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Clutch sizes and hatching success of Canada geese nesting in Canterbury, New Zealand

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Dedicated to Earnest Selwyn Bucknell (Buck) 1926–2001, outdoorsman, colleague, tutor, and friend.

Abstract: Nesting outcomes of Canada geese (*Branta canadensis maxima*) in Canterbury, New Zealand were recorded from a sedentary population nesting at coastal Lake Forsyth (1967–70) and from a seasonally migratory population nesting in headwater valleys of the Waimakariri River (1966–80). Mean clutch size in 462 Lake Forsyth nests was 5.3 (*sd* = 1.3) eggs, with clutches of 4, 5, and 6 eggs comprising 17%, 30% and 30% respectively of the total. Goslings hatched from 67.4% of 1,602 eggs in 298 monitored nests, and the entire clutch hatched successfully in 42.6% of the monitored nests. Mean productivity at hatching was 3.6 (*sd* = 2.3) goslings per nest. Mean clutch size in 1,211 Waimakariri River headwaters nests was 4.5 (*sd* = 1.3), with clutches of 4, 5, and 6 eggs comprising 25%, 32%, and 20% respectively of the total. Goslings hatched from 63.3% of 3,952 eggs in 871 monitored nests, and the entire clutch hatched successfully in 30.5% of the monitored nests. Mean productivity at hatching was 2.9 (*sd* = 1.9) goslings per nest. Relative to Canada geese in their native North American range, geese nesting at Lake Forsyth laid clutches of similar size, had similar hatching success but higher nest success whereas geese nesting in the Waimakariri River headwaters laid, on average, conspicuously smaller clutches, had similar hatching success, but higher nest success.

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INTRODUCTION

Following an importation of 50 birds in 1905, and a plethora of liberations of their captive-raised progeny, wild populations of Canada goose (*Branta canadensis maxima*) soon established in scattered headwaters of New Zealand's eastern South Island rivers, from North Canterbury to central Otago (Imber & Williams 2015). As their numbers increased, so did the antipathy of pastoral farmers on whose lands the birds grazed, the geese being viewed as grazing competitors with their farm stock, polluters of pastures, and damagers of newly-sown grass and of autumn-saved pastures being withheld to support stock through winter. Introduced to provide sport for hunters, the goose's troublesome feeding choices saw it declared unprotected in 1931, merely 25 years after its introduction. While not an auspicious start to life in a new land, it was, nevertheless, a portent of the travails to follow, and

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which persist to this day (McDowall 1994; Spurr & Coleman 2005; Williams 2011).

The persistent challenge for historic wildlife management agencies (Acclimatisation Societies, Wildlife Service of Department of Internal Affairs) was to limit Canada goose populations to numbers pastoral farmers could reluctantly tolerate but which also ensured adequate sporting opportunity for gamebird hunters. Population "control" was attempted, mainly, by pricking or destroying eggs in nests of geese breeding in headwater valleys of some Canterbury rivers (e.g. Waimakariri, Poulter, Rakaia, Wilberforce, Harper, Avoca), by culling of moulting birds, and, between 1963–72 by late-summer hunting at Lake Ellesmere and in its environs, including at Lake Forsyth (Imber & Williams 1968).

Canterbury's Canada goose population was, by the 1960s, perceived to be seasonally migratory. It was known that most nesting occurred in headwater tributary valleys of major Canterbury rivers, especially Waimakariri River, and once nesting and brood rearing had been completed, the geese dispersed to autumn and winter pastoral and lake-side habitats at lower elevations, or to coastal wetlands (Imber 1971a, 1985). The Canterbury-wide population at this time was estimated to be *c.* 20,000 (Imber 1971a) and the majority were thought to share an annual residency at Lake Ellesmere (Te Waihora) on Canterbury's east coast. It was at this lake that many failed breeders, non-breeders and pre-breeding geese of this population moulted each year, and to which many successful breeders brought their fledglings in late February-early March annually. A small (400–500) and presumed sedentary population of Canada geese resided at adjacent Lake Forsyth.

To assess the reproductive performance of Canada geese coincidental with the attempted "control" measures, nesting studies were initiated by the former New Zealand Wildlife Service (NZWS). Records of these studies, at Lake Forsyth 1967–70 and in Waimakariri River headwaters (Esk River and Cox River catchments) 1966–80, were lodged in (now archived) files of the NZWS (IAD 25/4/10) where they remained unevaluated. Retrospectively, and to the extent that the archived records allow, we summarise these nesting records, the only nesting study of Canada geese in New Zealand to date.

STUDY AREAS

Lake Forsyth (Te Roto o Wairewa) is a small (620 ha), shallow and hypertrophic barrier-bar lake impounded by coastal gravels at the south-western flank of Banks Peninsula (43.805°S, 172.741°E) and lies 4 km east of Lake Ellesmere. From within a catchment of 108 km^2, it is fed by the small Okana and Okuti Rivers (which coalesce to form the short Takiritawai River) and by drainage from its flanking hills. Its catchment is entirely of steep pastoral slopes. Resident geese nested on the lower 100 m of the steep pastoral slopes on the lakes' eastern flank and grazed pastoral flats at the head of the lake (Fig. 1).

Figure 1. Lake Forsyth looking south towards its terminal barrier and coast. Arrows delimit Canada goose shoreline nesting area. A sliver of Lake Ellesmere, 4 km distant, is visible in upper right corner of this image. Photo: Kelvin Nicholle.

