feeding locations thereafter. Ducklings are never kept within the confines of a Shelduck territory, but in the vast majority of cases are taken to entirely separate nursery waters. Only in the few cases where, by coincidence, adults held territories along such nursery waters was there any possibility of confusion, but colour-ringed birds confirmed that even here territory had no relevance to the rearing of ducklings.

From 1964 to 1966 inclusive, prolonged observation in February and March from before first light showed that the tendency was for pairs to visit and adopt territories before making regular visits to upland nesting areas. By the second or third week in March pairs spent short periods on the territories, generally from around first light (c.05.00 hrs.) until farming and other activities often disturbed them about 07.00 hrs. Territorial attachment is not strong at this season and when disturbed, pairs range over the grazing marshes. Some make brief visits to nesting localities, others merely circle towards them before wheeling, to seek out social gatherings on the larger flood-water pools of the grazing marshes or in the estuary creeks.

Social organisation of breeding birds

The term communes was applied to persistent groups of breeding adults in the nesting areas (Hori 1964a). They are distinct from many of the larger gatherings of breeding adults which occur on the fresh grazing marshes early in the season, in the locality of territories and, of course, from the gatherings of non-breeding birds. The widespread occurrence and persistence of communes indicate that they are of considerable importance in Shelduck social organisation.

Attachment to territories and nesting areas develops steadily and by the beginning of April visits to territory are regular and purposive. During this period birds were seldom recorded on territories at dusk, but most were there at first light. At this stage the commune bond appears to become dominant; early each morning birds leave territories in pairs and fly direct to traditional assembly areas, for example four to six pairs from one fleet would move off adjacent territories each morning between 04.40 hrs. and 05.00 hrs. and fly towards known assembly areas. Colour-ringed birds were often watched off their territories and then followed by car to the assembly areas. On arrival at the latter, pairs join others which settle at varying distances from nesting sites. In one relatively remote locality, a grazing marsh commune often assembled outside or on the roof of a shed which contained two or three nests annually. In contrast, upland communes often assembled fifty or a hundred yards from subsequent nesting sites.

At this time the majority of adult pairs spend most of the daylight hours in communes. When disturbed, the latter usually move a short distance, perhaps only one field. Most of the late morning and afternoon is spent sleeping in groups in the nesting locality. Thus although most pairs have discrete territories and are within a month of laying, little time is spent in isolation. This behaviour persists until egg laying commences.

The complexity of the social organisation which produces inter-pair hostility on territories and, within a very few minutes, social gatherings of the same individuals underlines the suggestions made by Crook (1964) that analysis of such systems requires extensive experimentation and attention to the dynamic interaction of a large number of factors.

Unlike similar organisations described by Carrick (in Andrewartha 1961) for the Australian Magpie *Gymnorhina dorsalis*, communes were not exclusive. For example, when seriously disturbed, members often flew to the assembly area of another commune and joined them for the remainder of that morning. Colour-ringed individuals forced to find new nesting sites, for example when the previous year's sites were destroyed, were apparently able to join other communes readily.

During the remainder of April and early May, visits to nest sites become more purposive and pairs spend long periods searching hay and straw stacks. These birds attract other potential breeding pairs and cause grouping at such sites.

When clutches are complete nesting pairs act with considerable independence and seek the isolation of their home range. But the commune bond again becomes apparent if nests are destroyed. Such re-assembly made possible a preliminary judgement on the nesting success of communes. Thus a commune of 5 pairs in 1966 re-assembled daily on upland pasture during early June. An old hay stack, known to contain at least one nest, had been burnt the week before. A further stack left over from 1964, around which the commune often assembled, was found to contain four deserted nests.

Communes in which all nests failed were believed to break their tie with the home range and, after a short while, join the flocks of non-breeders which migrate first (Greenhalgh 1965, Hori 1966). The remainder of the breeding population then consists of three classes, pairs in which the female is incubating and which still have a bond to the commune, pairs in which the females, having laid their eggs in the nests of others or having lost nests, are tied to communes, and other pairs, believed to be in a small minority, which have isolated nests and no commune bond. The breeding chronology of the latter class is fairly obvious, but it was not discovered until late in the study that the commune bond remained intact in the two former classes. Thus commune members who lose nests or are nest parasitic, temporarily lose daily contact with incubating pairs, but instead of rejoining the non-breeding population they tend to stay in the breeding range and resort to the vicinity of the main duckling nursery. The presence of these birds was detected by colour-ringing during the brood season and previous work (Hori 1964b) suggested that they may stimulate brood adults to desert their ducklings. Groups of pairs following broods and crêches on the duckling waters are probably mainly parasitic pairs or failed breeders. In a number of instances known communes remained near duckling waters up to 12 days, until all members had broken their ties by brood attacks or by simple desertion. At the latter stage of the breeding cycle many instances were noted where sexes associated freely instead of in pairs, for example three or four adult females feeding or preening close together whilst the remainder of the commune might be 10 yards away. Marked females, including some who had freshly deserted broods, were also seen in such communes without their mates; whenever such groups were watched for prolonged periods the drakes were seen to return after feeding on the inter-tidal zone.

The commune bond thus exists at least from the end of March until adult pairs leave on moult migration. It has so far proved impossible to demonstrate the existence of such groups within the winter flocks, although pair bonds are obvious enough.

Multiple nesting (See Plate I, p. 32)

The phenomenon of a number of females laying in the same nest has been frequently reported in Shelduck, but its widespread occurrence and significance have received little attention.

Weller (1959), in a comprehensive study of parasitic behaviour in North American diving ducks, differentiated between nest and egg parasitism and suggested that the term parasitic could be logically applied where advantage or disadvantage to the participants occurred. Disadvantage was difficult to demonstrate in Shelduck, although females which did not incubate were clearly in better condition to undertake the moult migration and it is apparent that conditions similar to Weller's dump nests could arise. The largest number of eggs found in a single nest during this study was 32 but this was robbed. Surprisingly, hatching success in 21 clutches larger than 12 eggs did not differ from that in smaller clutches (Table I). The disadvantages of multiple nests postulated by Weller were thus not apparent.

