Breeding of Ducks at Loch Leven, Kinross

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This paper describes the nest-spacing, laying seasons, clutch-sizes and success of ducks breeding at Loch Leven in east-central Scotland. This large, shallow, eutrophic loch has long held the largest concentration of nesting ducks in Britain. In 1966–1973 these consisted mainly of Tufted Duck *Aythya fuligula* (500–600 pairs) and Mallard *Anas platyrhynchos* (400–450 pairs), with smaller numbers of Gadwall *Anas strepera* (25–30 pairs), Wigeon *Anas penelope* (25–30 pairs), Shelduck *Tadorna tadorna* (11–13 pairs), Shoveler *Anas clypeata* (up to 10 pairs) and Teal (up to 10 pairs). Most of these birds nested in one huge colony on the biggest island (St. Serf's), to which the present study was largely restricted. The main aims were (a) to find what led to such dense nesting in species which usually nest in a more dispersed manner; and (b) to collect as much information as possible on laying dates, clutch-sizes and other aspects of breeding, which are less readily obtained from smaller populations nesting elsewhere in Britain. Boyd & Campbell (1967) described the first year's findings, Jenkins (1972) some aspects of Shelduck breeding, Laughlin (1974, using some of the same data as here) the bioenergetics of Tufted Ducks, and Allison & Newton (1974) the waterfowl population in general; while the intensive studies into eutrophication and productivity made at Loch Leven as part of the International Biological Programme were described in the symposium volume 'Loch Leven'.

Lying in the fertile Kinross plain, Loch Leven has a water surface of 13·3 km^2, a perimeter of 17 km and is comparatively shallow, with half its area less than 3 metres deep. It has seven permanent islands. Some 14 km to the south lies the Firth of Forth and 17 km north the Firth of Tay, both also exceptionally good for waterfowl, while within 30 km are many other smaller lochs and reservoirs. The farming in the area is mixed, with a large proportion of cereals and root crops.

St. Serf's island, near the eastern end of the loch, covers 42 ha (105 acres) (Figure 1 and 1a). Its northern part is overgrown in some areas with *Phalaris* reeds and in others with a mixture of *Phalaris* reeds and *Salix* bushes, with scattered patches of nettles *Urtica dioica* and other tall herbs. This vegetation gives way to the south as the ground rises, first to a zone of *Deschampsia* tussocks and then to short grass pasture, which covers the rest of the island, apart from a few patches of rushes. Almost all the ducks nested in the *Phalaris* or *Deschampsia*, which together covered 14 ha, though Shelducks used old Rabbit *Oryctolagus cuniculus* holes on the short-grass areas.

Of many other bird species on the island, six were especially important to nesting ducks. Black-headed Gulls *Larus ridibundus* nested in a colony of 5,000–6,000 pairs which extended over part of the *Phalaris* and *Deschampsia* areas, and attracted many nesting Tufted Ducks. Jackdaws *Corvus monedula* and Moorhens *Gallinula chloropus* were important as predators on eggs. Visiting Herring Gulls *Larus argentatus*, Lesser Black-backed Gulls *Larus fuscus* and Great Black-backed Gulls *Larus marinus* were important predators on small ducklings. About 250 sheep were put on the island each summer and grazed chiefly the short grass. The only important wild mammals were Rats *Rattus norvegicus*, which were deliberately kept scarce by use of selective poisons. Rabbits were extinct.

Methods

The nesting area was marked out in 50 m squares using thick posts hammered into the ground and left for the duration of the study. The rows of posts were numbered from north to south, and lettered from west to east, so that each nest could be related to a particular grid square and, if necessary, its exact position recorded. In most years, the whole island was searched carefully, and known nests checked, 1–2 times each week through the season. Most nests were found by flushing the hen, and each nest was then marked with a numbered bamboo cane placed a set distance and direction away. This helped to locate the nest again when the female might be trapped using a net on the end of a long pole. (The cane indicated where the net should be dropped.) Females were ringed and sometimes weighed before release, and it was later

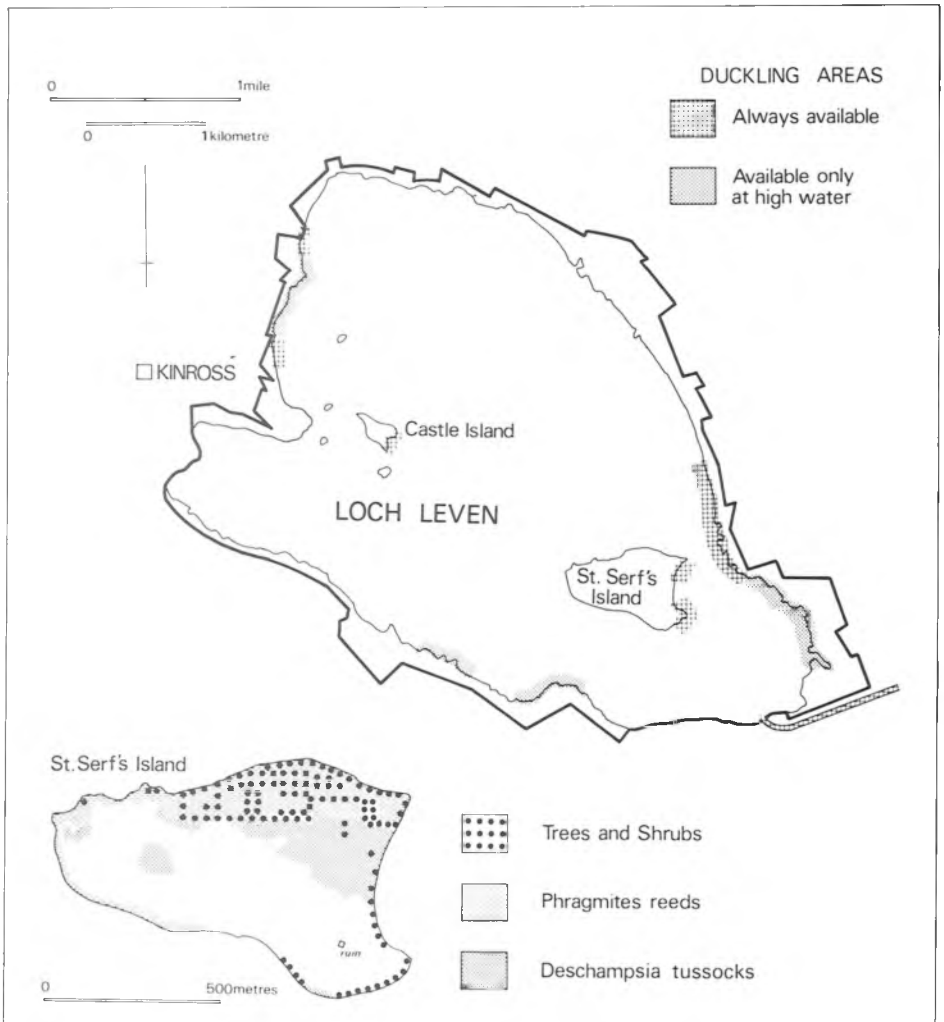

Figure 1. Map of Loch Leven and St Serf's Island. Areas good for ducklings are stippled.

found that no more nest failures had occurred among trapped than among untrapped birds. Two eggs from each clutch were candled to find the approximate stage of incubation.

After the event, hatched nests could be distinguished from failures by the presence of detached shell membranes, and the species involved identified from down, nest feathers and shell-fragments. Two projects were therefore undertaken at the end of the season to assess the data on success obtained earlier. One involved a further search of certain areas, on hands and knees where necessary, to find every nest. This was done on a series of transects, 2 m wide and 25 m apart, through the whole nesting area, and resulted in 12% of the ground being thoroughly covered. The aim was to find whether the success of the nests found earlier, in quick searches, was representative of the population as a whole. The second project involved setting aside an undisturbed 'control' area, in which no work was done till the end of the season. The aim here was to find whether our activities over the rest of the island had reduced nesting success there. One 100 metre square of *Deschampsia* was left undisturbed in 1969–1971 and the whole island in 1972–1973. In the event, neither project gave results that were unbiased, but they still helped to evaluate the main data. In total, nesting success in disturbed conditions alone was studied in 1966,

Figure 1a. St Serf's Island, Loch Leven, seen from the top of Vane Hill (*Pamela Harrison*).

1967 and 1968, in undisturbed conditions alone in 1972 and 1973, and in both conditions in 1969, 1970 and 1971. Henceforth, the term 'disturbed' is applied to areas worked during the nesting season, and 'undisturbed' to areas worked only at the end. In general, no one except ourselves entered the colony.