The Waimakariri River headwaters study area (hereafter referred to as "headwaters") included three sites within the tributary catchments of Esk River and Cox River. Within the Esk River catchment, the broad dry alluvial terraces, and boggy flats, of the tributary Pūkio Stream (pre-2016 name Nigger Stream) adjacent to Little Flora Knoll (42.962°S, 172.067°E) and about Flora Stream (42.950°S, 172.054°E) were where nest searches were concentrated initially. This comprised a terrace of 2.52 km^2 and boggy flats 1.85 km^2 in extent, both at an altitude of 750 m. Surveys extended over 5–10 km of main stem Esk River's extensive braided flats (Fig. 2) and those of tributary streams (650–700 m altitude), mostly upriver from the river's confluence with Ant Stream (42.955°S, 172.116°E). The section of Cox River valley surveyed was at 650 m altitude, and comprised 2.27 km^2 of braided river flats extending upriver of Ball Creek Hut (42.893°S, 171.968°E) to Montgomery Stream (7 km) and approximately 2 km downriver of the hut in a valley that, but for an ancient landslide, was an extension of the Pūkio Stream valley.

Figure 2. Esk River valley, looking upriver from near the river's confluence with Pūkio Stream. Photo: J.S. Adams

The two nesting areas contrasted climatically and topographically. At Lake Forsyth September – November temperatures averaged 9–12°C, and rain about 11 mm monthly. Orientated SW–NE, the lake's narrow valley funnels winds averaging 16 km/h. The headwaters area comprised broad (1.5–2.0 km) sub-alpine valleys flanked by ridges rising 500–600 m above the valley floors. Mean daily September – November temperatures averaged 5.5–10°C with 10–14 mm of precipitation monthly, including snowfalls which, in most years, extend to mid-October.

METHODS

Prior banding

The study was supported by annual banding of geese moulting at Lakes Ellesmere and Forsyth. Banding at Lake Ellesmere commenced in 1957 (Imber & Williams 1968) but only after 1966 were yearlings discriminated (by bursa probing: Elder 1946) and colour banded to denote year class. Additionally, and commencing in 1969, tags were inserted in the webs of newly-hatched goslings at the headwaters nesting sites allowing those caught the following year, or later, moulting at Lake Ellesmere to have coloured leg bands applied to denote year class. Banding commenced at Lake Forsyth in 1966 where, annually, most of each year's cohort of goslings were captured (and colour-banded to denote year class) together with their moulting parents and some pre-breeders. The colour bandings at both moulting sites, and web-tagging of goslings, were to allow ages of nesting birds to be identified in the field.

Nesting study

Visits to the study areas commenced once nesting was well underway (Lake Forsyth, mid-October) or when spring thaw of winter snow permitted vehicular access to the remote headwaters sites, which was seldom before the third week of October. Observers were continuously present in the headwaters sites until approximately 20 November each year, whereas at Lake Forsyth the nesting area was visited for 3-day periods usually four times between 12 October and 20 November.

Initial nest searches comprised methodical pattern searches of the landscape and all nests detected were indicated with markers of some kind e.g. colour-tipped bamboo stakes, marking tape on nearby conspicuous vegetation etc. Once located, the nest was revisited on subsequent days to confirm laying had ceased (and thus clutch completed), thereafter infrequently during incubation sufficient to assess egg fertility (by field candling: Weller 1956) and deduce likely hatching date, and then, near and during hatching, daily to confirm hatching success. Where goslings hatched and departed a marked nest without being observed, hatching outcome was assessed from number of egg-shell membranes and unhatched eggs present in or alongside the nest bowl.

Details of colour bands observed on nesting adults were recorded alongside their breeding records, and banded non-breeding geese observed were recorded also.

For 1977–80 inclusive, the approximate location of all surveyed nests within Pūkio Stream and Cox River were plotted on large-scale field maps (1:31680 = 2 inches-to-the-mile). These maps were too crude to allow inter-nest distances to be calculated but the margins of the surveyed areas were sufficiently well defined on the maps to allow a coarse estimation of nesting density. For Pūkio Stream, this was done by constructing a minimum convex polygon to encompass all nests and calculating its area using Google Earth measuring tool; for Cox River, the area of riverbed surveyed was consistently 2.27 km^2. No nest location maps were compiled for the Esk River study site, nor for Lake Forsyth. However, at Lake Forsyth, the 100 m contour along 2.5 km of the its eastern shore delimited almost all nest placements (see Fig. 1) and this area was also calculated using the Google Earth measuring tool.

The data set

Nest records from Lake Forsyth were accumulated over four summers 1967–70 inclusive. The annual nest summaries and field notebooks provided dates of nest visits and details of nest content at each viewing. Nest status (e.g. laying, incubating, abandoned, hatched) was reported and an assessment of egg fertility was recorded, usually when incubation had extended for at least one week. The number of nests monitored annually

(105–123) was considered to comprise most nesting attempts at Lake Forsyth.

Archived nest records from the headwaters area were from 1966 to 1980 but varied between the three valleys and in their completeness between years. For Pūkio Stream, complete nest records were for 1966–68, 1971–73, 1975, 1977–80 with summarised data reported for 1974 and 1976. For Esk River, complete nest records were from 1977–80 with summarised data for 1971–73. For Cox River, complete nest records were from 1976–80 with summarised data for 1971–74. Complete nest records provided details of dates of nest visits, details of nest content at each viewing, and nest status (laying, incubating, abandoned, hatched). An assessment of egg fertility was recorded soon after incubation had commenced (consistently only for Pūkio Stream nests). Summarised data reported numbers of nests encountered, mean clutch size, and sometimes mean number hatched per nest (there are no hatching records for Esk River and Cox River sites other than 1977–80 inclusive). Nest records from all three valleys have been amalgamated for this analysis.