Assuming that clutches or broods greater than 12 were the result of multiple nesting (see later), at least a quarter of the broods produced came from such nests (see Tables V and VI on p. 16).

Parasitic egg laying by Shelduck was entirely intra-specific and its origins are obscure. Commune organisation facilitated members following each other to nest sites, particularly where sites were rather restricted. As suggested by Weller, the sight of eggs appeared to be the stimulus to parasitic birds. Other species could be likewise stimulated, for example an egg of a Stock Dove *Columba oenas* was

Table I. Comparative hatching success in individual and multiple nests.

	1963	*1964*	*1965*	*1966*	*1967*
No. of clutches $\leq$ 12 eggs compared	8	12	9	8	6
Hatching success % (laid/hatched)	90	93	87	92	88
No. of clutches $>$ 12 eggs compared	8	2	2	6	3
Hatching success % (laid/hatched)	91	95	90	89	85

found on a pile of 22 Shelduck eggs, and Mallard eggs were frequently found in Shelduck nests in trees and haystacks. There appeared to be exact synchronisation of laying between host and parasitic female Shelduck and this would also appear to result from commune organisation.

Observations of commune females visiting multiple and other nests were commonplace. Females believed to be parasitic were also observed sitting, and even laying eggs, beside incubating females. A typical commune in which pairs are 'clumped' or over concentrated with regard to available nest sites was in successive years centred on a shepherd's shed in an undisturbed area of grazing marshes. This contained up to four nests annually, always begun in the latter part of the laying period, probably as a result of the poor nature of the site. Commune pairs assembled immediately outside the door and continued to do so throughout the incubation period, for example on 26th June 1966 five adult females and three adult males were gathered outside the shed and a female was sitting on one of two proven multiple nests with clutches of 15 and 14 eggs. When the ducklings were taken to the nursery water the whole commune moved with them.

Another aspect of behaviour considered to result mainly from multiple nesting is down-stripping away from the nest. Piles of down resulting from this habit were only found in areas used by communes and breeding pairs, often those under observation for periods of up to three weeks. In all cases location and direct observation confirmed that breeding adult birds were involved. Only subjective estimates of the quantity of down stripped could be made, but it was possible to date the occurrence of maximum quantities of fresh down (Table II). The maximum frequency of this habit occurs two to three weeks after the peak laying date. It therefore marks the virtual end of egg laying in the population. This suggests that the large drifts of down, spread over 30 to 40 yards, are the work of parasitic birds excluded from the multiple nests when one of their number begins to incubate. Many of these birds move to the nursery waters and it is near these that the large quantities of down are found. It might be possible to gain an impression of the annual extent of multiple nesting by recording the volume of down. Small puffs and piles of down, such as one might expect from single birds, are found in territorial areas, and the time spread suggests that these result from the destruction of individual nests during the incubation period.

Individual histories

Sixty adult females were caught at nests and marked with numbered metal rings and plastic colour rings on one or both legs. Experiments in 1963 with spirit soluble dyes were not entirely successful because such dyes were only recognisable for a few weeks. Some individuals were known either every breeding season or in various seasons for the last six years of the work. Table III shows examples of traditional attachments (Hochbaum 1955) to the home range.

Not only were these Shelduck traditional in returning to the home range, but they retained a tenacity towards various components of it. Approximately 7% to 25% of the breeding population of females were handled each year and, allowing for the difficulties of detecting colour rings on pasture and soft mud, these data suggest that most of the population acted in the same way. Work on other hole-nesting ducks has shown similar tendencies in Goldeneye *Bucephala clangula* (Siren 1957), Bufflehead *Bucephala albeola* (Eskine 1961) and North American Wood Duck *Aix sponsa* (Bellrose, Johnson and Meyers 1964).

Some remarkable examples of tenacity and tradition occurred in the Shelduck. One female, AJ 62813, used exactly the same hole for the three years 1962 to 1964. In 1965 a Wood Pigeon *Columba palumbus* laid there first. The Shelduck laid in the nearest available hole, in the same tree screen 40 yards from the original site. In 1966 this hole remained full of

Table II. Occurrence of down-stripping away from the nest.

	1962	*1963*	*1965*	*1966*
Maximum down-stripping	17/6	9/6	12/6	4/6
Spread of occurrences	31/5— 24/6	not recorded	5/6— 13/6	27/5— 5/6
Peak laying	29/5	12/5	24/5	23/5

Table III. Examples of home range tenacity.

	No. of breeding females involved in stated activity					
	1963	*1964*	*1965*	*1966*	*1967*	*1968*
On same territory as previous year	1	6	6	7	not investigated	
Same nesting locality as previous year	1	9	5	7	4	5
In same nest site as previous year	1	9	4	7	3	4
Broods taken to same nursery water as previous year	1	4	7	6	not investigated	
Cumulative no. of adult females ringed at end of previous nesting season	5	17	25	36	44	49

winter rain water and the female returned to the first site. In 1967 the female again used this site which, being a vertical hole in the centre of the trunk, was eroding relatively quickly. This made it difficult to catch her and moreover resulted in one duckling being abandoned in the nest. For this reason the hole was filled with hardcore and wood litter during the winter 1967-68 to a depth which would make capture easy again and in 1968 the bird nested in the same hole once more. Unfortunately the clutch was destroyed by Magpies *Pica pica* and it seems likely that the raising of the nest made it a little too readily seen from outside. This bird therefore nested for seven consecutive years in virtually the same spot. Throughout these years her territory remained on a freshwater fleet about 1,200 yards from the nest, and she and her mate were also to be seen feeding on the inter-tidal zone. The date of her first egg varied, being 23.5, 26.4, 1.5, 11.5, 20.5, 25.5 and 21.5, and so did clutch size and hatching success, 8/8, 6/10, 7/8, 9/9, 8/9, 8/8, 0/10. The incubation period was always 30 or 31 days, making the dates of brood exodus 3.7, 7.6, 14.6, 22.6, 2.7 and 23.6. The broods were always taken to the same place on the main nursery water and usually deserted within 10 days.