The breeding cycle

During a breeding cycle, ducks at Loch Leven used (a) initial home ranges or 'territories' where pairs spent most of their time before nesting and where the drake waited for the duck during the laying period; (b) a nesting area; and (c) a brood rearing area. While on some wetlands all three phases of breeding might take place on the same area, at Loch Leven most ducks completed the three phases of breeding in two or three widely-separated areas.

Initial territories

In surface-feeding ducks the first sign of approaching breeding came when pairs separated from winter flocks and spaced themselves around shorelines, far apart on straight featureless stretches (more than 100 metres between pairs) and closer on indented stretches (as close as 20 metres where neighbours could not see one another). As well as feeding places, each 'territory' contained one or more loafing spots, where the pair spent long periods resting, and from which the drake started the aerial chases (or 'three-bird flights') which were apparently important in achieving spacing (McKinney, 1965). The different surface-feeding species spaced themselves along shorelines largely independently of one another, and often two species shared the same loafing spots. Drakes remained on these areas until during incubation, when they spent increasing periods in bachelor flocks, then left altogether. Tufted Ducks spaced themselves on open water, instead of shorelines, and were less aggressive than surface feeders; pairs were furthest apart when feeding, and came closer together when resting. No aerial chases were seen, but the paired drakes kept an area round their females clear of other drakes, of which there was an obvious surplus. As these various observations did not differ importantly from those of Hochbaum (1944), Lebret (1961), McKinney (1965), Dzubin & Gollop (1972) and others, the initial spacing of pairs at Loch Leven was not studied in detail.

Nesting areas

Most females at Loch Leven, instead of nesting on shore near their initial territories, moved to St. Serf's island, up to 3 km away. The evidence for this was that: (a) searches in two years revealed extremely few nests around the loch shores; (b) many more nests were found on the island than could be accounted for by pairs territorial round its shores; (c) pairs were often seen to fly from shoreline territories to the island; and (d) females put off nests on the island often made straight for the loch shore. The preference for

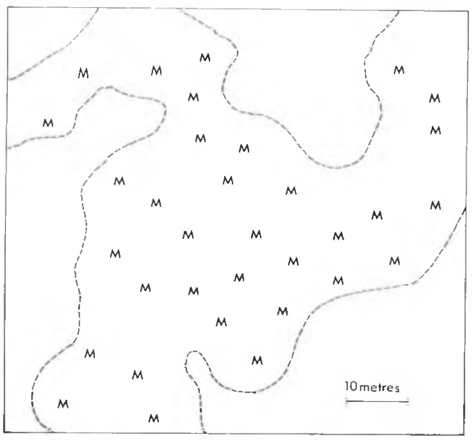

Figure 2. Regular spacing of Mallard nests on part of St. Serf's Island, 1st–16th April 1971. Dashed lines enclose suitable *Deschampsia* cover.

nesting on islands, when available, is well known in other ducks (McKinney, 1965; Duebbert, 1966), and St. Serf's was especially attractive because of good nesting cover.

In 1971 we made precise measurements of nest-positions on St. Serf's in a fairly uniform area of *Deschampsia* tussocks. The aim was to find how the nests of each species were spaced, first with respect to other concurrent nests of the same species, and second with respect to those of other species. Whenever a nest was found, its position was recorded by measuring the distances to the two nearest grid-posts. Nests in use at given dates were then plotted on to maps (Figures 2 and 3), distances between nearest neighbours were measured, and tested to see if they differed significantly from random. Two tests were used, both based on the square of the distance to nearest neighbour. One entailed calculating the variance of this measure, the other the geometric mean (see Appendix 1), and in both, significance levels were obtained by computer simulation. Significance levels derived by the first method were more disturbed by the occasional outlying nest than were those derived by the second method, so it is the latter that are quoted below.

In 1971, the earliest Mallard began nesting in mid-March, when scattered nests were found throughout the area, but none closer than 5 metres to the next. As the days passed, more nests appeared in vacant spaces until, by mid-April, a regular distribution was found ($p < 0{\cdot}005$), with most nests 5–10 metres from their nearest neighbours (Figure 2). Occasional nests were as close as two metres, yet bore the usual spatial relationship with their other neighbours. Such nests were usually started on about the same date, as though two ducks had simultaneously occupied the space normally filled by one. In nearly all such close nests, one was deserted, probably before the clutch was complete. Later in the season, when some nests were finished and others

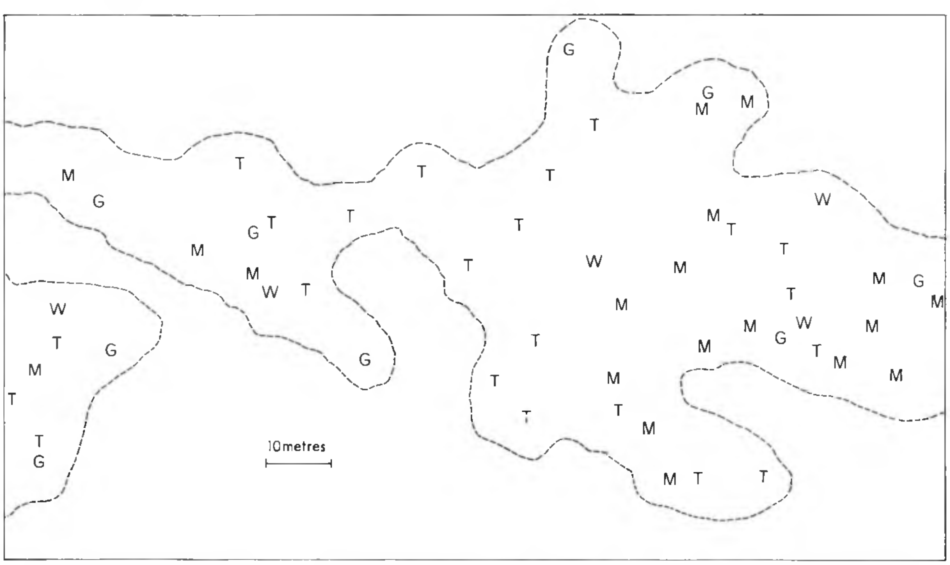

Figure 3. Locations of nests of various duck species on part of St Serf's Island, 16th–31st May 1971. Dashed line encloses suitable *Deschampsia* cover. G = Gadwall, M = Mallard, T = Tufted Duck, W = Wigeon. Nests of any one species are regularly spaced with respect to one another, but not with respect to nests of other species.

started, and when other species had begun nesting in the same area, spacing among Mallard nests became slightly less regular, but was still significantly more regular than random ($p < 0{\cdot}04$) (Figure 3).

An average of 7 metres between Mallard neighbours would permit densities of more than 180 concurrent nests per hectare, but in practice patches of unsuitable habitat within the general nesting area prevented this being reached, except very locally. The greatest number of occupied nests found at one time in a hectare was 43, and over the season as a whole 81, a situation produced partly by different females nesting successively in the same places. We three times caught a second female from the same tussock later in a season, and many other times found a new nest on a recently used one.

Selection of the nest-site was apparently by the female, as found by Hochbaum (1944), Sowls (1955) and others. Prospecting pairs usually settled on short grass at the edge of the *Deschampsia* and, after a few minutes, the female walked in. Usually the drake waited but sometimes he followed. The female wandered around, examining tussocks and finding where nests were already established. Fighting occurred, and near most nests tufts of female feathers were found, as evidence of a recent battle. Only one fight was witnessed, however, and the drake of the prospecting pair did not participate, while the ducks fought fiercely.

Wigeon moved into the area from mid-April, Gadwall from late April and Tufted Ducks from early May. The spacing of nests in all these species was significantly different from random, though in Wigeon only just (Appendix 1). Most Gadwall nests were 16–28 metres from their nearest neighbours ($p < 0{\cdot}02$), and most Tufted 5–11 metres ($p < 0{\cdot}005$), while Wigeon ranged from 15–40 metres ($p < 0{\cdot}05$) (Table 1). Possibly many Wigeon nests were missed, and a larger sample in another year might show greater regularity. One pair of Gadwall nests was only 8 metres apart but, as in close nests of Mallard, were the usual distance from their other neighbours. In all species, the longer distances between nests might have resulted from intermediate nests being missed, as was especially likely if such nests failed at an early stage.

In *Deschampsia,* nests could have been built less than one metre apart (the distance between tussocks), yet no nests of any species were closer than two metres. It was as though several different spacing patterns, one from each species, were superimposed without relation to one another, except for this two metre radius. Hence, we concluded that, in fairly uniform *Deschampsia,* the females of each duck species spaced out their nests, and tolerated other species closer than their own. This was independent of prior spacing along shorelines, in which drakes were active, but again pairs of different species were generally closer together than pairs of the same species. In addition, Tufted Ducks nested at much greater density in the gullery (Table 12 and Figure 3a), with only 2–3 metres between nests, compared with 7–11 outside, so the

Figure 3a. High density duck nests, indicated by bamboo stakes, in the gullery, St Serf's Island (*Pamela Harrison*)

Table 1. Spacing among simultaneous duck nests in *Deschampsia* tussocks on St. Serf's Island, Loch Leven, 1971.

