Moult migration, site fidelity and survival of Canada Geese *Branta canadensis* caught at Lake Windermere, Cumbria

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Abstract

Analyses of 2,108 re-encounters made during 2013–2021 of 1,042 Canada Geese *Branta canadensis* marked at Windermere, Cumbria, in summers 2013–2021 are used to describe their post-moult migration site linkages. Birds moulting at Windermere were subsequently sighted in 34 counties, although post-moult migration was mainly to the counties of Lancashire, Cheshire and Cumbria itself. The proportions of re-encounters in each direction away from Windermere differed statistically from the pattern expected for random dispersal, for seven out of eight directions. Resightings at Windermere showed that the number of marked individuals returning to moult decreased during the study, although numbers moulting on Windermere remained consistent throughout. We also provide new and updated information on the survival and mean dispersal distance for non-breeding Canada Geese. The mean dispersal distance away from Windermere for all marked individuals was 76 km (95% CI = 14.2). Annual mean survival rates ranged between 0.510 and 0.875 over the study period, with a geometric mean of 0.654 ± 0.199 (95% CI = 0.556–0.751). The results significantly improve our knowledge of the demography of the non-native British Canada Goose population.

Key words: *Branta canadensis*, Canada Goose, colour-marking, moult, survival, Windermere.

Most wildfowl species undertake a complete annual wing moult, which lasts for 4–6 weeks and renders them flightless for most of this period. Prior to the commencement of wing moult, some birds undertake movements, known as moult migrations, to sites that provide adequate safety and plentiful food resources during this vulnerable period (Salomonsen 1968; Kjellén 1994). In Britain, the Canada Goose *Branta canadensis* is a non-native, introduced species first recorded in St James's Park, London in 1665 (Lever 1977) and is now widespread, with a 68% increase in count totals in the 25 years between 1993/94 and 2018/19 (Frost *et al.* 2021) and a population estimate of 165,000 birds (Woodward *et al.* 2020). Previous studies of the moult migration of this introduced population found highly directional movement patterns, with the birds migrating north to moult and subsequently returning south once moult was completed; *e.g.*, Canada Geese from Yorkshire and the East Midlands carried out moult migrations to the Beauly Firth in the Scottish Highlands (Dennis 1964; Walker 1970; Austin *et al.* 2002).

Lake Windermere (hereafter Windermere or "the Lake", see Methods for definition) in Cumbria is an important moulting location for both Canada Geese and Greylag Geese *Anser anser* (Brides *et al.* 2019), hosting up to 2,000 individuals of both species combined from early June to mid-July (Figs. 1 & 2). Responding to public criticism of a proposed cull of geese on Windermere in 2012, the Lake District National Park Authority (LDNPA) and local landowners allowed the RSPCA to capture and ring both Canada Geese and Greylag Geese, to determine their movements away from Windermere post-moult and their return rate in subsequent years. Here we use ringing, resighting and count data to describe post-moult movements of Canada Geese from Windermere. Also presented are the results of the first survival estimate, specifically using mark-recapture methods, to be undertaken on resident Canada Geese in Britain. The results from a previous similar study carried out at Windermere on British Greylag Geese (Brides *et al.* 2019) are also available and we use results from both studies to compare movements, site fidelity and survival of the two species.

Methods

Capture, marking, resighting and recoveries

In this paper, Windermere or the Lake refers to the waterbody and its near shore areas (*i.e.* not including the nearby town of Windermere), which extends up to 18.1 km in length by 1.6 km in width, and contains 18 islands. Each June between 2013 and 2020, over several days each year, non-breeding flocks of Canada Geese were displaced by catch teams from waterside feeding areas onto the water at Windermere (52°22'N 2°56'W; Fig. 1) during the flightless phase of moult. The birds were then surrounded using motorboats and kayaks and herded into funnel nets, erected on land, for catching and colour-marking. Smaller numbers of birds, from the breeding population at Windermere, were caught on the nest using a hand net during the late stages of incubation, and several birds were hand-caught at feeding areas. The geese