Individuals experienced varied breeding success from the complete success of AJ 62813 to almost the opposite. An unusually timid bird incubating a multiple nest under a water tank in 1963 deserted as a result of colour dyeing experiments. She returned with the commune in 1964 and began laying in a dutch barn some 50 yards away from the previous site where she was caught by mistake after laying only five eggs and deserted. In 1965 she used the barn again, where she was examined and carried on incubating, but unaccountably deserted six days later. In 1966, in spite of at least three successive years of total nest failure, she returned with the commune and completed a clutch in a prepared site in the same barn. All seemed well, she was examined several times during incubation and hatched 10 of her 12 eggs. But her timidity again caused failure. This clutch had been injected with colour dye and at 06.30 hrs. on 30th June the pair was seen leading two coloured ducklings in the direction of the main nursery water. The pair had been disturbed by farm-workers whilst calling the ducklings off. The remainder emerged by themselves the next day and were later found following hens in the farmyard. Ironically this female turned out to have loose brood ties and her two coloured ducklings were found five days later with another family group.

Behaviour of broods and attendant adults

Shelduck ducklings can be heard cheeping as the eggs chip, but I have not recorded a female communicating with the young at this stage. However, as the time to leave the nest approaches considerable vocalization occurs. The female uses a soft 'arrnk' or 'arrk' note which, with varied amplitude and frequency, is used for contact, indicating safe conditions to the brood, as a call note or as an alarm, in much the same way as dabbling ducks (Beard 1964, Collias and Collias 1956). The period of vocalization at the nest appears to last only a few hours, but during this time ducklings apparently learn to differentiate between the notes. In studies of Mallard and Wood Ducks, Gottlieb (1965) has suggested that audible imprinting occurs at this time.

Since many Shelduck nests are hidden from the light, vocalization is clearly essential. Ducklings may have difficulty in finding their way out of dark labyrinths or, in tree holes, may find it physically difficult or impossible to climb out. In 1964 in a nest under hay bales in a small dark shed, eleven eggs began hatching on 22nd June and all ducklings were dry by the evening of the 23rd. Next morning at 04.55 hrs. the female was heard calling inside the shed. Besides the monosyllabic 'aarrk' note was another very soft running 'ugg, ugg, ugg'. The former was more frequent and was reminiscent of a domestic hen calling young, it seemed to be a combination of contentment and contact notes. Both calls were used almost continuously for the next 50 minutes; occasionally a duckling would appear briefly outside the shed. Calling was now interspersed with a further note, a quiet but hard bubbling 'ak ak ak' variant of the 'following' call, giving the impression of rising excitement as the female came closer to the door. At 06.59 hrs., after at least two hours calling, the female led the brood through a hole at the bottom of the door calling with a gentle 'arrnk, arrnk' note whilst the ducklings 'peeped' continuously as they ran hesitantly in single file behind her. Even so, two ducklings were left behind in the shed.

The calls described are of extremely low volume and can only be heard under quiet conditions when the observer is very close to the brood. In the open it is extremely difficult to detect contentment, contact and initial alarm notes of the female and ducklings; one usually hears only the later alarm and distraction notes of the female. Collias and Collias (1956) also noticed that low pitch, weak intensity, repetitive notes used for calling ducklings are similar to the clucking of domestic hens and found that Canvasback *Aythya valisineria*, Redhead *Aythya americana* and Mallard ducklings could easily be attracted by such clucking on their first day.

In difficult tree sites, vocalization is used to induce ducklings to climb and jump considerable heights. In one such nest where the ducklings had to get from a hole inside a hollow branch, they invariably fell into the bottom of the hollow trunk. In 1962 and again in 1964 persistent calling by the female induced three or four of the brood to climb out, but the remainder had to be rescued. In 1966 another female was unable to call any of her ducklings off this site and all ten were found dead in the trunk.

Shelduck ducklings are taken direct and rapidly to traditional nursery waters. Marked females and ducklings in their first day out of the nest moved up to three miles from the nest to the nursery; the maximum overland journey known was approximately two miles. The only divergence from behaviour previously described for this phase (Hori 1964a) was that several females led broods from upland nesting areas without accompanying males. Circumstances where a female calls a brood off during the mate's absence seem to occur with some regularity. In such cases the broods are often taken to the nursery water via the territory area where the male can join them.

On arrival at the nursery water, ducklings join a complex family and crêche organisation. Study of brood behaviour during the first five years of this work was greatly facilitated because approximately 80% of each season's ducklings were taken to one large fleet in the grazing marshes. This is unusual in estuarine Shelduck populations and possibly the relatively small area and non-tidal situation of this nursery produced inter-action not always present on tidal mudflats used by other populations. However, when a major shift of nursery occurred in 1966, brood and crêche behaviour appeared similar. The ducklings' initial brood tie may last only a day or two. It was confirmed that brood attacks (Hori 1964b) in which both parents drive their own ducklings away, are one of the basic methods by which ties are broken. Most brood attacks apparently occurred as a result of conflicting tendencies in the adults to break the brood tie and yet remain in nursery areas; possibly to rejoin communes which had assembled nearby. The rapidity with which brood ties are broken is in marked contrast to the dabbling ducks. For example, on 22nd June 1965 a colour-ringed female and her mate took 9 ducklings from the nest and on the next two days gave protracted and violent distraction displays on the main nursery water. The following day the pair had only four ducklings and on 28th June, although still at the same place, they had none, but were swimming close to a crêche. When disturbed the female flew straight out of sight towards the estuary, her mate followed for about 100 yards, but then came back as though still drawn to the ducklings. Observations on brood abandonment in Wood Ducks by Mendall (1958) and in Hooded Merganser *Mergus cucullatus* (Beard 1964) show interesting similarities to the brood attack behaviour witnessed in Shelduck.