Distance to nearest neighbour (m)

Number nests	Mean	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Mallard—Mallard, 1–15 April	6 9	64	—	2	4	2	9	8	17	5	5	6	4	1	1	—																					
Mallard—Mallard, 16–31 May	8 4	36	—	—	2	2	4	4	5	2	5	1	6	—	1	1	1	2	—																		
Mallard—any other duck, 16–31 May	6 6	36	—	2	3	6	6	4	2	4	2	2	—	3	—	—	1	1	—																		
Gadwall—Gadwall, 16–31 May	20 0	15							—	2	—	—	—	—	—	—	—	2	—	—	3	1	—	—	2	1	1	—	2	1	—						
Gadwall—any other duck, 16–31 May	4 9	15	—	3	3	3	—	2	1	1	1	—	—	—	1	—																					
Wigeon—Wigeon, 16–31 May	24 7	11*													—	—	2	—	2	—	—	2	—	—	—	—	—	—	—	—	1	1	—	—	—	2	—
Wigeon—any other duck, 16–31 May	6 1	11	—	1	1	3	1	—	—	3	—	2	—	—	—																						
Tufted Duck—Tufted Duck, 16–31 May	10 1	44	—	2	2	—	2	2	3	2	9	8	4	1	2	—	2	1	—	—	—	—	2	1	—	1	—										
Tufted Duck—any other duck, 16–31 May	8 3	44	—	2	3	5	7	6	3	1	2	3	2	—	4	—	2	1	—	1	—	1	—	—	—	—	—	—	—	1	—						
Any duck—any other duck, 16–31 May	5 7	107	—	10	13	19	16	13	8	9	8	7	—	—	3	—	—	1	—																		

Note. * Includes one extra at 40 metres.

Table 12. Hatching success in different cover-types in disturbed area, 1966–1971.

	Mallard		Gadwall		Wigeon		Shoveler		Tufted Duck		All species	
	No. of nests of known fate	No. (%) hatched	No. of nests of known fate	No. (%) hatched	No. of nests of known fate	No. (%) hatched	No. of nests of known fate	No. (%) hatched	No. of nests of known fate	No. (%) hatched	No. of nests of known fate	No. (%) hatched
Areas without gulls												
Tussocks	903	478(53)	112	47(42)	109	58(53)	16	10(63)	388	189(49)	1528	782(51)
Reeds	351	201(56)	24	8(33)	12	9(75)	4	2(50)	306	176(58)	697	396(57)
Reeds/Bushes	164	87(53)	13	6(46)	7	3(43)	5	1(20)	60	35(58)	249	132(53)
Others	13	6(43)	1	0	3	1(33)	1	1(100)	5	3(60)	23	11(47)
Totals	1431	772(52)	150	61(41)	131	71(54)	26	14(54)	759	403(53)	2497	1321(53)
Areas with gulls												
Tussocks	198	117(59)	12	8(67)	17	11(65)	0	0	754	426(57)	981	562(57)
Reeds	88	51(58)	6	3(50)	0	0	0	0	179	128(71)	273	182(67)
Totals	286	168(59)	18	11(61)	17	11(65)	0	0	933	554(59)	1254	744(59)

Note. * The better success in areas with gulls was significant only in the Tufted Duck ($x^2 = 6{\cdot}46$, $P < 0{\cdot}01$), and in the combined data for all species ($x^2 = 13{\cdot}75$, $P < 0{\cdot}001$).

mean inter-nest distance varied in different situations.

Successive nest positions of individual females

Ringed females of all species were caught on the island in more than one year, and each time note was made of which 50 metre square the nest was in. This was not precise enough to tell whether any females returned to the same site in successive years, but many returned to the same area. About two-thirds of recaptured Mallard and Tufted were in the same 50 m square or in the square adjacent to where they were caught the previous year. Failed females tended to shift more than successful ones but, on the data available, this trend was not significant statistically (Table 2). If any ducks moved off St. Serf's island to nest in a later year, we would not of course have noted them (except for one Mallard found by a farmer on a nest 5 km from where it first nested). Similar trends have been noted elsewhere in Mallard (Sowls, 1955) and in Tufted Ducks (Mihelsons *et al.* 1968).

Shoreline brood rearing areas

Most of the shoreline of Loch Leven was bare and subject to violent wave action, and the main brood rearing areas were a 2 km stretch of sallow and reeds on the east shore, and a few short stretches elsewhere along the shore and round the islands, which together totalled about 4 km (Figure 1). In the first three years, when the water was high, some of these areas extended more than 50 metres back from open water, but this distance was less in other, drier years. All these areas were separated from St. Serf's by more than one kilometre of open water, during the crossing of which many young were taken by large gulls (especially Great Black-backed and Herring) and some by Pike *Esox lucius*. Predation by gulls was facilitated by the frequent rough water, which tended to scatter the young, and make them easier to pick up. On several occasions we saw whole broods taken within minutes. Feeding conditions, on the other hand, were probably excellent, for large hatches of chironomids took place on the loch through the summer, and prevailing westerly winds piled these insects up against the east shore until at times low emergent vegetation was black with them. Some surface-feeding ducks held territories on these same shores, but the broods were generally taken further into cover from open water. Young Tufted spent much more time on open water than did surface feeders, and often formed crêches.

Laying seasons

The laying seasons of different species are shown in Figure 4 as the number of clutches started in each 5-day period, March–July, all years combined. For nests found during laying, the starting date was found by back-dating, assuming that one egg was laid per day (Sowls, 1955). Estimates made in this way were the most accurate, but would have been in error if any eggs had been removed unknown to us by predators, or if extra eggs had been added by other females. For successful nests found during incubation, the starting date was estimated from the date of hatch, using published figures of incubation periods (Witherby *et al.* 1938); and for unsuccessful nests found during incubation, the starting date was estimated from the state of

Table 2. Successive nesting areas of ringed female Mallard and Tufted Ducks.
The figures refer mainly to females caught in two successive years, but include a few Mallard caught on two nests in the same year.

		Second nest in same or adjacent 50 metre square	Second nest further away
Mallard	First nest successful	36	13
	First nest failed	9	8
	Total	45	21
Tufted Duck	First nest successful	10	3
	First nest failed	5	4
	Total	15	7

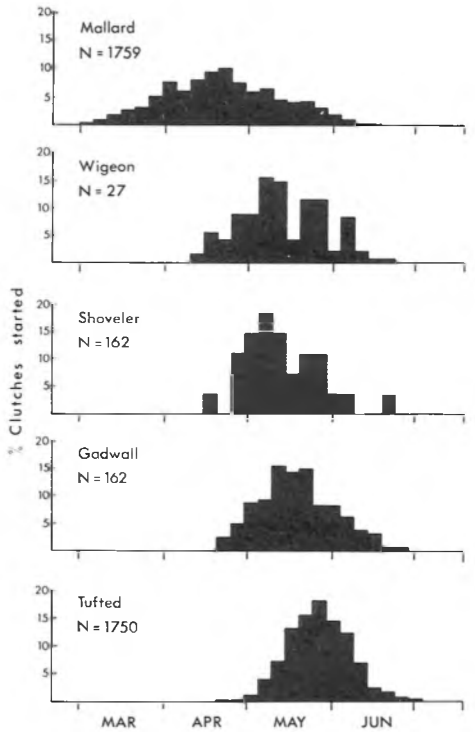

Figure 4. Laying seasons of ducks at Loch Leven as shown by the proportions of clutches started in each 5-day period through the season, all years combined.

incubation recorded by candling the eggs on the previous visit. For most nests in these last two categories, the date of hatch or failure was not known accurately, but was assumed to lie midway between two visits. Probably few estimates were in error by more than one 5-day period, and could not have appreciably altered the overall picture. But for nests not found till after failing or hatching, the laying date could not be estimated.

In general, Mallard began earliest and had the longest laying season (up to 16 weeks), while the Tufted began latest and had the shortest season (up to 10 weeks). Other species were intermediate, both in starting date and in length of season, in the order Wigeon, Shoveler and Gadwall. Too few Teal nests were found to be sure where this species would be in the sequence. In surface-feeding ducks repeat laying was frequent (see later), and the number of clutches started in different periods presumably depended partly on the number which failed in previous periods. Hence, the pattern of nesting shown in Figure 4 probably differed from that in other areas where predation differed. Also, the combining of all data masked annual differences. Thus in Mallard, the timing of onset varied by up to three weeks in different years, correlated with February temperatures (Table 3), but in the other (later nesting) species, such differences were barely apparent. Also, in any one year, the Tufted season was more concentrated than Figure 4 implies, more than 80% of all clutches being started within a 6-week period. Since the Tufted did not lay repeat clutches, this meant that individuals varied by more than 6 weeks in the date they started.