Definition of terms

Key terms used in this account are: clutch size – the maximum number of eggs observed in a nest; number hatched – number of goslings that emerged completely from eggs in the nest; hatching success – percentage of eggs from which a gosling emerged (equivalent to egg success in some literature); nest success – percentage of total nests in which one or more eggs hatched.

RESULTS

Nesting environment and nest density

At Lake Forsyth most nests were constructed on sloping ground and in association with low vegetation e.g. rushes (*Juncus* spp.) or small prostrate herbs/shrubs in an otherwise pastoral environment. Narrow ledges on the slopes and bared areas of former small landslips were common nest sites. Most nest sites afforded the incubating and guarding adults a wide uninterrupted view. No nest density assessment was reported but nests were scattered along approximately 2.5 km of the lake's south-eastern hillside (see Fig. 1) and at low elevation (< 100m above lake level). In effect, all nests were established within a long, narrow hillside area of approximately 0.4–0.6 km^2, equivalent to a density of approximately 200 nests/km^2. It was a quasi-colonial distribution despite some altitudinal separation between nesting pairs and the hillside and shoreline indentations ensuring many nests were established out of direct sight of others.

Nest sites of headwaters geese were all on the valley floors and affording a wide vista. The Pūkio Stream nesting environment, especially the alluvial terrace, had a patchy covering of *Halocarpus bidwillii* shrubs amongst extensive grassland comprised of *Agrostis capillaris, Festuca novae-zelandiae, Anthoxanthum odoratum* and *Holcus lanatus. Chionocloa rubra* was prominent on the boggy flats (Hustedt 2002). Most nests were associated with low or prostrate herbs in dry sites (Fig. 3) and with *Carex* spp. and *Poa cita* in wet areas. Nests established on the Esk River and Cox River flats were often on bare shingle but associated with woody debris, small hummocks of river sediment, or sparse plant clumps. Although nests were widely distributed and proximity of neighbours highly variable (as interpreted from the nest distribution field maps), the overall nest density in years 1977–80, was 20–30 nests/km^2. Within Pūkio Stream valley, nest density on the drier alluvial terrace was more similar across these four years (range 23.1–27.5 nests/km^2) than on the boggy flats (range 18.3–35.1 nests/km^2). On the Cox River flats, the range of nest densities was 18.5–25.6 nests/km^2. It was not possible to deduce nest density on the Esk River flats from the filed records nor the precise limits of the surveyed area in any year.

Figure 3. Typical headwaters nesting environment on the dry valley floor of Pūkio Stream. Photo: J. L. Kendrick, NZ Wildlife Service.

Nesting chronology

Initial visits to both study sites post-dated the commencement of nesting in every year.

At Lake Forsyth, initial visits in each year 1967–70 were between 12–15 October. At this time 79%, 48%, 84%, and 84% of the nests in 1967, 1968, 1969, and 1970 respectively from which clutch size information was obtained were active, most of which at that time (83%, 62%, 70% and 74% respectively) were being incubated. Only in 1968 were new nests (6) established later than 25 October.

The timing of snow thaw and ability to traverse challenging vehicle tracks meant access to headwater areas was rarely possible prior to 23 October, by which date the first eggs were beginning to hatch (see hatching results below). Of 705 nests monitored in Pūkio Stream valley across all years of study, just 39 (5.5%) were established later than 27 October.

Clutch size

Lake Forsyth

Over four years 1967–70, clutch sizes in 462 nests averaged 5.3 (*sd* = 1.3) eggs and ranged from 1 to 10 eggs (Table 1). Clutches of 5 and 6 eggs were the most common, each 30% of total clutches. Clutches of 1 and 2 eggs (4 and 6 nests respectively) were all recorded as being incubated but, as with all nests, prior egg loss cannot be excluded. For larger clutches of 8–10 eggs (14 nests) there was no record to indicate any comprised eggs from multiple females.

Variability in mean annual clutch size ranged from 5.1 (*sd* = 1.4) in 1969 to 5.5 (*sd* = 1.0) in 1970. The mean clutch size in 1969 was significantly lower than in the previous or subsequent year (1968 v. 1969, $z = 2.261$, $P = 0.023$; 1969 v. 1970, $z = 2.964$, $P = 0.003$) but not 1967 ($z = 0.643$, $P = 0.520$), and was a consequence of the higher number of 4-egg clutches laid in 1969 (Table 1). Clutches of ≤4 eggs comprised 27.6%, 21.1%, 30.8%, and 14.9% of total known clutches across the four years, and 23.6% overall.

For female geese of known age, mean clutch sizes were 4.7 (*sd* = 1.5, n = 3) for 2-year-olds, 4.8 (*sd* = 0.9, n = 27) for 3-year-olds, and 5.3 (*sd* = 1.0, n = 15) for 4-year olds.

Headwaters

Between 1966–80, clutches in 1211 headwaters nests averaged 4.5 (*sd* = 1.3) eggs and ranged from 1 to 8 eggs (Table 2). Clutches of five eggs comprised almost one-third, and those of four eggs almost one-quarter, of total clutches. Clutches of 1 and 2 eggs (93 (7.7%) nests in total) were all recorded as being incubated. There were no records reporting a clutch had been contributed to by multiple females.

At Pūkio Stream, the only headwaters valley surveyed in all years, there was non-significant annual variability in mean clutch size of nests (Table 3) (e.g. 1967 v. 1971, $z = 1.816$, $P = 0.069$, *NS*)

Mean sizes of clutches of females of known age and found 1977–80, were 3.0 (*sd* = 1.6, n = 5) for 3-year-olds, 4.1 (*sd* = 0.8, n = 8) for 4-year-olds, and 5.0 (*sd* = 0.9, n = 19) for >4-year olds. Three 2-year-old females were recorded alongside sparse nest bowls which never contained eggs.