Most females deserted their broods each year. The few who raised their ducklings to fledging in discrete family broods generally appeared to be those which reached the nursery water earliest in the season. So that apart from parasitic females and failed commune members the adult pairs remaining on the nursery water were crêche adults. The identity of the latter has been conjectural. Hori (1964b) suggested that pairs which loafed on the nursery water and which often followed broods or crêches might be failed breeders or parasitic females anxious to adopt ducklings. In four fully documented cases since then, females in charge of crêches were adults which had successfully hatched their own broods the same year. Thus female AJ 87938 hatched all her 11 eggs in 1964. She led the ducklings out at 07.00 hrs. on 24th June and took them to the main nursery water some 80 yards from the nest. At 05.00 hrs. the next morning this female and her mate had a crêche of 55 uniformly sized Class I ducklings at exactly the same spot. Daily observations, between 05.40 hrs. and 08.00 hrs. but at 11.50 hrs. on 28th June, showed the numbers to be varying, 56, 52, 18, 65, 68, 28, 24, 6, 35, until 5th July when there were 22. The pair were not seen subsequently on 12th or 19th July. The following year this female appeared on 20th June 1965 on the main nursery water with 6 tiny Class I ducklings. Once again she and her mate became crêche parents, having 15 on 23rd June, 23 on 24th June, 10 on 10th July, 14 on 25th July and 20 on 1st August. The first wave of adults had left on moult migration before the last observation on AJ 87938 in 1964, and clearly in 1965 the pair, who were known to be members of a commune in both years, again stayed behind with the ducklings. This holds generally; for crêche adults the bond to ducklings is stronger than the commune bond and the migratory urge. It has not yet been established whether crêche adults make a moult migration later.

Daily life in broods and crêches on the main nursery water was the most sedentary observed. Feeding, preening and sleeping periods were all led by the adult female during the first two or three weeks. Typically, AJ 87938 would spend 15 to 40 minutes feeding and then gradually swim towards the bank, where, after a few minutes spent standing in shallow water preening breast and flanks, she would walk on to the bank, followed by the ducklings. During bad weather ducklings were brooded by the female. Activity of the brood appeared to be diurnal during the first week or two, and as darkness fell ducklings were kept on the bank with the female sheltering them under both wings.

Whenever broods were disturbed on their journey to the nursery water and during the first few days thereon, both adults gave violent and protracted distraction display. On dry land the adult display was equally as spectacular as a Mallard's and usually included injury feigning. This reduces to tolling (Hori 1964b) as broods develop, and it was generally noted that at this stage parents which subsequently deserted broods simply flew wide circles without any display or vocalization.

For the first few days broods and crêches are tight gatherings which follow the adults closely, but they soon become increasingly independent. Medium and larger sized Class II ducklings were often seen at first light on the banks with adults, but as the light increased and particularly during warm spells, they ranged widely. In consequence, they join the nearest brood or crêche when disturbed and this creates the impression that crêche sizes vary more than they actually do. By the time they are c.16-20 days old, ducklings were often largely independent, brooding each other at night and associating at other times in groups without adults. Occasionally males of brood or crêche pairs leave the group to feed on the intertidal zone and may be absent for an hour or more. Less often the female was absent. Movement of ducklings between broods and crêches was detected by regular counts of undisturbed groups, by movements of dyed ducklings in 1966 and by prolonged direct observation. This interchange is contrary to behaviour reported from the Ythan estuary in Scotland by Young (1965), and is almost certainly dependent upon the density of broods and crêches.

Adults in the nursery area were extremely passive towards ducklings, especially those without accompanying adults and only three exceptions were observed during six seasons. Whenever wandering Class I ducklings approached strange adults they were treated as though they belonged to the birds concerned. Three or four adult females might stand or swim around such an apparent orphan, examining it minutely and touching it gently with their bills. Even when accompanied by adults, ducklings were treated passively.

When the water referred to as the main nursery water became less suitable, as it did towards the end of this study, it was found that the tradition of attachment to the creek was still intact, but the ducklings now resorted to its tidal reaches. Though the mass of ducklings could invariably be found in the creek on an early morning high tide, provided they had not been disturbed, they would regularly float out as the creek emptied on the ebb and might range two or three miles down the shore. Duckling behaviour on exposed mudflats and on saltings was similar to that recorded in the freshwater nursery except that on high tides birds used the saltings widely to hide when danger threatened. Adults would lead broods or crêches to side creeks or runnels and then into the grass/purslane saltings. However, when suddenly surprised such groups would invariably make for open water, running at high speed across the mudflats or swimming and diving down the creeks.

PART II: POPULATION DYNAMICS

The changing habitat

Usually habitat changes are too slow to be considered in ecological studies. Although the same is largely true of the present work, certain significant changes did occur in the period 1960 to 1966. By far the most important was in the physiography of the area called the main nursery water (Figure 3).

Prior to 1953 this had been the largest saltwater creek on the island and a traditional nursery. Its attractions as duckling habitat were its location in that part of the island least accessible to man, the shelter it afforded from prevailing winds, the shallow gradient of mud towards the edge of the saltings and the food supply.

This habitat was virtually halved when, following the 1953 sea floods, a dam was constructed across the creek to rationalise the previous sea wall system. Thus in 1955 the majority of the creek's length became non-tidal and a transition to fresh vegetation started: a sewage outfall kept the water level high and no doubt contributed to food supply, whilst the shallow water's edge gradually became almost perfect for ducks and waders. Construction operations prevented the area being useful to Shelduck until 1956. Thus the period of the present study, 1960-1966, commenced when that part of the duckling nursery above the dam had developed to an extremely favourable environment and the tradition of using the tidal portion of the creek as a nursery was being modified to take advantage of it.

During the period 1960-62 inclusive, at least half the broods taken to the nursery area stayed for long periods above the dam, in 1963 about two-thirds did so and in 1964 and 1965 something like three-quarters of those using the nursery were above the dam. Even many of the broods which later used the creek spent their first few days above the dam. However, by 1965 changing plant communities began to affect the situation and this was made strikingly obvious in 1966. The population then virtually returned to using the tidal creek as a nursery. The maximum count of ducklings above the dam dropped to 20% of the total in the nursery area.