Differences in laying season between species were presumably related to differences in the periods that their particular food supplies were most plentiful, either for laying females or for growing young, but only for the Tufted was detailed information collected at Loch Leven. This species fed primarily on Chironomid midges, and its laying period coincided with the season when the greatest biomass of larvae were available on the loch floor (McLusky & McFarlane, 1974).

Clutch sizes

Clutch sizes were hard to determine accurately because we were never certain that the contents of a nest represented the total produc-

Table 3. Relationship between February temperatures and the start of egg-laying in Mallard. Dates refer to first eggs, and years are listed in order of spring warmth.

	Mean February temp (°F)*	First clutches begun on March	Mean date of all March clutches
1969	30·3	21–25	26
1968	31·2	16–20	25
1970	33·9	6–10/21–25†	24
1966	38·1	11–15	21
1971	39·3	6–10	20
1967	41·4	1–5	19

* Calculated as the average between the means of the daily maxima and minima.

† A break occurred between the first two nests and the rest, associated with a short cold spell.

tion of a single female. Some females, which failed during laying, finished their clutch in a new nest (on which they were recaught), while at other times two females used the same nest (found from laying frequency and egg type). In addition, if any eggs were taken by predators and the duck continued sitting, the recorded clutch size would have been too low. With these limitations, Mallard were found incubating apparently genuine clutches of 4–14 eggs (with five instances of 15–19), Gadwall 6–11, Wigeon 5–12 and Tufted Ducks 5–16 (but see below). Females of all species except Tufted were proved, by ringing, to re-lay after the loss of a previous clutch, and annual variations in mean clutch size depended largely on the (unknown) proportion of repeats in the sample, in turn dependent largely on the predation rate. One significant trend, however, was a seasonal decline in mean clutch size, which took place in all species for which adequate data were obtained (Table 4). At the start of the season, mean clutch size in the Tufted Duck was around 13–15 eggs, in the Mallard around 11 eggs, in the Gadwall around 10 eggs and in the Wigeon around 9, declining in all species to around 7 by the end. In surface-feeding ducks this trend resulted partly from the increasing proportion of repeats in later samples. Nonetheless the trend had set in well before much repeat laying occurred and in Tufted was apparent even in the absence of repeat laying (see later). Evidently the females which were latest to come into laying condition were also those least apt to produce large clutches.

Too few clutches of Shoveler and Teal were seen for us to examine seasonal variation, but of 16 Shoveler clutches, one was of 12 eggs, nine of 10, four of 9, and two of 8 (mean 10·0); and of eleven Teal clutches, one was of 12 eggs, four of 10, four of 9, and two of 8 (mean 9·5).

Excluded from Table 4 were some obviously multiple clutches of Tufted Ducks, containing 17–42 eggs. They were found every year, mainly in the gullery where Tufted nested at greatest density, and were especially frequent in 1971, when they formed at least 10% of 215 nests in 1 ha. Such multiple laying probably resulted partly from shortage of nesting sites in favoured areas. Tufted also occasionally laid in the nests of other species, as found elsewhere by Hildén (1964) and others.

Table 4. Season trends in clutch-size, 1966–1971

		Tufted Duck			Mallard			Gadwall			Wigeon		
		No.	Mean	s.e.	No.	Mean	s.e.	No.	Mean	s.e.	No.	Mean	s.e.
March	1–5												
	6–10				11	10·9	0·6						
	11–15				21	10·6	0·4						
	16–20				38	10·3	0·3						
	21–25				57	10·9	0·2						
	26–30				80	10·2	0·2						
April	31–4				106	9·4	0·2						
	5–9				88	9·3	0·2						
	10–14				115	9·3	0·2						
	15–19				136	8·7	0·1						
	20–24	1	9·0		127	8·3	0·1	9	9·9	0.3	7	9.0	0.7
	25–29	2	15·0		81	8·0	0·2						
May	30–4	18	12·6	1·0	73	7·6	0·2	18	10·1	0·6	16	8·6	0·2
	5–9	65	11·8	0·3	73	7·7	0·2						
	10–14	92	11·1	0·2	69	8·0	0·2	28	8·8	0·3	25	8·4	0·3
	15–19	176	10·9	0·2	49	7·1	0·2						
	20–24	209	10·5	0·2	42	7·2	0·2	21	8·4	0·7	20	7·6	0·3
	25–29	273	9·7	0·1	41	7·4	0·3						
June	30–3	224	9·2	0·1	31	7·6	0·3	17	7·4	0·3	22	7·3	0·2
	4–8	190	8·3	0·1	24	7·1	0·3						
	9–13	108	7·7	0·2	11	7·1	0·3	7	7·9	0·6	8	7·1	0·3
	14–18	38	7·7	0·3	1	7·0							
	19–23	23	7·1	0·3				2	7·5	1·5	2	5·0	
	24–28	12	6·5	0·3									
July	29–3	4	7·0	0·4									
	4–8	1	6·0										

Re-nesting

The trapping of certain female Mallard on two nests in the same year confirmed that repeats were attempted, but gave only maximal estimates of the re-nesting interval (period between the end of one attempt and the start of the next). This was because we were never certain that other attempts had not been made in the interim nor, in re-nests after a perious hatch, of the age at which the young were lost. In three nests which failed during incubation, however, the recorded re-nesting interval was 20–23 days, 29–34 days and 35–38 days respectively; while in six attempts that failed after hatch, this interval was at most 15, 15, 20, 23, 23 and 30 days. The two at 15 days were probably close to the minimum required by birds at this stage (see Sowls (1955) for Pintail *Anas acuta*).

One each of Gadwall and Wigeon were caught on two nests in the same year, but the numbers of these species ringed were small. For Tufted, however, 299 birds were caught on nests and 52 re-caught in subsequent years, yet none was found on more than one nest in the same season. We thus concluded that, if repeat laying occurred in Tufted, it must have been extremely rare, as would be expected from the shortness of its season.

Hatching success

Effects of observer

Our aim was to find how many of the clutches started subsequently hatched, and how many failed. But it was first necessary to know (a) whether the success of nests found was representative of the population, and (b) whether our continual presence in the area had had any effect on success. For this, we had three sets of results (Tables 5–8). One was from nests found during the season in quick searches, and the other two were from used nests found at the end of the season during thorough searches aimed to find all nests in part of the study (= disturbed) area and in the control (= undisturbed) area. A nest was classed as successful if at least one egg hatched.

Success was much better among the samples of nests examined at the end of the season, in both disturbed and undisturbed areas, than among those found during the season. This was not entirely because the early samples were unrepresentative, but because successful nests survived longer than failed ones, so were more likely to be found in end-of-season searches. In addition, failed nests were often re-used by successful birds, so at the end of the season would be registered as successful, even though the same site had earlier held one or more failed nests, which passed unnoticed. These effects, which biased the end-of-season results in favour of success, were most marked in Mallard, which had the longest season.

On end-of-season results, success was still significantly better ($x^2 = 18{\cdot}1$, $P < 0{\cdot}001$) in undisturbed than in disturbed areas, implying that our activities in the study area had reduced success there. The difference between within-season searches in the disturbed area and post-season searches in undisturbed areas (18–32% in different years) gave a maximum estimate of the extent of our influence, while the difference between post-season searches in the disturbed and undisturbed areas gave a minimum estimate of this extent (9–14%). Even in areas completely free of disturbance, the maximum possible success was 75–86% in different years, these being the end-of-season figures.

Some differences in success between years were associated with differences in the timing and frequency of our visits. In 1966, when the hatch was significantly better than in other years ($x^2 = 4{\cdot}70$, $P < 0{\cdot}05$), especially in Mallard ($x^2 = 5{\cdot}83$, $P < 0{\cdot}05$), work was not started until late April, when many Mallard nests (included in the totals) were well through incubation. Otherwise, the level of disturbance remained about the same through the study period. Nonetheless several trends emerged, showing that other factors, besides human disturbance, influenced success. These trends are discussed in later sections.

In all species, most failures were apparently due to predation (Table 5), but some nests classed as preyed upon may have been deserted first. On St. Serf's, where egg eaters were very numerous, it was impossible to get an accurate measure of desertion. Likewise any eggs left in a nest after hatch quickly disappeared, so no good measure was obtained of what proportion of eggs hatched in successful nests. Also the fact that many nests failed did not in surface-feeding ducks imply a corresponding reduction in the number of ducklings produced, because repeats were laid, and each adult could have had one or more failures and still produced young.