Table 1. Annual and overall percentage frequency distribution of clutch sizes, and annual and overall mean ($\bar{x}$, *sd*) clutch sizes of Canada geese nesting at Lake Forsyth 1967–70.

Clutch size	Year				All years
	1967	1968	1969	1970	
1	2.9	0	0.8	0	0.9
2	2.9	0.8	1.7	0	1.3
3	4.8	7.3	5.8	0.1	4.8
4	17.1	13.0	22.5	14.0	16.7
5	24.8	28.5	32.5	34.2	30.1
6	31.4	31.7	24.2	35.1	30.5
7	14.3	13.0	10.0	14.0	12.8
8	0.9	4.1	2.5	1.8	2.4
9	0	0.8	0	0	0.2
10	0.9	0.8	0	0	0.4
$\bar{x}$	5.2	5.5	5.1	5.5	5.3
sd	1.5	1.4	1.3	1.0	1.3
n	105	123	120	114	462

Table 2. Percentage size frequency distribution of 1,211 clutches of Canada geese nesting at three Waimakariri River headwaters valleys 1966–80 (combined data from Pūkio Stream 1966–68, 71–73, 75, 77–80; Esk River 1977–80; Cox River 1976–80).

Clutch size	1	2	3	4	5	6	7	8
Frequency (%)	0.6	7.1	12.5	24.8	32.1	20.2	2.5	0.2

Table 3. Mean ($\bar{x}$, *sd*) annual clutch sizes of Canada geese nesting at Pūkio Stream 1966–80. (nr = not recorded).

year	1966	1967	1968	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980
$\bar{x}$	4.5	4.2	4.6	4.7	4.3	4.5	4.3	4.4	4.7	4.4	4.4	4.5	4.4
sd	1.0	1.3	1.0	1.2	1.3	1.3	nr	1.2	nr	1.0	1.1	1.3	1.1
n	42	45	32	50	47	59	47	61	57	58	66	54	90

Comparison between areas

Mean clutch size at Lake Forsyth was significantly larger than at any one of the three headwaters sites, and all headwaters sites combined (z = 11.51, P < 0.001). When this comparison is restricted to the two years when data were collected from both areas coincidentally (1967, 1968), mean clutch size at Lake Forsyth was 5.4 eggs (sd = 1.4, n = 228) and at Pūkio Stream 4.3 eggs (sd = 1.2, n = 77), a highly significant difference (z = 5.91, P < 0.001).

A principal difference between the two study areas was in the proportions of small clutches, i.e. those containing ≤4 eggs (Lake Forsyth 23.7%, headwaters 45.0%) and ≤3 eggs (Lake Forsyth 7.0%, headwaters 20.2%; Tables 1,2).

Hatching

Lake Forsyth

Visitation frequency and duration did not allow a hatching chronology to be compiled. However, no hatchings were recorded prior to 25 October in any year but by 10 November annually, eggs had hatched in 47–74% of monitored nests.

Over the four years combined, hatching outcomes were recorded for 298 nests (Table 4); these nests contained 1,602 eggs, of which 1,079 (67.4%) hatched, an overall mean hatch per nesting attempt of 3.6 (sd = 2.3) eggs.

In 127 (42.6%) nests all eggs hatched and in 59 (19.8%) nests none hatched. Of the latter, 32 were recorded as being "abandoned", including consequent to cattle trampling the nest (3), and "predation" (27). References to some nests being "abandoned/predated" indicates these were not necessarily exclusive categories.

In 112 (37.6%) nests, which in total contained 629 eggs, less than the full clutch hatched. In 48 nests just 1 egg failed to hatch of which 17 contained a near full term embryo, 16 a gosling that was unable to emerge completely from its shell, and 15 recorded as "addled" or "infertile". In 64 nests multiple eggs failed to hatch successfully (191 (52.5%) of 364 eggs); of 106 egg fates recorded, 18 goslings failed to emerge, 24 eggs contained a near full-term embryo, 25 were early embryo deaths, and 39 recorded as "infertile" or "addled". Reported scavenging and predation by black-backed gulls (*Larus dominicanus*) of eggs remaining in recently hatched nests suggests the status of some unhatched eggs may not have been identified.

There was no consistent evaluation of egg fertility; many nest records were devoid of a fertility assessment, some reported evaluations of unhatched eggs only, while in others, assessments were at variable times during the laying-incubation periods. However, there were 138 nests whose total of 741 eggs were candled to determine evidence of embryo development during days 10–24 of the incubation period; 586 (79.1%) eggs were recorded as "fertile".

Hatching rates (percentage of eggs hatching) were significantly lower in nests containing small clutches (2–3 eggs) than in all others (e.g. in 5-egg clutches, χ^2 = 14.18, P < 0.001), and was a consequence of their higher nest failure (Table 4). In 13 (68%) of 19 2–3 egg clutches no eggs hatched compared to 14 (10%) of 140 6–7 egg clutches, a significant difference (χ^2 = 7.08, P = 0.008). Hatching success in 5-egg clutches was significantly lower than in 6-egg (χ^2 = 25.33, P < 0.001) and 7-egg (χ^2 = 21.09, P = 0.0001) clutches, a statistical outcome arising from the higher whole clutch failure within this cohort (Table 4).

Hatching outcomes from nests of known age females were: 2-year-olds, n = 3, 1 partial hatch (3 of 5 eggs), 2 failed; 3-year-olds, n = 13, 2 complete hatch, 9 partial hatch (33 of 43 eggs), 2 failed; 4-year-olds, n = 6, 2 complete hatch, 4 partial hatch (16 of 20 eggs); older females, n = 12, 6 complete hatch, 4 partial hatch (17 of 23 eggs), 2 failed.