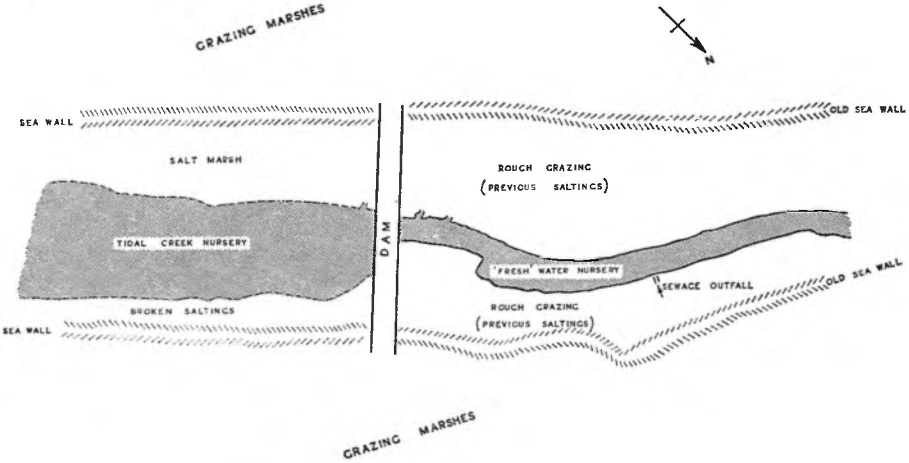

Figure 3. Principal features of the main nursery water. (Scale: 1 in.=approx. 600 yds.).

The change was brought about by the spread of sea club-rush *Scirpus maritimus*, as plant succession above the dam turned that water into a typical Thames marshland fleet. This reed, although providing food for surface feeding ducks, was disadvantageous to Shelduck and to Pochard *Aythya ferina*. Spreading from the upper reaches of the fleet and colonising shallow water first, it gradually obstructed the edge so that ducklings were unable to negotiate it easily and adults were no longer able to maintain a view of broods and crêches from the bank. The number of ducklings found dead, apparently killed by foxes *Vulpes vulpes*, stoats *Mustela erminea* and weasels *Mustela nivalis* increased, and the new reed beds probably aided these predators by concealing their approach. In 1966 none of the marked females which had been observed closely in previous years remained on the old main nursery. The population, which in 1964 successfully exploited the new habitat, had thus largely completed a cycle of adaptation and re-adaptation in the space of twelve years.

Other human pressures affected the habitat noticeably. Destruction of nest sites was apparent in the annual felling of trees, the clearance of derelict buildings and the intrusion of holiday camps and caravan parks into previously undisturbed areas. This must in the long term affect a species with such strikingly coloured females, but in the span of this study the population prospered. It is interesting to note that something like a third of the nesting sites in this study were provided by man and that Shelduck are to this extent parasitic on him. Some pastoral communities have recognised this as a ready means of farming the birds for eggs, and I found no difficulty in inducing birds to lay in nests which I prepared for them. This could be a method of conserving Shelduck populations in the future and provides interesting conjecture as to whether breeding populations such as that on Sheppey will ultimately become semi-feral. Whilst there was as yet no evidence of any change in the relative importance of nest locations, it was apparent that the use of trees will gradually decline. All the tree sites were in elms *Ulmus procera* and many in holes caused by the Dutch Elm disease. Although elm screens on the island were thick when Hasted (1797-1801) noted that Shelduck were frequently seen on Sheppey, re-planting to replace those which deteriorate badly stopped some years ago and all subsequent re-planting has been with other species; suitable tree holes are thus becoming less common.

Clutch size

Clutch data are shown in Table IV. These include data for obvious multiple nests and those which had been tampered with, 'milked', which were excluded in previous work (Hori 1964a), and give an overall mean, for 130 nests, of 11.1. Such means are useful in estimating laying dates and incubation periods from brood studies, but since they include multiple nests they do not give an accurate result if used for population deductions. Estimating the proportion of breeding females which use multiple nests remained a major difficulty and could only be approached by intensive study of individual clutches. In a sample of 60 nests in which eggs were counted daily and the behaviour of adults studied in detail, all clutches greater than 12 eggs were proved to be the work of more than one female. This was supported by the finding that in 69 additional nests in relatively solitary sites, with no evidence of visits by other

Table IV. Number of eggs in nests examined.

Year	*Nests counted*	*No. of nests containing eggs shown*													*Mean*
		<8	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*>18*	
1962	13	1×4 1×5	6	1	1	—	—	1	—	—	—	—	1	1×20	9.7
1963	25	1×3	2	4	3	1	2	2	3	3	—	1	1	1×22 1×25	12.6
1964	22	2×7	5	3	6	3	—	—	—	—	—	1	—	2×19	10.4
1965	19	1×6	5	6	3	2	—	—	1	1	—	—	—	—	9.5
1966	25	1×6 1×7	3	4	6	1	2	—	1	2	1	—	—	1×20 1×21 1×23	11.7
1967	13	1×6	3	2	1	—	1	—	2	—	1	1	—	1×32	12.5
1968	13	1×4	2	2	3	2	—	1	—	—	1	—	—	1×23	11.0

Table V. Individual and multiple nests and clutch sizes.

	1962	*1963*	*1964*	*1965*	*1966*	*1967*	*1968*
Individual mean clutch size	7.6	9.2	8.0	8.9	9.3	8.8	9.0
Multiple mean clutch size	17	16.3	18.3	14.5	17.4	18.6	17.3
% of multiple nests	23	48	14	11	28	38	15

females, clutches never exceeded 12 eggs. Re-analysis of nests in Table IV according to this criterion is shown in Table V.

Brood size

Ducklings were classified in three age groups: Class I — tiny downies up to approximately three days old; Class III—those having most of their feathers, but not necessarily flying; Class II — all ages between Class I and Class III. Every duckling count included records of family and crêche grouping, of location and of the parent female's identity when known. Ducklings were counted on two days each week throughout the brood season and every day during the peak of this season. During the latter peak, counts were augmented by motor boat surveys along the whole length of the Swale channel. It was then possible, for limited periods, to differentiate between broods; so that tabulations maintained on this basis enabled the season's aggregate of ducklings to be deduced, i.e. the total number taken to saltwater nursery areas in any one season. Precautions necessary to obviate duplication probably gave aggregates slightly lower than actual numbers which reached nursery waters, but these errors were considered to be consistent. To assess further the incidence of multiple nesting, broods were separated according to whether they contained more or less than 12 ducklings. Data shown in Table VI refer to sample sizes of 290 and 294 brood days for Class I and Class II ducklings respectively. Wherever there was reason to believe that a group of ducklings might be a crêche, either from its large size or from marked disparity in the size of ducklings, the data have been excluded.

