Second-brooding in semi-captive Barnacle Geese

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The precise integration of physiological state and behaviour with annual cycles in the environment is of great adaptive value. Many studies have shown that changes in circulating levels of hormones are important in ensuring the normal sequence of events and behaviour during the breeding season in waterfowl (Campbell *et al.* 1978; Balthazart & Hendrick 1981; Dittami 1981; Dawson & Goldsmith 1982). This note describes a phenomenon hitherto unrecorded for geese; that of the laying of a clutch of eggs while rearing young from a previous clutch. Copley (1963) described such an occurrence in a pair of Black-necked Swans *Cygnus atratus*. The pair produced a second clutch of five eggs while caring for a cygnet from a previous clutch. However, midway through incubation the pair rejected the cygnet, preventing it from approaching the nest. There have been a few other examples among captive swans (Kear 1972 and pers. comm.).

Study site and methods

The Wildfowl Trust at Slimbridge, Gloucestershire, in southern England, maintain a free-flying flock of more than 200 Barnacle Geese *Branta leucopsis*. The flock was established from several wild birds in the early 1960s and has now bred through a maximum of five generations. The birds nest within a 40 ha area which is surrounded by a fox-proof fence. They are provided with grain twice a day, together with a high protein supplement before and during the breeding season. This is in addition to a grass diet gained from grazing high quality lawns. All geese are marked with plastic leg bands which are engraved with unique number and letter combinations.

The geese were observed intensively throughout the nesting period; the dates of egg laying and other nesting parameters were routinely recorded. Hormone levels were determined by radio-ammunoassay. Plasma was separated from blood samples and analysed at Bristol University by a team led by Prof. B. K. Follett.

Results

During 1980 and 1982–5 five different pairs of Barnacle Geese laid a second clutch after successfully rearing a gosling(s) from a first clutch (Table 1). One pair has shown this behaviour twice. These second clutches have been termed "second-broods". Two females, D2 and UT, hatched their second clutches and reared goslings from both broods together. The second-brood goslings of CV/D2 died before fledging, but TC/UT reared goslings from their first and second broods to maturity.

The goslings in the first brood and the males usually remained close to the nest while the female laid and incubated the second clutch of eggs (Fig. 1). Although incubation extended into the normal

Table 1. Data on first clutches and second-broods for pairs of Barnacle Geese in the years 1980 and 1982–5 at the Wildfowl Trust, Slimbridge.

			FIRST CLUTCH					SECOND-BROOD			
Year	Pair M/F	Age M/F	Date 1st egg day/mnth	Clutch size	Hatch date day/mnth	No. reared	Renesting interval	Date 1st egg day/mnth	Clutch size	Hatch date day/mnth	No. reared
1980	CV/D2	13/10	27/4	5	30/5	1	24	23/6	6	25/7	0
1982	TC/UT	2/3	15/4	5	13/5	2	30	11/6	3	09/7	3
1983	LG/PP	7/7	10/5	6	13/6	1	33	15/7	6	–	0
1984	UH/GL	5/9	16/4	5	15/5	5	31	15/6	?	–	0
1985	VA/UJ	6/5	25/4	5	25/5	1	36	1/7	4	–	0
1985	LG/PP	9/9	28/4	7	1/6	1	28	29/6	4	–	0