Table 4. Hatching outcomes relative to clutch size, and overall, in 298 Canada goose nests at Lake Forsyth, 1967–70.

Clutch size	All nests			All hatch		None hatch	
	No. nests	No. eggs	% eggs hatching	No. nests	% all nests	No. nests	% all nests
2	3	6	33.3	1	33.3	2	66.7
3	16	48	31.3	5	31.3	11	68.8
4	50	200	64.5	21	42.0	10	20.0
5	83	415	58.6	32	38.6	21	25.3
6	97	582	73.7	45	46.4	9	9.3
7	43	301	75.1	21	48.8	5	11.6
8–10	6	50	70.0	2	40.0	1	20.0
Totals	298	1,602	67.4	127	42.6	59	19.8

After hatching, almost all broods of young goslings and their attendant adults congregated on pastoral flats at the head of the lake feeding as a flock or as large creches.

Headwaters

The continuous presence of observers during the nesting period allowed a hatching distribution to be compiled (Fig. 4); in 68% of 725 successful (and assumed successful) nests eggs hatched in the first 12 days of November while, by 18 November, only in 16% of nests were eggs yet to hatch, thus indicating a high level of nesting synchrony. [An approximate nesting chronology can be deduced from this hatching distribution by taking into account an egg-laying frequency of 1 egg each 1.5 days and an average 28 days of incubation (Brakhage 1965); initial egg-laying in late September and peak egg-laying during 1–10 October is implied.]

Hatching outcomes were recorded for 871 nests (Table 5); these nests contained 3,952 eggs, of which 2,502 (63.3%) hatched, an overall mean hatch per nesting attempt of 2.9 (*sd* 1.9) eggs.

In 266 (30.5%) of nests all eggs hatched and in 141 (16.2%) nests none hatched. In the other 464 (53.3%) nests, which in total contained 2,199 eggs, less than the full clutch hatched. In 218 just 1 egg failed to hatch successfully and records of 154 of these report the unhatched egg contained a fully-formed gosling that had either failed to break the eggshell or could not escape from it (74), the egg was infertile or early embryo death had occurred (68), or the egg was broken or predated (12). In 246 nests multiple eggs failed to hatch successfully (668 (54.8%) of 1,220 eggs); of 301 egg fates recorded, 105 were "dead in shell" (gosling either failing to emerge successfully from egg or a full-term embryo not having pipped the egg), 28 were "early embryo deaths", and 168 recorded as "infertile" or "addled".

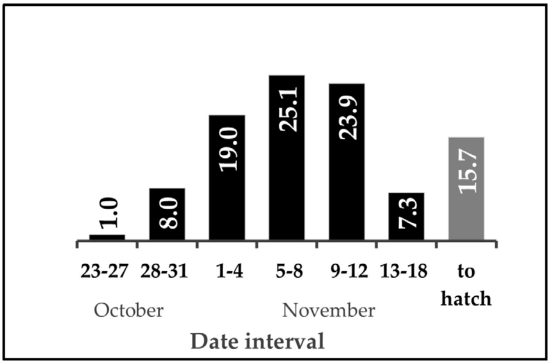

Figure 4. Percentage frequency distribution of hatching dates of 725 headwaters Canada goose nests, 1966–80.

Of the 141 (16.2%) nests that failed to hatch any eggs, 61 were abandoned (mostly during incubation) and 80 suffered apparent predation of some or all eggs both during egg laying and incubation (black-backed gulls were identified as an egg predator).

A fertility assessment of incubated eggs at Pūkio Stream 1971–73 recorded 511 of 571 (89.5%) eggs in 127 nests as "fertile".

Hatching rate (the percentage of eggs hatching) was similar across all clutch sizes (Table 5), except for 6-egg clutches being significantly higher than for 2-egg ($\chi^2 = 10.04$, $P = 0.0015$), 3-egg ($\chi^2 = 12.29$, $P = 0.0004$) and 4-egg ($\chi^2 = 11.99$, $P = 0.0005$) clutches, and 5-egg clutches exceeding that of 2-egg clutches ($\chi^2 = 5.34$, $P = 0.027$).

Across nine of the years between 1968–80, annual hatching rate in Pūkio Stream nests averaged 69.7% (*sd* = 7.5%), varying between 62.2% and 78. 5%.

Hatching outcomes from nests of known age females 1976–80 were: 3-year-olds, n = 4, 1 complete

Table 5. Hatching outcomes relative to clutch size, and overall, in 871 Canada goose nests at three Waimakariri River headwaters valleys combined, data from 1966–80.

Clutch size	All nests			All hatch		None hatch	
	No. nests	No. eggs	% eggs hatching	No. nests	% nests	No. nests	% nests
2	69	138	54.3	26	37.7	21	30.4
3	106	318	57.2	37	34.9	25	23.6
4	210	840	60.2	67	31.9	40	19.0
5	285	1,425	64.3	76	26.6	34	11.9
6	176	1,056	67.9	54	38.4	18	10.9
7–8	25	175	62.3	6	24.0	3	12.0
Totals	871	3,952	63.3	266	30.5	141	16.2

Table 6. Comparative hatching outcomes for Canada geese at Lake Forsyth and headwaters study areas. (Statistical comparisons: [1] $z = 4.73$, $P < 0.001$; [2] $\chi^2 = 14.51$, $P < 0.001$; [3] *NS*; [4] $\chi^2 = 8.14$, $P = 0.004$; [5] *NS*; [6] $\chi^2 = 5.08$, $P = 0.024$.).