Predators

Up to 400 Jackdaw pairs bred in old rabbit holes in the short grass part of the island, and others came in daily from the mainland to feed. (Numbers were lower from May 1970, however, when many were killed by use of poisoned eggs, though not enough to reduce predation rates.) To judge from gut analyses and observations, they took chiefly chironomid midges and other invertebrates from the grassland, but also took duck and gull eggs when the chance arose. Most often, duck nests destroyed by Jackdaws were partly pulled out, nest material and shell pieces were scattered around, surrounding cover was flattened, and the nest bottom was wet with egg contents. This resulted when several Jackdaws fought over the eggs. At other times nests were found intact, but devoid of contents. This resulted when fewer birds were involved, when there was little fighting, and when the eggs had been carried away. Accumulations of shells were found below several bushes on the island, and also along the north shore, where bushes overhung the water. Those nests found containing all broken shells were proved in a few instances to result from predation by Moorhens. These were unsuspected, until a late snowfall in one year revealed their footprints around some Mallard nests which had been destroyed. About 100 Moorhen pairs nested each year on the island. One or two pairs of Carrion Crows *Corvus corone* also nested, but could not have made any appreciable impact compared to that made by the numerous

Table 5. Overall hatching success each year in the disturbed area, from data collected during the nesting season.

	1966	1967	1968	1969	1970	1971	All years
Mallard							
No. of known fate	233	439	322	309	295	119	1717
No. (%) hatched	182(78)	227(52)	148(46)	165(53)	148(50)	70(59)	940(55)
No. (%) predated	47(20)	195(44)	126(39)	123(40)	137(47)	41(34)	669(39)
No. (%) deserted	4(2)	17(4)	48(15)	21(7)	10(3)	8(7)	108(6)
Gadwall							
No. of known fate	34	45	24	22	29	14	168
No. (%) hatched	21(62)	19(42)	11(46)	9(41)	6(21)	6(43)	72(43)
No. (%) predated	13(38)	25(56)	12(50)	13(59)	23(79)	8(57)	94(55)
No. (%) deserted	0	1(2)	1(4)	0	0	0	2(2)
Wigeon							
No. of known fate	36	34	21	19	27	11	148
No. (%) hatched	30(84)	16(47)	14(67)	7(37)	7(26)	8(73)	82(55)
No. (%) predated	6(16)	18(53)	7(33)	12(63)	20(74)	2(18)	65(44)
No. (%) deserted	0	0	0	0	0	1(9)	1(1)
Shoveler							
No. of known fate	6	9	5	4	1	1	26
No. (%) hatched	5	2	4	1	1	1	14(54)
No. (%) predated	1	6	1	3	0	0	11(42)
No. (%) deserted	0	1	0	0	0	0	1(4)
Tufted Duck							
No. of known fate	215	354	179	315	395	234	1692
No. (%) hatched	99(46)	197(56)	120(66)	157(50)	279(71)	105(45)	957(57)
No. (%) predated	110(57)	141(40)	52(30)	140(44)	88(22)	114(49)	645(38)
No. (%) deserted	6(3)	16(4)	7(4)	18(6)	28(7)	15(6)	90(5)
All species							
No. of known fate	524	881	551	669	747	379	3751
No. (%) hatched	337(64)	461(52)	297(54)	339(51)	441(56)	190(50)	2065(55)
No. (%) predated	177(34)	385(44)	198(36)	291(44)	268(36)	165(44)	1484(40)
No. (%) deserted	10(2)	35(4)	56(10)	39(5)	38(8)	24(6)	202(5)

Notes: All species together did significantly better in 1966 than in the remaining years ($x^2 = 4 \cdot 70$, $P < 0 \cdot 05$); but in individual species this difference was significant only in Mallard ($x^2 = 5 \cdot 83$, $P < 0 \cdot 05$). Overall the Gadwall did significantly worse than the remaining species ($x^2 = 9 \cdot 16$, $P < 0 \cdot 01$), and the Tufted Duck did significantly worse in 1971 than in 1970 ($x^2 = 4 \cdot 00$, $P < 0 \cdot 05$).

Table 6. Overall hatching success each year in the disturbed area, from data collected after the nesting season.

	1969	1970	1971	All years
Mallard				
No. of known fate	33	42	38	113
No. (%) hatched	26	33	30	89(79)
Other dabbling duck				
No. of known fate	6	8	4	18
No. (%) hatched	3	4	2	9(50)
Tufted Duck				
No. of known fate	50	67	73	190
No. (%) hatched	26	48	46	120(63)
All species				
No. of known fate	89	117	115	321
No. (%) hatched	55(62)	85(73)	78(68)	218(68)*

Note. * Most of these nests had been found and recorded earlier in the season. Among those that had been missed, hatching success was the same (67% of 21 nests successful).

Table 7. Overall hatching success each year in the undisturbed area, from data collected after the nesting season.

	1969	1970	1971	1972	1973	All years
Mallard						
No. known fate	57	70	63	33	28	251
No. (%) hatched	49(86)	57(84)	57(90)	28(84)	24(84)	215(86)
Gadwall						
No. known fate	2	4	2	2	3	13
No. (%) hatched	1	3	1	2	3	10(77)
Wigeon						
No. known fate	2	3	5	2	4	16
No. (%) hatched	1	2	4	2	3	12(75)
Shoveler						
No. known fate	0	1	0	1	1	3
No. (%) hatched	0	1	0	1	1	3(100)
Tufted Duck						
No. known fate	21	21	29	28	25	124
No. (%) hatched	17(81)	18(86)	23(79)	18(64)	19(76)	95(76)
*All species**						
No. known fate	84	99	100	68	61	412
No. (%) hatched	69(82)	81(82)	86(86)	51(75)	50(82)	337(82)

Note. * Includes a few unidentified and excluded from the totals above. The "undisturbed area" comprised one hectare in 1969–71, and transect samples from the whole island in 1972–73.

Table 8. Summary of hatching success (all species) in disturbed and undisturbed areas, from data in Tables 5–7.

	Data collected during the nesting season		Data collected just after the nesting season			
	(a) Disturbed area		(b) Disturbed area		(c) Undisturbed area	
	No. nests of known fate	No. (%) hatched	No. nests of known fate	No. (%) hatched	No. nests of known fate	No. (%) hatched
1966	524	337(64)	—	—	—	—
1967	881	461(52)	—	—	—	—
1968	551	297(54)	—	—	—	—
1969	669	339(51)	89	55(62)	84	69(82)
1970	747	441(56)	117	85(73)	99	81(82)
1971	379	190(50)	115	78(68)	100	86(86)
1972	—	—	—	—	68	51(75)
1973	—	—	—	—	61	50(82)
Totals	3751	2065(55)	321	218(68)	412	337(82)

Notes. The disturbed area comprised the whole island in 1966–1968 and the whole island minus the one hectare undisturbed area in 1969–1971; the undisturbed area comprised one hectare in 1969–1971, and transect samples from the whole island in 1972 and 1973 (see text).

Significance of differences in overall success indicated by the three sets of data were as follows: between (a) and (b), $x^2 = 51{\cdot}9$, $P < 0{\cdot}001$; between (b) and (c) $x^2 = 18{\cdot}1$, $P < 0{\cdot}001$; and between (a) and (c), $x^2 = 107{\cdot}6$, $P < 0{\cdot}001$.

Jackdaws. Other potential avian predators included Black-headed Gulls (5,000–6,000 pairs on the island), and visiting Herring Gulls (up to 25 in March–May, and several thousands by late June), Lesser Black-backed Gulls (up to 12), and Greater Black-backed Gulls (up to 100). Perhaps duck nests were too well hidden for these gulls, for no evidence was found that they took eggs, though the large species took ducklings. Potential mammalian predators included Rats and Water Voles *Arvicola amphibius*. The numbers of Rats were deliberately kept low through selective poisoning, and in most years we saw none. Water Voles were abundant and, while no evidence was found that they took eggs, such evidence might anyway have been difficult to get. To conclude, the most important predators on eggs were apparently Jackdaws, and to a lesser extent Moorhens, both of which could get only unguarded eggs. It was presumably their being well covered that allowed eggs to survive during the laying period, when the female duck was mainly absent.

Experiments with artificial nests

The main way in which predation occurred under our disturbance was through providing extra chances for predators to take eggs while the mother was away, and we often saw Jackdaws removing eggs from nests just visited. Predators might also have found nests with the help of marker canes, as found by Picozzi (1975), who studied Crow predation on Red Grouse *Lagopus scoticus* nests. The situation at Loch Leven differed from Picozzi's, because the main predators were Jackdaws, not Crows, and nest densities reached 200 or more per ha, much higher than Red Grouse, so even a short search by predators on St. Serf's was likely to be rewarding. Also our canes were left in place till the end of the season so, as the weeks passed, an increasing proportion were at finished nests, rather than occupied ones. Nonetheless, it was desirable to test for any possible influence of canes.