Apart from 1961 when the sample was comparatively small, Class II brood size in Table VI correlate well with Class I data. The percentage of broods greater than 12 ducklings, i.e. those assumed to result from multiple nests also show reasonable correlation with the sample in Table V. Both sets of data show the same

Table VI. Brood data for Class I and Class II ducklings.

	1961	*1962*	*1963*	*1964*	*1965*	*1966*
Mean brood size for all Class I broods	6.8	8.5	9.6	9.3	9.1	8.5
Mean brood size for Class I broods not exceeding 12 ducklings	6.1	6.5	6.7	7.2	7.8	6.9
% of Class I broods larger than 12 ducklings	6	20	27	25	14	17
Mean brood size Class II broods not exceeding 12 ducklings	8.2	6.5	5.2	6.8	7	6.2

Table VII. Dates for main aspects of breeding cycle.

	1961	*1962*	*1963*	*1964*	*1965*	*1966*
Start of laying	2/5	30/4	25/4	22/4	15/4	19/4
Peak of laying	22/5	29/5	12/5	26/5	24/5	23/5
Span of laying season (days)	60	59	65	80	90	78
Span of incubation season (days)	78	84	81	85	91	80
First brood	5/6	10/6	7/6	29/5	26/5	28/5
Peak number of ducklings on nursery waters	9/7	14/7	7/7	1/7	5/7	9/7

pronounced increase in the incidence of multiple nesting in 1963.

Timing of breeding phases

Incidence and duration of the main phases of the breeding cycle are shown in Table VII, in which the following terminology is used: *Start of laying:* date on which the first egg was laid, in the whole population. This was obtained either from nest records or by deduction from the appearance of the first duckling using previously derived data (Hori 1964a). *Peak of laying:* the date at which the majority of birds in the breeding population were laying, determined by deduction from the incidence of Class I ducklings. *Span of laying season:* the period between laying of first and last eggs by the population, extreme dates being determined by direct observation or deduction from Class I broods. *Span of incubation season:* the period during which females in the population were incubating.

Meteorological data collected at H.M. Meteorological Station at Grain, 8 miles NW. of the breeding area, were examined, but no satisfactory correlation was found between these and breeding success or any aspects of the breeding season included in Table VII.

Non-breeding adults

Recent suggestions have included the hypothesis that in some Shelduck populations a varying number of the mature adults do not attempt to breed every year (Young 1965). The basis for such suggestions is not clear, particularly the identification of breeding and non-breeding populations. A fundamental consideration is the ability accurately to differentiate between adult and immature birds. The ready assumption that this was possible by body plumage, bill shape and intangibles such as 'gravid appearance' has probably led to substantial errors in the past. Experience indicates that the only consistent method of identification is the wing pattern (Hori 1965).

The following counts were made in the Sheppey study area using techniques already described (Hori 1964a), to determine the breeding and non-breeding portions of the population:

i) Regular estimates of the total population during February, March and April to obtain a first estimate of the summer population and to determine the date when breeding and non-breeding populations separated.

ii) Estimates of the non-breeding population from mid-April to the end of May by prolonged observation at gathering grounds.

iii) Estimates of the potential breeding population by counts of 'communes' and territorial pairs, consisting entirely of adults, during the same period as (ii); with (ii) these estimates provide a first check on (i).

iv) As the non-breeding population, together with some failed breeders, made their moult migration before the majority of the adult population, counts of the bulk of the breeding population could afterwards be made with high accuracy at their pre-moult concentrations. Making allowance for part of the failed breeders, these estimates gave further verification of counts in (iii).

v) Estimates of nesting pairs were made to determine whether there was a substantial variation between these and the total of paired adults. They were based on: a) nest finding, which annually accounted for 20-30% of those estimated to be present; b) nest site identification by conclusive evidence of nesting, e.g. incubating birds hissing, adult females without down regularly entering holes, etc.; c) flight line observations and prolonged observation of territorial and commune birds as a check on (b) and to discover pairs using nesting areas which had not been searched; d) detailed duckling counts.

Table VIII gives data accumulated on nests. The number found includes all failed nests even though these might have been deserted during laying. The number identified includes all those estab-

Table VIII. Number of nests in relation to breeding population.

	1962	*1963*	*1964*	*1965*	*1966*
Estimated breeding pairs	70	73	65	115	147
Number of nests found	18	25	35	38	40
Number of nests identified	61	64	60	100	125
Proportion of pairs identified with nests	87%	88%	92%	87%	85%

lished beyond reasonable doubt plus those inferred from regular observation. Thus estimates of the total population of adult pairs showed close agreement with the total of nests identified in all years. On Sheppey, at least, there does not appear to be a substantial and varying proportion of the adult population which does not breed.

Population regulation

In the evolutionary time span, density dependent factors could account for the overall distribution of Shelduck. For example, Olney (1965) has shown this species to be overwhelmingly dependent on *H. ulvae* as a winter diet. Correlation between Shelduck distribution and habitat containing plentiful supplies of this mollusc is obvious for Western Europe and for the British Isles. For the Kent shore of the Thames estuary, Newell (1965) has shown the mollusc to be densely distributed in the black muds west of Whitstable, but to decrease sharply on approaching the clean sands of Herne Bay. This distribution corresponds precisely with the eastern limit of Shelduck distribution in Kent. Upstream distribution is limited by the virtual end of appreciable inter-tidal mudflats and the start of industrial development at Gravesend.