Study area	No. of nests	$\bar{x} \pm sd$ hatchlings per nest[1]	% nests all eggs hatch[2]	% nests no eggs hatch[3]	Hatching rate (%)		
					in all nests[4]	in clutches ≤4 eggs[5]	in clutches 5–7 eggs [6]
Lake Forsyth	298	3.6 ± 2.3	42.6	19.8	67.4	57.5	69.2
Headwaters	871	2.9 ± 1.9	30.5	16.2	63.3	58.9	65.6

hatch, 2 partial hatch (3 of 6 eggs), 1 failed; 4-year-olds, n = 7, 2 complete hatch, 4 partial hatch (11 of 18 eggs), 1 failed; older females, n = 14, 2 complete hatch, 6 partial hatch (19 of 31 eggs), 6 failed.

In the early aftermath of hatching, goslings and their parents remained in discrete family units, mostly alongside each valley's watercourses.

Comparison between areas

Hatching outcomes differed between the two study areas (Table 6). Only hatching rate of clutches ≤4 eggs and percentage of nests in which no eggs hatched were similar whereas the differences for all other comparisons were statistically significant (Table 6). Additionally, amongst successful nests (those in which at least 1 egg hatched), the proportion in which all eggs hatched at Lake Forsyth (53.1%,) was significantly higher than in headwaters nests (36.4%; $\chi^2 = 20.82$, $P < 0.001$). The relative proportions of single to multi-egg failures in successful nests did not differ between the study areas ($\chi^2 = 0.62$, $P = 0.43$, *NS*).

DISCUSSION

Study context and intent

The field study reported here sought to record nesting outcomes of geese at a time when extensive "control measures" were being applied; egg pricking or whole nest destruction within some Canterbury headwater valleys (but not in Esk and Cox River valleys), widespread culls of moulting geese, hunting without kill limits during the annual gamebird hunting seasons (May–July), and, between 1963 and 1972, immediate post-moult hunting of the largest moult aggregation at Lake Ellesmere (also including Lake Forsyth). The study was intended to be complemented by an estimation of age-specific annual survival rates of geese from analyses of bands returned by hunters and from recaptures of already banded geese at moulting sites, thereby extending the analyses of Imber & Williams (1968).

The choice of two study areas, Lake Forsyth and Waimakariri River headwaters, was strictly pragmatic. Lake Forsyth was a readily accessible nesting and capture location whereas the headwaters valleys, where most nesting occurred, were remote and challenging to access. There was no prior expectation that nesting outcomes might differ between study areas other than, perhaps, as a consequence of their differing age structures (Imber 1971a). The single perceived difference between geese nesting at the two locations was their annual dispersion: Lake Forsyth geese were year-round residents whereas, after nesting, the headwaters geese dispersed across inland and coastal Canterbury, but mainly to Lake Ellesmere.

The anticipated importance of the age composition of nesting females was responded to by banding goslings at hatching or before fledging. At Lake Forsyth, following four years of banding all goslings before fledging, females 4-years old or younger comprised 21% of those nesting in 1970 but age-related breeding performances of only 45 females had, by then, accrued. A more prolonged period of annual banding of goslings was, at that point, considered necessary so the nesting study was stopped with the intent of recommencing four years later. Annual banding of goslings continuing to 1982 but, for reasons unrecorded, the nesting study was never recommenced.

The headwaters nesting study proved even more daunting in this respect. Between 1969 and 1977, 2,196 goslings were tagged at hatching but, by 1980, just 270 (12.3%) had been recaptured at Lake Ellesmere. Between 1967 and 1973, 1,569 yearling females were captured and banded with an age-denoting colour band at Lake Ellesmere. Despite this effort, known-aged females comprised a mere 5.9–7.4% of those nesting in the study area annually in years 1977–80.

While NZWS staff persisted with the headwaters nesting study throughout the 1970s, farmer agitation for a reduction in goose numbers ensured the focus on Canada goose management gradually shifted to annual aerial surveys across areas of inland Canterbury, increased culls of geese moulting at inland lakes, and to an assessment of grazing impact on farming economics (references in Spurr & Coleman 2005). In effect, the extensive nesting study reported here ceased to be directly relevant to contemporary goose management and the intended survivorship analyses were never pursued.

Interpreting between-area differences

A conspicuous outcome of the study was the differing clutch sizes and hatching outcomes at the two areas. Geese nesting at Lake Forsyth laid larger clutches, hatched more of their eggs in more of their nests, and thus were significantly more productive. Was this a consequence of different age structures of nesting females, or might other factors have contributed?

Age composition of nesting females

North American nesting studies (e.g. Brakhage 1965; Cooper 1978), confirm that young Canada geese lay smaller clutches than those of older age. Age-related clutch size data from this study, while minimal, are in accordance. Thus, small clutches (of ≤4 eggs), which were twice as frequent in headwaters nests than at Lake Forsyth, could indicate the presence of, proportionately, many more young nesters there.

One pathway by which a difference in age structure of nesters could have arisen was by restriction of breeding opportunity. At Lake Forsyth, high nesting density could have excluded young breeders from nesting amongst older, more dominant, and experienced nesters. By this means the relative contribution of young geese, with their smaller clutches, to the annual mean clutch size would be restricted. Conversely, the expansive headwaters nesting grounds may have imposed little or no restriction on nesting opportunity for young geese and, thus, their smaller clutches would contribute proportionately more to the overall annual mean clutch size. The significantly different proportions of clutches of ≤4 eggs in the two populations (Forsyth 23.6% (1967–70) *c.f.* headwaters 45.0% (1966–80), and Pūkio Stream alone 1966–68, 50.4%) are, nevertheless, stark, but for age composition to be a primary explanation for their difference implies other vital statistics (e.g. age-related survival, mean adult longevity) must have been profoundly different also. Regrettably, those survival characteristics were not appraised beyond 1967 (Imber & Williams 1968).