Two experiments were carried out in 1969 and two more in 1970. They all involved setting out in Deschampsia a series of 20 artificial clutches, each of 5 hens' eggs, to look like natural 'covered' duck nests. Half were marked with canes (placed 1 m to the north) and half were not, then the rate at which these clutches disappeared was assessed from visits every third day. The clutches were laid out in two rows, 20 m apart and 10 m between clutches. In the first year alternate nests in each line were marked, starting in one line

Table 9. Survival of marked (with cane) and unmarked (no cane) 'clutches' of hens eggs, set out to look like natural duck nests.
The figures show the number of clutches extant at different visits.

	1969a		1969b		1970a		1970b	
	Marked	Unmarked	Marked	Unmarked	Marked	Unmarked	Marked	Unmarked
At start	10	10	10	10	10	10	10	10
After 3 days	8	7	9	9	3	4	2	2
After 6 days	5	4	8	7	2	0	0	1
After 9 days	3	4	1	5	1	0	0	1
After 12 days	1	2	0	0	1	0	0	1
After 15 days	0	0	0	0	0	0	0	0

with a marked nest and in the other with an unmarked. In the other year, all the nests in one line were marked and all those in the other were unmarked. On average, in both years marked and unmarked clutches disappeared at about the same rate (Table 9), implying that predators were not using canes as indicators of eggs. If the same applied to natural duck nests, the rate of predation resulting from our disturbance must have resulted primarily from the increased exposure of (covered) eggs, rather than to the use of marker canes.

Differences between species

In the disturbed area, no marked differences in overall success were noted between species, except that Gadwall were significantly less successful ($x^2 = 9{\cdot}16$, $P < 0{\cdot}01$) than the rest (Table 5). This was not apparent in the undisturbed area (Table 7), so was presumably due to the Gadwall being more susceptible than other species to human disturbance. The apparent greater success of Mallard in the undisturbed areas was probably not genuine, because it had the longest season and most often nested on previously failed nests, so that data on its success from these areas were likely to be most biased. Otherwise the striking feature in data from all three sources was the lack of marked differences in success between species.

Seasonal trends

In all duck species, hatching success declined through the season (though in Shoveler too few nests were found to confirm this trend statistically). They all showed about 70% success at the start of the season, and declined to less than 40% at the end. But the extent of this decline is partly masked in Table 10, where data are grouped by months. The decline in success was not due to some common factor acting simultaneously on all species. Human disturbance remained constant through the season, at one or two visits per week; in some years the decline took place when predator numbers were expanding (through breeding) and in others when predator numbers were declining (through control), and anyway nests became less, not more, conspicuous through the season as cover thickened. Almost certainly, the decline in success was due to some seasonal change in the behaviour of the ducks themselves, such that late nests were most vulnerable. Moreover, it took place independently in different species, according to when they bred. Thus in May, when Mallard were halfway through their season, only 47% of nests were successful, but in Wigeon, which had only recently started, 60% of nests were successful. In both species success declined to around 40% in the last month of their season.

Influence of cover type and gulls

To recapitulate, the main nesting areas on St. Serf's consisted of (a) mixed *Phalaris* reeds/*Salix* bushes, (b) *Phalaris* reeds alone, (c) *Deschampsia* tussocks. In addition, the Black-headed Gull colony extended over part of the *Phalaris* and *Deschampsia,* bringing the total nesting habitats to five. An indication of the extent to which these various areas were used is given in Table 11, which shows the total number of nests found per ha of each habitat in 1966–1970, when searching effort was spread equally over the whole island. *Deschampsia* was much the preferred cover type, followed by *Phalaris* and *Phalaris*/

Table. 10. Hatching success in different months in disturbed areas, 1966–1971 combined.

	March	April	May	June	Whole season*
Mallard					
No. of known fate	224	788	473	92	1577
No. (%) hatched	173(77)	461(58)	220(47)	36(40)	890(56)
No. (%) predated	37(16)	265(34)	231(48)	52(56)	585(37)
No. (%) deserted	14(7)	62(8)	22(5)	4(4)	102(7)
Gadwall					
No. of known fate		11	106	32	149
No. (%) hatched		8(73)	49(46)	12(38)	69(46)
No. (%) predated		3(27)	56(53)	19(59)	78(52)
No. (%) deserted		0	1(1)	1(3)	2(2)
Wigeon					
No. of known fate		26	90	20	136
No. (%) hatched		19(73)	54(60)	8(40)	81(60)
No. (%) predated		7(27)	35(39)	12(60)	54(39)
No. (%) deserted		0	1(1)	0	1(1)
Shoveler					
No. of known fate		3	19	3	25
No. (%) hatched		2	11(58)	1	14(56)
No. (%) predated		1	7(37)	2	10(40)
No. (%) deserted		0	1(5)	0	1(4)
Tufted Duck					
No. of known fate		3	923	603	1529
No. (%) hatched		2	583(63)	352(58)	937(61)
No. (%) predated		1	294(32)	221(37)	516(34)
No. (%) deserted		0	46(5)	30(5)	76(5)
All species					
No. of known fate	224	831	1611	750	3416
No. (%) hatched	173(77)	492(59)	917(57)	409(54)	1991(58)
No. (%) predated	37(16)	277(33)	623(38)	306(42)	1243(36)
No. (%) deserted	14(7)	62(8)	71(5)	35(4)	182(6)

Notes. * For many nests of known fate, the starting date was not known, so they were excluded from this table, yet included in Table 1, hence the differing totals. The significance of the seasonal decline in success was examined in Mallard by testing March data against June ($x^2 = 16{\cdot}38$, $P < 0{\cdot}001$), in Gadwall by testing the first half of the season against the second half ($x^2 = 4{\cdot}03$, $P < 0{\cdot}05$), in Wigeon by testing April against June ($x^2 = 3{\cdot}83$, $P < 0{\cdot}05$), and in Tufted Duck by testing the first three weeks against the last three ($x^2 = 7{\cdot}41$, $P < 0{\cdot}01$).

Table 11. Number of nests per hectare in different main cover-types. The figures show the range of mean values obtained in different years, though locally much higher densities were obtained.

	Deschampsia tussocks without gulls	*Deschampsia* tussocks with gulls	*Phalaris* reeds without gulls	*Phalaris* reeds with gulls	*Phalaris* reeds/ *Salix* bushes
Mallard	13–21	17–20	8–10	6–13	1–8
Tufted Duck	7–10	40–100*	5–8	10–15	1–3
All ducks	26–34	54–118*	15–17	19–29	1–73

* Excludes 1971 when about 250 nests were found (nearly all Tufted) in one hectare of *Deschampsia* gullery.

Salix, but the occupancy of these last areas varied greatly from year to year, depending on water level. When the water was high, much of these areas was flooded and unsuitable for nesting, but *Phalaris* growth was then good, and cover for the next year plentiful. (Most nests were placed in dead growth from the previous year.) In general, *Phalaris* offered better cover, and was used more, in the first three years than in the last five. Tufted Ducks nested at much greater density in areas with gulls than in equivalent cover elsewhere. Surface-feeding ducks showed no such preference, and all species nested at about the same density in the gullery as outside (except Shoveler, for which few nests were found, none in the gullery).

No significant differences were noted in hatching success between the various cover types lacking gulls, but all ducks were more successful in the gullery than outside (Table 12). The difference was significant in the Tufted Duck ($P < 0{\cdot}01$), and even more so in the combined data for all species ($P < 0{\cdot}001$), but not in individual surface-feeders. The attraction of Tufted Ducks to gulleries has often been seen elsewhere (Hildén, 1964) and, while a protective function has been assumed, this is apparently the first time the link with hatching success has been checked (but see Olsson (1951) for Eider *Somateria molissima*). It presumably occurred because the gulls, while not themselves serious predators on hidden duck clutches, kept out other species, like Jackdaws, that were. Most of the duck nests destroyed were on the edges of the gull colony, with few in the middle.

The decrease in Tufted Duck success between 1970 and 1971 ($x^2 = 4{\cdot}00$, $P < 0{\cdot}05$), was associated with unusual crowding in the gullery (at least 215 nests in one hectare). There were more desertions than usual and multiple laying in 10% of nests. If the eggs in a multiple clutch were laid over the same period, so all started incubation together, they sometimes all hatched, and up to 24 ducklings were seen in a nest at once. This was unusual, however, because (a) nearly always some eggs were pushed out, (b) incubation was inefficient, so some embryos died through chilling, and (c) eggs were sometimes added during incubation and, because the female left with the first hatched young, these later eggs were abandoned. The net result was that, in successful nests, a much smaller proportion of eggs in multiple clutches (< 60%) than in normal clutches (> 90%) hatched. The exact proportions could not be assessed, because of the rapid removal of abandoned eggs by predators. Hence, while in general nesting success among Tufted Ducks was higher in the gullery than outside, the reverse was so in 1971, when exceptional numbers nested there.