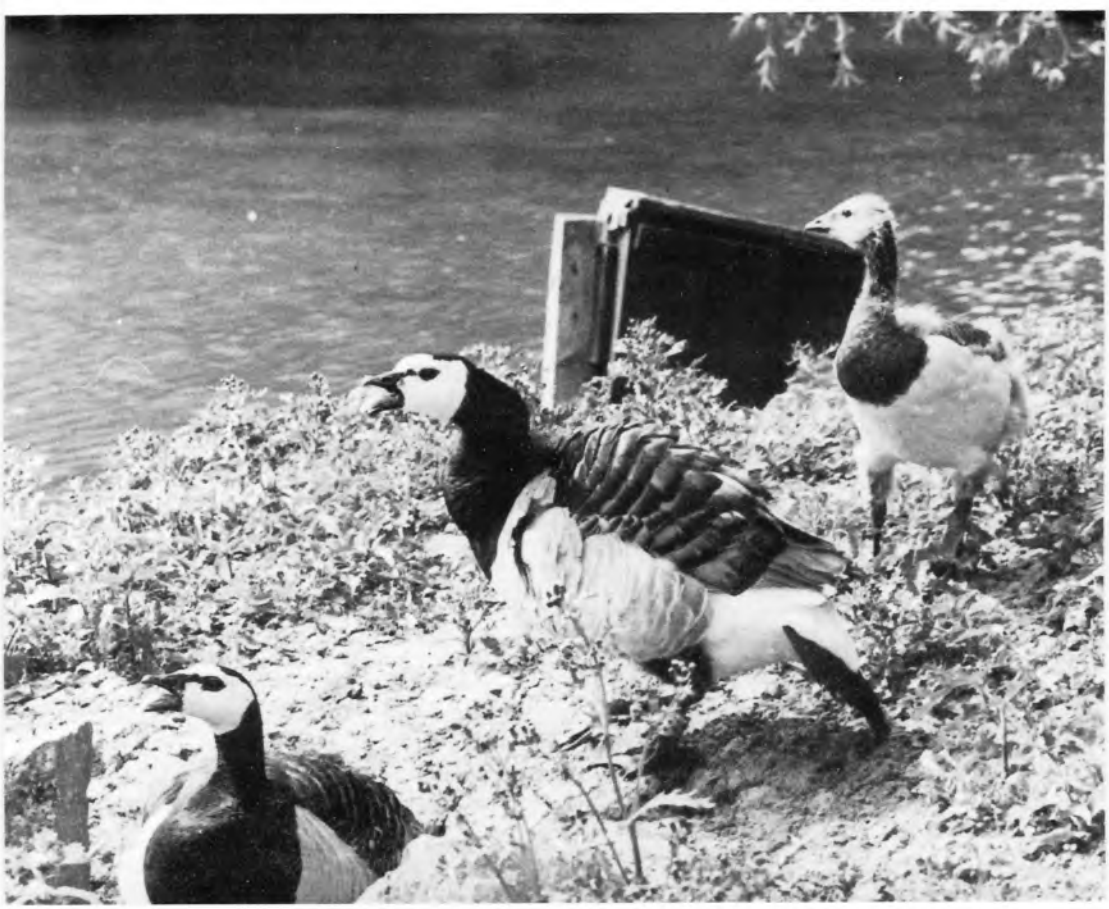
moulting period for the remainder of the flock, all females delayed moult until after incubation. However, the male CV in 1980, and VA in 1985, accompanied by their goslings from the first clutch, left their females during incubation and fed with the rest of the flock away from the nesting area. These males moulted their primaries while their females were incubating the second clutch; VA was flightless by the fourth day of incubation.

It would be expected that the presence of the gosling(s) would stimulate a hormonal condition in the parent birds that would prohibit renesting. The pattern of secretion of Luteinising Hormone (LH) in adults successfully rearing goslings from the first clutch but not renesting is shown in Fig. 2. Also shown is the relative time of laying of the first egg of the second-brood in the pairs described. Clearly these clutches were laid at a time when, in normal successful breeders, LH levels are low.

Usually second clutches in waterfowl are laid, if at all, when first clutches are destroyed or removed. Renesting after the loss of the first clutch is a common occurrence in Barnacle Geese at Slimbridge. In pairs renesting, a close positive correlation ($r = 0.729$, $P < 0.001$) has been found between the duration of incubation and the time taken to renest. Interestingly, of the 6 second-broods, 5 were laid after longer renesting intervals than that expected for pairs renesting due to clutch loss after a full term incubation. This may be due to the inhibitory effect of having a brood.

In the Bar-headed Goose *Anser indicus* elevated levels of prolactin have been found in parent birds (Dittami 1981). Prolactin is known to have an inhibitory effect on LH secretion. In the Mallard *Anas platyrhynchos*, prolactin levels increased during incubation coinciding with a pronounced drop in LH secretion (Goldsmith &

Figure 1. One of the second-brooding pairs in 1985 – VA and UJ – at the nest with their gosling from the first clutch. Note that VA is flightless, having moulted all the primary feathers of its wings.