However, when local populations are examined in the shorter term, density dependent regulation does not appear to fit the observed facts. It seems, as one might expect intuitively, that a mechanism capable of determining dispersion does so rather coarsely, and that other factors control finer adjustments. On Sheppey the breeding population was far below that which the food supply could have supported. Even if it is argued that delayed density dependent regulation occurred so as to provide for the needs of winter flocks, direct observation suggests that the latter do not come near to taxing available food supplies. Whereas *Hydrobia* appear to be widely and fairly uniformly distributed through the mud of the inter-tidal zone, Shelduck group together during feeding. Two large flocks mass on each rising tide, ride the high water in packed rafts and then, as the tide falls, they exploit the tidal cycle of the mollusc.

From 1959 to 1962 the summer population experienced a stable phase with estimates of 220, 250, 270, 260 birds. The severe winter of 1962-63 brought heavy mortality and at least 5% of the winter population perished at this time. Heavy mortality was reported from other areas, for example a total of 400 corpses were counted on the Kent shore of the Thames estuary (*Kent Bird Report* No. 12, 1963) and Shelduck suffered heavily throughout the British Isles (Dobinson and Richards 1964). The heavy losses were undoubtedly accentuated by the species' narrow winter feeding ecology. The effect was discernible on Sheppey in the total summer population of 1963 which totalled 245, but it did not materially affect adult numbers; winter casualties must therefore have been predominantly sub-adults.

In 1963 an adult summer population numerically equal to the level which had come to be regarded as normal produced the largest number of ducklings ever recorded on Sheppey (Table IX). Again, a similar result occurred nationally (Hugh Boyd, pers. com.). The ability of bird populations quickly to restore their numbers after major depletion has often been noted (Lack 1954). The effect on Sheppey was a ' step ' in the summer population of 1964 to 390 as the previous season's ducklings became sub-adult non-breeders. Further increase in summer totals, to 465 in 1965 and to 495 in 1966, occurred as the breeding population was augmented.

In 1963 the breeding population produced more than twice as many ducklings per pair than it did in 1962 or 1964. From Table VII it will be seen that the peak of laying was at least ten days earlier than usual yet the peak number of ducklings was reached at the usual time. This suggests that the early ducklings survived unusually well. The losses in the 1962-63 winter were thus more than compensated. In 1965 and 1966 the effect of the large number of ducklings born in 1963 became apparent in the adult population, and

Table IX. Duckling production per pair of the breeding population.

	1962	*1963*	*1964*	*1965*	*1966*
Estimated breeding population (pairs)	70	73	65	115	147
Total number of ducklings reaching nursery stage/season	245	515	243	285	244
Ratio, ducklings/breeding pair	3.5	7.1	3.5	2.5	2.0

duckling production per pair by the latter dropped progressively (Table IX). So, although external factors such as territory and nesting density, food supply and meteorological conditions were apparently constant, regulation occurred which was consistent with the size of the winter population. This widely different performance by a relatively constant breeding population suggests that density dependent regulating factors, for example food supply during the breeding season, territory and nest site availability, were ineffective.

Table V shows that individual clutches were large in 1963, but not uniquely so. This result was also corroborated in the histories of six birds known for at least three years (Table X). However, the Class I broods (Table VI) which, being only a few days old, should correlate closely with clutch sizes and are drawn from much larger samples, do not show any rise in 1963. Thus, while some individuals may have responded to the population check with larger clutches, this was not general throughout the population and this could not explain the overall increase in duckling output of 100% which occurred that year.

Table X. Clutch sizes in individual females.

Female			*Clutch size*				
	1962	*1963*	*1964*	*1965*	*1966*	*1967*	*1968*
AJ 62813	9	10	8	9	9	8	10
AJ 87943		12	8	8			
AJ 87909		12	10		10	11	11
AJ 87941		9	19*	10			
AJ 87908		14 (M)	8	10	12		
AJ 87904		14 (M)	17 (M)	12	10	9	13 (M)

Note: (M) indicates multiple nest
* indicates nest 'milked'

The present study does not support suggestions that there is a variable proportion of the adult population which does not breed in some years (p. 17) and which might therefore provide an 'emergency reserve'. However, commune organisation could be a possible regulating mechanism. The latter may produce over concentration with regard to available nest sites and it encourages multiple nesting. Effects on individual birds are difficult to measure, but studies of American diving ducks have suggested numerous possibilities. Weller (1959) and others found that parasitic egg laying limited the clutch size in parasitised nests; presumably by depressing ovulation. It has also been suggested that hatching success would vary and be lower in the larger multiple nests because of the physical size of the clutch as well as accidental ejection and damage to eggs resulting from numerous females visiting nests. The latter could also disturb incubating birds to the extent that desertion might occur. In the Redhead, Williams and Nelson (in Weller 1959) regarded 'community' nesting as the most important single cause limiting production in Utah. Other investigators have reported evidence of widespread nest failure resulting from parasitism.

However, Shelduck breeding season social organisation is entirely different from that of most other ducks with, as already described, special provision for facilitating and encouraging gregariousness. So, although the behaviour is referred to as parasitic, it is considered that at the level witnessed on Sheppey it is actually advantageous to the population. Thus, disturbance during incubation was considered to be low in the Shelduck because of the parasites' precise synchronisaton of laying and the intra-specific tolerance observed. Synchronisation of laying dates within communes was extremely precise by comparison with the wide span of such dates through the population (Table VII). The span of laying in the whole population varied from 59 to 90 days, whereas the span in nests known to belong to the same commune did not exceed 29 days. This is illustrated by the dates for the first eggs, for example: Commune A — 1.5, 4.5, 15.5, 17.5, 18.5; Commune B — 2.5, 7.5, 12.5, 14.5, 14.5, 18.5; Commune C — 17.5, 23.5, 25.5, 5.6; Commune D — 12.5, 16.5, 18.5, 22.5, 27.5, 30.5; Commune E — 17.5, 23.5, 26.5, 26.5; Commune F — 10.5, 20.5, 20.5, 29.5. Also, additional eggs were never found in multiple nests after incubation had been in progress for more than four days. The requirement for precise synchronisation, to prevent incubation interference, may help to explain the remarkably long period between the return of breeding pairs to the home range and the laying of first eggs in this species; approximately nine weeks. This period contains considerable group and inter- and intra-pair display which could achieve social stimulation. Similarly, egg wastage by dump nesting which is common in American diving ducks and which has been recorded in Shelduck, was only observed once in the present work. There appeared to be no difference in hatching success between individual and multiple nests for the clutch sizes which were given in Table I (i.e. up to 22 eggs). Although larger multiple clutches than this occurred, nest failures, etc., precluded measurement of hatching success in these. It is extremely doubtful, however, that the clutch of 32 recorded in 1967 could have been hatched with comparable success. This was the only nest recorded which resembled a dump nest, and it was robbed of 20 eggs just after incubation started.