Fledging success

The previous estimate of 67% young surface-feeding ducks reaching the flying stage at Loch Leven in 1966 (Boyd & Campbell, 1967) is erroneous because it was based solely on the reduction in mean brood-size (6·5 to 4·4) during the growth period, and took no account of broods depleted to nil. We were unable to make a good assessment of duckling survival, but circumstantial evidence suggested that it was poor, at least among surface feeders. Firstly, broods were counted on various dates through the duckling period, with one observer on shore to drive the young out and another in a boat. Usually less than 100 ducklings were seen, and often fewer than 50, nearly all less than a week old. In view of the large number hatched, the number seen should have been greater and should have included more large birds. Secondly, counts of the total surface-feeding ducks on the loch in late August, by which time all young were well grown, indicated populations only 1·5 to 2 times higher than at the start of breeding, which implied a ratio of 0·5–1 young per adult. Thirdly, the ratio of young to old Mallard among shot birds in autumn varied in different years between 0·7 and 1·3, and since young Mallard were probably about 1·5 times more vulnerable to gunfire than old ones in autumn (Geis *et al.* 1969), this implied a young to adult ratio in the population of only 0·5–0·8 to one in different years. Ringing showed that Mallard were resident in the Loch Leven area through the year, with no appreciable immigration from abroad, so these figures probably reflect poor local production. Too few ducks of other species were shot to deduce anything from age-ratios, but from observations and counts, their production seemed also to be low.

In Tufted Duck, on the other hand, survival was probably better. Many more young were seen on brood counts, and at least once each year, more than 500 young were counted. Late summer counts were of little value in assessing production, because of early dispersal to other waters. In some years, numbers doubled between May and August/September, and in others they fell (Laughlin, 1974).

Discussion

Limitations on numbers of breeders

Two aims of this study were to find (a) what lead to such dense nesting in species which, over most of their range, nested in more dispersed manner; and (b) whether any limitation on breeding numbers is likely to have been imposed at Loch Leven. Dense nesting probably occurred because of the proximity of a highly suitable nesting area (St. Serf's Island) to a large water surface with a shoreline long and broken enough for several hundred pairs to establish territories there in spring. So far as we know, no modification of the normal spacing and aggressive behaviour was needed to permit such dense nesting, for initial territories and nesting areas were generally well separated. Similar findings were made on Gadwall in North America, where islands were used for nesting by birds which flew in from 'territories' on the mainland (Hammond & Mann, 1956). Homing behaviour and good breeding success would of course ensure the continuation of such a colony, and make it independent of continual immigration (McKinney, 1965).

Since spacing occurred both along shorelines and in nesting areas, either could have limited breeding numbers. The shoreline areas were occupied by spaced (= aggressive) birds for only a few weeks, so the same areas could then have become available to other pairs. We have no evidence that successive pairs occupied the same sites at Loch Leven (as this was not studied), but such replacement was reported from the prairies, where in one year many Mallard were forced through drought to share the same small ponds (Dzubin, in McKinney, 1965). Replacement was also observed by Sowls (1959) among Blue-winged Teal *Anas discors,* and by McKinney (1967) among Shovelers in crowded pens, while Smith & Hawkins (1948) discussed the possibility of three turnovers of pairs during a 6-week breeding season. Likewise in the nesting area on St. Serf's, not only were vacant sites usually available, but some were used successively by more than one hen. Hence, neither spacing of initial territories along shorelines, nor spacing of nests on St. Serf's Island, necessarily limited total breeding numbers to what could be accommodated at one time. If crowding occurred, its first effect would be to reduce the number of birds that could nest at the start of the season.

Tufted pairs which did not space themselves along shorelines, but on open water, were less aggressive than surface-feeders. It is thus hard to say whether any limitation on density was imposed on the water, especially as pairs were often seen close together. On St. Serf's, some nest sites were occupied by more than one female in a season, though less often than by surface-feeding ducks, because of the shortness of the season. For these various reasons, we consider it unlikely that the breeding numbers of any species at Loch Leven were near the maximum that space would allow, but further study is needed.

If a female surface-feeding duck failed late in incubation, her mate had usually deserted the territory, joined a flock, and perhaps started to moult. She might then have to find a new mate. In Mallard, breeding drakes usually began to moult before bachelors, and the latter were seen, in mid-summer, attempting to pair with females still in breeding condition. These surplus drakes, evident in many duck populations, may well be necessary to achieve maximum production in areas where nest predation is heavy and repeats frequent. But to our knowledge, proof from ringing that the same duck may have different mates for successive nests in a season has so far been established only for Mallard, Gadwall and Pintail, by Sowls (1955). Again, it is hard to say whether shortage of drakes could ever limit the number of breeding attempts, but where predation was heavy it might.

Limitations on production of young

The advantage of island nesting is generally held to be reduced predation on eggs, especially from mammals, like Foxes *Vulpes vulpes*. This view could not be tested at Loch Leven because we did not study mainland nests, but in undisturbed conditions on the island, no more than 76–86% of nests in different years produced young. This was of the same order as in island nesting ducks elsewhere, and much higher than in mainland nesting ducks in most situations (Hammond & Mann, 1956, Dzubin & Gollop, 1972). At Loch Leven a major influence on the success of ducks was our own disturbance, which probably accounted for at least 9–14% of all clutches started and possibly twice as much. This was because Jackdaws, the main egg-eaters, were abundant and opportunist, raiding nests whenever the female was off. Similar bias presumably applied in some degree to much, if not all, previous data collected on the nesting success of ducks, yet few attempts were made to assess its extent (exceptions include Balat, 1969; Reed, 1970; MacInnes & Misra, 1972). Irrespective of disturbance, however, several trends emerged. The most pronounced were the declines in clutch size and hatching success through the season, shown by all species. Within each species, early nesting individuals laid larger clutches, less often deserted and suffered less predation than late nesting birds. In surface-feeders, the reduced clutch size was partly because later samples contained increasing proportions of repeats, but the trend also held in Tufted which did not repeat. The same trends have been noted in other waterfowl (Sowls, 1955; Hildén, 1964; Mednis, 1968; Havlin, 1971; Dzubin & Gollop, 1972; Reynolds, 1972; Newton & Kerbes, 1974), and are evidently widespread. Perhaps the date of laying, clutch size and how much the duck goes off to feed, leaving the nest exposed, all depend partly on one common factor, namely body condition. On this view, ducks with most reserves would nest earlier, lay more eggs, and leave their eggs less in order to feed than would ducks with fewer reserves. A link between attendance at nests and egg-losses in Blue Geese *Anser caerulescens* has recently been established by Harvey (1971).

Brood counts, late summer numbers and autumn age ratios all pointed to poor survival of young at Loch Leven, especially in surface-feeders. The fact that areas suitable for surface feeding ducklings were restricted, led to crowding in a few short stretches of shore. In Finland, Raitusuo (1964) showed that, under conditions of crowding, female Mallard themselves were the worst enemies of young ducklings, as they savaged any strange young that approached their own brood. Frequent interactions, together with rape attempts by drakes, resulted in young scattering, getting lost and attacked, so that 34–40% of young died in the first two days alone, a loss far greater than that caused by predators. Strife between females of this and other species in crowded conditions was also noted by Collias & Collias (1956) and Beard (1964).

If brood density was low, individual broods could presumably avoid one another, but at Loch Leven, over an 8-week period, at least 200 Mallard broods are presumed to have made their way to 4 km of shoreline. If they all remained and survived, this is equivalent to a density of one brood per 20 m of shore, excluding other species. No observations were made of brood behaviour but, from Raitusuo's observations, conditions at Loch Leven were not the best for good duckling survival. Some females might have taken their broods further afield, and elsewhere brood movements of up to 5 km were recorded in seven days, and of 8 km in nine days, but they too resulted in heavy losses (Dzubin & Gollop, 1972). Hence, shortage of good brood rearing areas was probably the major bottleneck to production of Mallard and other surface-feeding ducks at Loch Leven. The problem was less acute in Tufted Ducks, because the females were less aggressive, and the young fed largely on open water. It is probably for these reasons that survival of young Tufted at Loch Leven appeared in most years better than that of other species. We were unable to assess how much the predation on ducklings by large gulls was influenced by restricted habitat, rough water and other predisposing causes. But relatively poor production of ducks nesting in large concentrations has been noted elsewhere in other species (Hildén, 1964; Dzubin & Gollop, 1972; Milne, 1973; Jenkins *et al.* 1975). The situations in which ducks can be most easily studied may thus be atypical as regards production.