Body condition

Clutch size in waterfowl reflects nutrient reserves of the female at time of laying (Lack 1967), although other demands of the breeding process, especially incubation and brood rearing, influence energy allocated to clutch formation (Winkler & Walters 1983; Erikstad *et al.* 1993). Ryder's (1970) elaboration of Lack's original idea as an "energy reserve hypothesis" found favour as an explanation for clutch size variation and evolution in many arctic-nesting waterfowl that fly long distances from winter feeding to spring breeding grounds, nesting immediately upon arrival (see Alisauskas & Ankney (1992) for review). By not relying on food on the nesting grounds to fuel egg production, their body reserves are mobilised instead. Could female Canada geese travelling to nest in the remote Waimakariri River headwaters valleys arrive there with, on average, lower energy reserves than those of resident geese preparing to nest at Lake Forsyth?

Lake Forsyth was a benign pastoral feeding, nesting, and brood-rearing environment. The pastoral flats at the head of the lake would have offered fresh and nutritious pre-breeding fodder. Not so the headwaters nesting areas wherein snow cover could linger into October and where first nests, established in the last third of September when snow remained lying in many areas, probably post-dated those at Lake Forsyth by two weeks. The immediate headwater nesting environs were most unlikely to have been significant pre-breeding assembly or feeding areas, and the geese would have needed to accrue or maintain body reserves on snow-free pastures either further down the Waimakariri River valley, or at their winter habitat of Lake Ellesmere, 80 km distant and at 700 m lower altitude.

There are no data from which to assess possible differences in body condition. However, one hatching outcome could imply the lesser condition of headwater nesting females – the significantly differing proportions of total nests in which all eggs hatched (Lake Forsyth 42.6% *c.f.* headwaters 30.5%) and, in successful nests, the significantly differing proportions hatching all eggs (Lake Forsyth 53.1% *c.f.* headwaters 36.4%). Among the many determinants of hatching success (which include female age and weather) is consistency of incubation. Body condition of incubating females demonstrably influences the frequency and duration of incubation recesses in Canada geese (Aldrich & Raveling 1983; Ankney *et al.* 1991). Cooper 1978 reported incubation constancy in Canada geese extending to 96% of each day, and incubating females spending as little as nine hours off the nest during the entire 26-28-day incubation period with less than one-third of that time devoted to feeding. In New Zealand conditions, however, incubation behaviour remains unreported.

Evolving population-specific response

The differences in clutch sizes and hatching outcomes between the two study areas might also reflect an evolving response arising from 40–50 years of breeding separation. Although a small introduction of geese directly to Lake Forsyth occurred in 1921, it is likely that the lake was colonised directly from nearby Lake Ellesmere at which initial headwaters releasees aggregated during autumn and winter from the early 1910s (Imber & Williams 2015).

Migratory Canada geese in North America demonstrate nesting ground philopatry, especially by females, and this is thought to have contributed to extensive genetic and morphological structuring within the *Branta canadensis* complex (van Wagner & Baker 1986, 1990). In a sedentary British population, there was especially strong natal philopatry by young female geese (Lessells 1985). The extensive marking of goslings at both Lake Forsyth and headwaters nesting areas provided evidence of nesting ground philopatry. For example, just five (1 male, 4 females) of 2,196 goslings tagged at headwater sites 1969–77 were amongst moulting adults caught annually along with goslings at Lake Forsyth 1971–80, while between 1974–80 just three females of 2,861 goslings colour-banded at Lake Forsyth 1968–78 were sighted at headwater sites.

Any evolving response to nesting alongside a consistent and year-round food supply may lead to an increase in average clutch size mediated via higher food quality and less energy expended to obtain it.

Comparisons with Canada goose nesting elsewhere

North America

Nesting studies of various Canada goose subspecies in North America were a popular professional and student pursuit in the 1940–1960 period with results summarised in relevant North American journals e.g. *Journal of Wildlife Management*, and in U. S. State and Federal agency publications e.g. California Department of Fish and Wildlife, U.S. Fish & Wildlife Service (see references in Hanson & Eberhardt (1971) and comparisons of early studies in Klopman (1958) and Brakhage (1965)).

How the nesting characteristics of the two Canterbury populations compared with those from some historic North American studies is summarised in Table 7. Lake Forsyth nesting outcomes matched many North American examples, e.g. Hanson & Browning (1959) and Geis (1956) reported mean clutch sizes and clutch size distributions almost identical to those from Lake Forsyth and whereas other North American comparisons differ slightly, they appear to reflect different field methodologies at sites also with differing predator impacts. However, headwaters clutches were significantly lower (t = -7.888, df = 3282, P <0.001) than the lowest of the compared North American clutch sizes (Guerena *et al.* 2016).

Both Canterbury populations distinguish themselves by their generally higher nest success, a consequence of proportionately fewer nests losing their entire contents relative to those in North American studies and, most likely, reflecting a lesser mammalian predator impact in New Zealand.

Great Britain and Fennoscandia

Canada geese have established feral populations in Great Britain and Fennoscandia and are presently expanding in lowland western Europe (Andersson *et al.* 1999). Nesting studies akin to those from North America are not extensively reported.