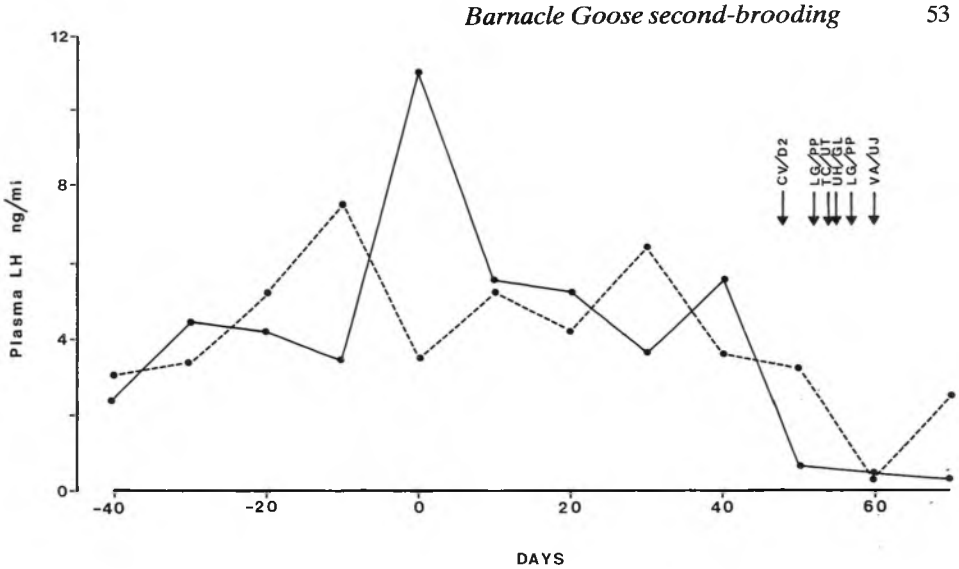


Figure 2. The pattern of secretion of Lutenising Hormone (LH) in adult male (dashed line) and female (solid line) Barnacle Geese in captivity at Slimbridge (N = 6 for both sexes). The figures on the X axis are the number of days before and after the laying of the first egg (0). Also shown are the relative dates of the first egg of the second-brood pairs.

Williams 1980), and injections of prolactin delayed renesting in the Barbary Dove *Streptopelia risoria* (Cheng 1977).

Photo-refractoriness prevents breeding attempts late in the season when it may be disadvantageous to do so (Lofts & Murton 1968). Due to the very short breeding season experienced by arctic nesting geese, second clutches are rarely observed in wild populations. Photo-refractoriness would certainly be expected to prevent late second clutches in pairs which had been unsuccessful first clutches and is probably also effective in preventing further breeding attempts in pairs rearing goslings from their first clutch.

Neither of the systems which control the reproductive cycle, parental hormones or photo-refractoriness, appears to inhibit the production of second-brood in the individuals described. There are two possible explanations.

Assuming that the genotypes of the captive birds are not markedly different from those in the wild, it appears that the environment in captivity in southern England allows the possibility of second-broods. This environment differs from that of arctic breeding area with respect to climate, the availability of food and the photoperiodic cycle. The attainment of nutrient reserves is an important factor in the control of reproduction in geese (Ankney & MacInnes 1978). The plentiful food supply at Slimbridge enables birds to regain the level of condition necessary for breeding. This may over-ride the inhibitory effects of parental hormones and of photo-refractoriness. It is difficult to predict the effect of the photoperiodic cycle of southern England on the onset of photo-refractoriness, perhaps it is delayed and may not now prevent renesting. Murton and Westwood (1977) suggested that anatids which require very long photoperiods before achieving full gametogenetic development may not exhibit true refractoriness under the short daylengths experienced in late summer in temperate latitudes. However, if altered environmental conditions were the only factors involved in the production of second-broods, they would be expected to occur more frequently.

An alternative explanation is that due to reduced selection pressures in captivity, birds with genetic changes in their control systems have survived. The hormonal condition of the parent bird may no longer

preclude renesting. Donham (1979) suggested that photo-refractoriness may be modified in domestic Mallard to allow an elongated breeding season. If second-brooding were due to genetic changes birds exhibiting the trait would be expected to be related. However, of the five different pairs only two are closely related. Further, male CV was brought to Slimbridge from Greenland as a gosling in 1967; one of the second-brood females, GL, is the daughter of CV and D2; and the vast majority of the Slimbridge geese have been parent-reared in the flock. The geese at Slimbridge are therefore only a few generations removed from wild stock which suggests that they may not be genetically very different from wild birds.

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Summary

Five different pairs of Barnacle Geese *Branta leucopsis* from a flock of 200 free-flying birds at the Wildfowl Trust in southern England each produced a second clutch of eggs while rearing goslings from the first clutch. "Second-brooding" occurred in five of the six years 1980 to 1985. Only two of the pairs were closely related and one of the males originated from an egg taken from the wild. In two cases, the second clutch was incubated to hatching and goslings from the two broods reared as one family.

This phenomenon, hitherto unrecorded in geese, could never occur in arctic-breeding geese in the wild because of the shortness of the season and limited food supply. It is suggested that a superabundant food supply enables these geese quickly to regain breeding condition following the hatching of the first clutch. This evidently over-rides the suppressing effects of parental hormones. An unnatural photoperiodic cycle at southerly latitides may also contribute by causing a failure of the geese to become photo-refractory after completing one nesting cycle.

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