In conclusion, as a habitat for adult ducks, Loch Leven provided abundant space for territories and good nesting cover, but for ducklings it provided only restricted areas, which led to crowding, and may have accounted for the presumed heavy losses. The major recommendations for management of Loch Leven as a Nature Reserve were thus to (a) keep human disturbance on the nesting area to a minimum, and more important (b) alter the shoreline, so as to establish more cover and improve it for ducklings.

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Summary

1. Loch Leven holds the biggest concentration of nesting ducks in Britain. In 1966–1973 the population consisted mainly of Tufted Duck *Aythya fuligula* (500–600 pairs) and Mallard *Anas platyrhynchos* (400–450 pairs), with smaller numbers of Gadwall *Anas strepera* (25–30 pairs),

Wigeon *Anas penelope* (25–30 pairs), Shelduck *Tadorna tadorna* (11–13 pairs), Shoveler *Anas clypeata* (up to ten pairs) and Teal *Anas crecca* (up to ten pairs).

2. Each spring, pairs of surface-feeding ducks spaced themselves around the shores of the loch, and pairs of Tufted on open water. For nesting, most females of all species then moved to St. Serf's Island, forming one huge colony in about 14 ha of suitable cover. Where the habitat permitted, nests of each species were spaced out regularly, and the spacing patterns of different species were independent, except that normally no two nests of any species were closer than two metres. Nest-spacing was apparently achieved by the females, and at least in Mallard involved fights. It was independent of the earlier spacing of pairs, in which the drakes were active. On both types of spacing each species tolerated other species closer than its own.

3. Ringed females of all species were caught on the island in more than one year, and usually returned to the same limited area to nest. Sometimes a nest-site was used by more than one female in a season.

4. Mallard began earliest each year and had the longest laying season (up to 16 weeks), while Tufted began latest and had the shortest season (up to ten weeks). Other species were intermediate, both in starting date and in length of season, in the order Wigeon, Shoveler and Gadwall. In surface-feeding ducks, repeat laying occurred after the loss of an earlier clutch, but in Tufted apparently not. In all species, mean clutch-size declined through the season.

5. Hatching success was reduced by our disturbance, which caused females to expose their nests to predators. Without disturbance, probably at most 76%–86% of clutches would have hatched in different years. The main egg-predators were Jackdaws *Corvus monedula* and to a lesser extent Moorhens *Gallinula chloropus*. Under disturbance, Gadwall were least successful. In all species, hatching success declined through the season, and was attributed at least partly to a seasonal change in the behaviour of the ducks themselves.

6. The hatching success of all species was better inside a large Black-headed Gull *Larus ridibundus* colony than outside it. This was probably because the gulls kept out other more serious predators. Tufted Ducks nested at greater density inside the gullery than outside, and in one year of exceptionally high density (215 nests in one hectare) its success was worse, not better, than outside. Under such crowding, many multiple clutches were laid and these had reduced hatching success.

7. Survival of young was almost certainly poor at Loch Leven, especially in surface-feeding ducks. Areas suitable for ducklings were restricted.

8. 'Colonial' nesting at Loch Leven was attributed to the proximity of an attractive nesting island to a shoreline and water area large enough for several hundred duck pairs to establish territories in spring.

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Appendix 1. A test of randomness of nest spacing

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Traditional tests of randomness of a configuration of nests in a 2-dimensional plane based on nearest neighbour measurements assume a random sample of nearest neighour distances (either random point to nest, or nest to nest) in an unbounded plane. In the research described in this paper there is a boundary beyond which ducks do not nest, and the use of all the information in the map of nest sites is desirable. Taking these restrictions into account, we asked: is it likely that this arrangement of nest sites has been generated by a process of randomly and independently positioning nests within the area of suitable habitat? The alternative considered was of some process tending to space out the nests; the alternative of clustering of nesting sites was of no interest.

We suppose the nearest nest to the ith nest in the collection of n nests to be at a distance d_i. Three test statistics were used initially:

$$\text{MSD} = \sum_{i=1}^{n} d_i^2/n$$

(Mean Square Distance) (1)

$$\text{SCVSD} = \frac{\sum_{i=1}^{n} d_i^4 - \left(\sum_{i=1}^{n} d_i^2\right)^2/n}{(n-1)\left(\frac{\sum_{i=1}^{n} d_i^2}{n}\right)^2}$$

(Square of coefficient of variation of d_i^2) (2)

$$\text{GMASD} = \frac{\left(\prod_{i=1}^{n} d_i^2\right)^{1/n}}{\left(\frac{\sum_{i=1}^{n} d_i^2}{n}\right)} \quad \left(\frac{\text{Geometric mean of } d_i^2}{\text{Arithmetic mean of } d_i^2}\right) \quad (3)$$

MSD, and mean linear distance to nearest neighbour, have been widely used in studies of this kind (Pielou (1969)); SCVSD was suggested by Eberhardt (1967), although he gave no method for significance testing; GMASD has been proposed by Moran (1951) in the context of renewal processes. The motivation of the first statistic has been dealt with extensively; the second is intuitively reasonable (regularity is indicated by little variation in nearest neighbour distances, in which case SCVSD will be small), and the motivation of the third involves a Gamma distribution model. For a random sample of nearest neighbour distances for an unbounded 2-dimensional Poisson Process, d_i^2 has an exponential distribution. A commonly used 2-parameter generalisation of this is the Gamma distribution:

$$f(t) = \frac{t^{k-1} e^{-t/\mu}}{\mu^k \, \Gamma(k)}$$

(if $k = 1$, reducing to exponential form). This form of the Gamma distribution is very flexible and could, for appropriate values of k, simulate the distribution of d_i^2 for arrangements of points with moderate regularity or clustering. The uniformly most powerful t2st of the null hypothesis $k = 1$ (i.e. Poisson process) against an alternative $k > 1$ is based on the test statistic GMASD. This model also connects statistics SCVSD and GMASD: the former is related to the moment estimator, and the latter to the maximum likelihood estimator, of k.

However, the sampling distributions of these statistics under the null hypothesis are impossible to obtain analytically or numerically in a region with an arbitrary boundary. In this paper they were estimated by computer simulation of the process of dropping n points at random in the region under study, and repeatedly evaluating the three statistics. Although the significance levels associated with a particular sample could not be determined exactly by this process, the approximations derived are likely to be sufficiently reliable for practical purposes. For example, if the estimated significance level were 0·05, then a 95% confidence interval on the true significance level would be 0·05 ± 0·02 if based on 400 simulations, or 0·05 ± 0·03 if based on 200 simulations.

Interpretation of results

(1) Significantly high values of GMASD and low values of SCVSD indicate *local regularity*. These two statistics have high power to detect local regularity, even when the pattern is clustered globally, provided the clusters contain more than one nest. Tests based on MSD are more affected by global pattern, which was of only secondary interest in this investigation.

(2) The boundaries could not be determined exactly in these surveys, and it was important to know how sensitive the analysis was to errors in determining the boundaries. Along with the reason given in (1), MSD was rejected as a possible test statistic because its sampling distribution is very sensitive to errors in determining the total area contained within the boundary, as well as its shape. SCVSD and GMASD are both slightly sensitive to small errors in the shape, but are independent of the area. Some simulation studies with rectangular shapes and chequer-board patterns indicate that, as the shape becomes less 'compact' (i.e. (boundary length)^2 for a given area included increases), the sampling distribution of SCVSD is shifted to the right and that of GMASD to the left i.e. away from the tails of the distributions used in determining the critical regions for a test against an alternative of regularity. If the boundary shape used in the test was more 'compact' than the actual boundary shape, the tests would therefore be conservative against an alternative of regularity. In order to check the results obtained using the best estimate of the boundary shape, possible errors in boundary estimates were recorded, and the most 'compact' boundary possible within these margins of error used in further simulations.

(3) For one case (Tufted Duck), the significance tests for GMASD and SCVSD do not agree, even approximately. Approximate power curves constructed by simulation indicate that, for some regular alternatives (bivariate normal deviations of different variances about a square lattice), the tests have approximately equal power in general. Some pilot studies suggest that SCVSD is less robust to the inclusion of isolated points in the sample than is GMASD (as might arise by there being only one suitable nest site in a fairly large area of habitat). Four Tufted duck nest sites lying at the upper and lower extremities of the area are isolated and, although not formally correct, further tests were performed after excluding these four nests to help with interpretation of the conflicting GMASD and SCVSD significance levels.

A more detailed discussion of the methods used will be published later.

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