In Great Britain where the species is essentially sedentary, Wright & Giles (1988) reported a mean clutch of 6.1 (sd = 1.4, n = 88), a nest success of 69% (n = 146 nests), a hatch of 433 goslings in 79 successful nests (5.5 goslings/nest), and a productivity of 2.9 fledglings per successful nest, outcomes broadly akin to those reported from Lake Forsyth and some North American studies (Tables 6, 7). Conversely,

Table 7. Comparative nesting statistics of New Zealand and North American populations of Canada goose. North America studies are, 1 – Hanson & Browning 1959 ([1]calculated from Fig. 4); 2 – Geis 1956; 3 – Steel *et al.* 1957; 4 – Cooper 1978 ([2]calculated from Fig. 3); 5 – Guerena *et al.* 2016 ([3]calculated from Table 1). $\bar{x}$ = mean, sd = standard deviation, nr = not recorded.

Location		**New Zealand**		**North America**				
Population/Source		**Forsyth**	**Headwaters**	**1**	**2**	**3**	**4**	**5**
Clutch size	n	462	1,211	1,032	358	361	466	2,073
	$\bar{x}$	5.3	4.5	5.4[1]	5.3	5.2	5.6	4.9
	sd	1.3	1.3	1.2[1]	1.3	nr	1.2[2]	1.8
Hatching rate	n	1,602	3,952	nr	2,501	1,810	2,912	10,075
	%	67.4	63.3	nr	55.6	69.3	68	61
Nest success	n	298	871	1,033	423	361	542	1,967
	%	80.2	83.8	70.9	61.5	79.5	75.0	59.0
Hatching rate in successful nests	n	1,321	3,376	3,947	1,364	1,458	1,871	nr
	%	81.7	85.4	92.0	89.5	86.0	96.6	nr
Hatch/ nest (all)	$\bar{x}$	3.6	2.9	3.5	2.8	3.5	3.8	3.0[3]

Johnson & Sibley (1993) reported a mean clutch of 5.1 (*sd* = 1.9, n = 71; calculated from their Fig. 4) and high nest failure with just 148 goslings hatched within 69 study nests (2.1 goslings/nest). Nevertheless, a 7–9% annual growth reported for the Great Britain population (Ogilvie 1977; Allan *et al.* 1995; Austin *et al.* 2007) indicates both high annual productivity and survival.

Sjöberg & Sjöberg (1992) reported mean clutch sizes over five years in four Swedish populations were between 4.8 (*sd* = 1.4, n = 102) and 5.3 (*sd* = 1.6, n = 133) with their annual variability ranging between means of 4.6 and 5.6. In two further Swedish nesting studies, hatching rates of 51% and 72% were reported (Fabricius 1983, quoted in Andersson *et al.* 1999).

These data on nesting of Canada geese beyond their native range indicate the two New Zealand populations had broadly similar nesting outcomes to those elsewhere. Despite the New Zealand and Fennoscandian introductions arising from small numbers released (Imber & Williams 2015; Heggberget 1991; Jannson *et al.* 2008) their nesting outcomes are akin to those recorded within North America, albeit influenced by their differing nesting densities and predator suites. Even so, the mean size of Waimakariri River headwaters clutches is the lowest reported.

Contemporary relevance of study

Since this study was undertaken, Canada goose numbers in New Zealand have increased significantly (Spurr & Coleman 2005; Robertson *et al.* 2007) both within long-established South Island regional distributions and in many North Island locations following deliberate 1980s introductions (Imber & Williams 2015). At one North Island site (Lake Wairarapa) their annual rate of increase over 20 years (1985–2005) was >12% (Spurr & Coleman 2005: Fig. 3). During the decade 2000–2010, and in the absence of deliberate culls, annual increases of some regional populations (e.g. Otago, West Coast, Marlborough, Waikato, Bay of Plenty) have ranged between 5–15% (relevant Fish & Game Councils, *unpubl. data*).

In the absence of modern assessments, outcomes of this 40–50-year-old nesting study can be used to infer productivity of Canada geese now nesting throughout New Zealand. The modern expansion of Canada goose distribution, especially in lowland North Island, has been typified by many initially small but rapidly expanding flocks derived from family groupings wherein pairs nest in near proximity and have limited feeding ranges. In these circumstances, which are akin to those reported for Lake Forsyth, each nesting female will lay 5–6 eggs and goslings will hatch from approximately two-thirds of all eggs laid. Gosling survival to fledging is unquantified in New Zealand but if it lies in the upper range reported in lowland pastoral English conditions (45–77%, Allan *et al.* 1995) then, on average, each nesting pair will fledge goslings from half of their eggs annually.

The Canada goose has been a remarkably successful, if somewhat controversial, exotic addition to New Zealand's avifauna. Evaluation of its contemporary breeding performance and survival, especially in lowland pastoral North Island and at peri-urban sites, would serve to prepare responses to its inevitable further expansion and concomitant decline in public endearment.

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Appendix: A record of egg size in Canada geese.

A sample of eggs was measured at each study area. These data were originally intended to contribute to an assessment of the race of Canada goose established in New Zealand (Imber 1971b) but were never published.

- From Lake Forsyth, 179 eggs had a mean length of 87.9 mm (sd = 4.1, range 75.6–103.2 mm) and a mean width of 58.3 mm (sd = 1.6, range 53.6 – 62.5 mm).
- From Pūkio Stream, 48 eggs had a mean length of 88.0 mm (sd = 4.9, range 76.5–98.5 mm) and a mean width of 58.0 mm (sd = 2.1, range 53.3–62.8 mm). The eggs sizes did not differ between the two study areas (length: z = 1.64, P = 0.55; width: z = 1.96, P = 0.36).
- Eggs laid at Lake Forsyth by females of known age included 76 eggs from 16 3-year olds which had mean dimensions of 88.9 (sd = 3.0) x 58.0 (sd = 1.7) mm, and 15 eggs from three 4-year-olds with mean dimensions of 88.1 (sd = 3.9) x 58.2 (sd = 1.1) mm.