When we consider complete nest failures, the multiple nests have an advantage. Thus in the four years 1963-1966, only 28% of 25 multiple nests were lost as compared with 47% of 88 individual nests. Further, multiple nesting might be more advantageous in some years than others. Situations were apparent where over concentration caused by the communes resulted in relatively few satisfactory nest sites being available for certain communes. In these situations multiple nests using the best sites would be advantageous, whereas appreciable nest loss could occur in marginally satisfactory individual sites. Such considerations are not merely concerned with the clutch. The chances of a predator noticing one very brightly coloured female's visits to a multiple nest over a six-week period are less than if the equivalent number of females were visiting single nests. Thus the use of multiple nests could be an important factor in limiting risks. Many instances were recorded where communes returned to a nesting locality to find hay and straw sites considerably changed from the previous year, for example in 1963 most haystacks had been removed before egg laying began. In some years birds went on searching for new sites well into May. Ultimately some laid in extremely precarious situations, for example under a single paper meal bag, or in rabbit and rat infested haystacks. Multiple nesting might also be advantageous because incubating females in such cases were experienced birds. Conflicting tendencies of commune association and incubation could cause higher desertion rates amongst birds breeding for the first time in individual nests. The latter effect may have been responsible for an apparent carelessness in laying and incubation which was detected in some years, but not in others.

The outcome of multiple nesting in Shelduck is subject to dynamic interaction of many factors. When the population was being regulated upwards in 1963, an unusually high proportion of the breeding population used multiple nests (Table V). It would appear therefore that in this population the advantages of more secure nest sites, stronger incubation attachment and the possible advantage of larger duckling groups more than outweighed the disadvantages of multiple nests. The hypothesis suggested by this study is that multiple nesting is the instrument by which commune organisation achieves regulation. This could have resulted from the fortuitous shortage of nesting sites, but could also occur by influencing the conflicting tendencies in adult females to incubate their own clutches or to assume parasitism and remain in full time association with other commune members. This could function by stimulation of the pituitary whose action has been shown by various studies to control the breeding drive (Nalbandov, Hochhauser and Dugas 1945). Principal contributors to pronounced regulation would be those commune pairs which vary their annual behaviour between parasitism and separate nesting as distinct from those adult females which incubate every year. The nature of the former group has not yet been discovered, but it seems possible that it may consist largely of the younger inexperienced birds.

Thus in a year when the population needs to be regulated upwards the commune bond would be strong and would induce many females to multiple nesting resulting in increased overall hatching success. Conversely, in seasons when the commune bond was weak, more females follow the tendency to incubate their own clutches and therefore use marginally satisfactory nest sites or lose clutches or ducklings in the nest through inexperience.

Regulation of the type suggested would require that adult females initially measured, or received stimuli from the size of the winter population or from the total of non-breeding and breeding birds in the summer population. Wynne-Edward's (1962) suggestion that the moult assemblies could affect such an epideictic function seems rather unlikely since for most of this time the birds are in their eclipse plumage and flightless. More probably the origin of the migration relates to a combination of ample supply of their specialised diet and the protection which an area like the Knechtsand affords conspicuously coloured flightless birds. Moreover the relevant reduction in population witnessed in this study had occurred in the winter immediately preceding the 1963 breeding season.

It is impossible at the present time to demonstrate when epideictic conditioning occurs. It must be remembered that there are indications that other factors may be involved, particularly nest site shortage and early nesting in 1963. But it is worth recording the widespread and intense group display in winter flocks on tidal water before the separation of breeding and non-breeding flocks which characterises the beginning of the breeding season. These displays can be seen during bright weather from late December to early February and often attract attention by the volume of female vocalisation which is greater than at any other time of the year. Vocalisation consists of the female's repulsion note, uttered whilst she performs inciting displays. The most important aspect of these displays is that they are of an inter-pair nature. They are thus completely unlike winter display in other species of anatidae. Pairs threaten each other and advance and retreat with females violently inciting as though defending territory, but in fact they may be floating fifty yards from the shore. The whole display is of the same nature as that seen early in the breeding season in groups on the fresh grazing marshes and in communes, but is then less intense.

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Summary

During the breeding seasons of 1964-66 inclusive, studies of social organisation, breeding biology and population dynamics were made on the summer population of Shelduck on the Isle of Sheppey, north Kent. Most breeding pairs change their feeding habits to food available in the territory in the spring instead of continuing the narrow highly specialised winter feeding ecology. Territorial occupation appears to be conventional as far as food supply is concerned. Territory may be a dispersion mechanism, but the simultaneous existence of a social organisation which causes nest grouping throws doubt on the effectiveness of territory in this respect. It is thought to be important on Sheppey in maintenance of the pair bond.

Commune organisation, i.e. the persistent grouping of breeding adults is described in relation to territorial occupation, incubation period, brood season and moult migration. The commune bond lasts at least from the end of March to moult migration. Multiple nesting was considered to result principally from this form of organisation. Such nesting was not disadvantageous to the species, making no difference in hatching success and reducing the number of complete clutches lost.

Histories of individual breeding birds are given in detail to illustrate home range usage, tenacity of attachment and individual behaviour and success in the brood season. The identity of those adults which attend crêches is demonstrated. Brood attacks were considered to be one of the basic mechanisms by which adults break the brood tie in order that they can make the moult migration.

Habitat and population changes during eight years' field work are discussed. A relatively constant adult breeding population produced a very varied annual duckling output and that when the population was severely depleted, immediate improvement of breeding success followed. It is not considered that a variable proportion of the adult population fail to breed annually. Commune organisation operating through the multiple nesting habit is suggested as being the principal regulating mechanism.

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