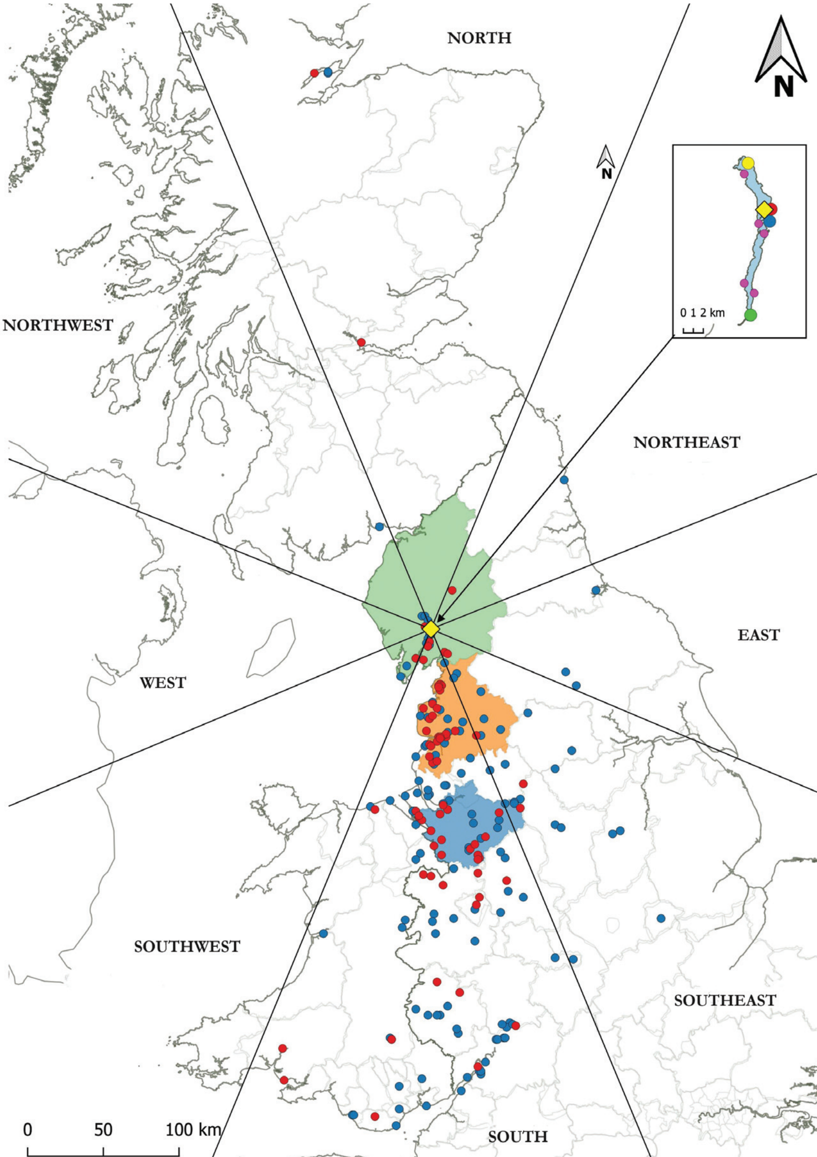

Figure 1. All re-encounters of colour-marked Canada Geese away from Windermere (yellow diamond) during August–May, including all years of the study: blue, sightings; red, ring recoveries from dead birds. The main counties where re-encounters occurred are shaded: Cumbria, green; Lancashire, orange; and Cheshire, blue. The inset shows Windermere and the sites where Canada Geese were captured: Ambleside, yellow circle; Rayrigg Hall, red; Bowness-on-Windermere, blue; Fell Foot, green; and breeding sites, pink.

Table 1. The number of individuals captured, resighted and recovered each year of the study. Each period refers to the interval between one summer moult and the next.

Time period	Total no. captures	No. new captures	No. recaptures	Total no. resightings	Total no. dead recoveries
2013–2014	115	115	0	40	2
2014–2015	327	218	109	165	15
2015–2016	170	97	73	183	12
2016–2017	176	158	18	202	25
2017–2018	1	0	1	455	12
2018–2019	1	0	1	377	14
2019–2020	21	12	9	89	4
2020–2021	0	0	0	68	6

were fitted with individually-coded red plastic leg rings (n = 1,042) that can be read without the need for subsequent recapture, and all birds also received individually-coded metal rings issued by the British Trust for Ornithology (BTO).

In total 2,108 re-encounters were reported to the Wildfowl & Wetlands Trust (WWT), to the BTO, or directly to the authors. An online automated reporting "App", hosted by www.waterbirdcolourmarking.org, was used to capture resightings data and to provide instant history feedback to observers, which included a map of the birds' movements. At one moulting site at Windermere (Rayrigg Hall, Fig. 1), the study used camera traps to increase the number of resightings (see Brides *et al.* 2018). Given a low resighting effort at Windermere by bird watchers, considerable effort was made by the authors to resight as many geese as possible during the moulting period, to determine which individuals returned to moult in subsequent years. Data presented here are based on recaptures, resightings and recoveries (Table 1) made between 16 August 2013 (the first recovery date) and 29 March 2021, inclusive of all months. Weekly counts of geese took place during May–July 2017 at all of the moulting sites at Windermere, to record the increase in the number of geese there as they arrived to moult, and also the subsequent decrease once moult was completed and the birds were leaving. This involved two teams of people, travelling by car around Windermere to visit the moulting sites and to record any geese that were in transit at the time, swimming between moulting locations. Once found, a total flock count was undertaken, using binoculars or a telescope and tally counters, noting the time and direction of swimming, so that any possible duplicate counts could be removed. In

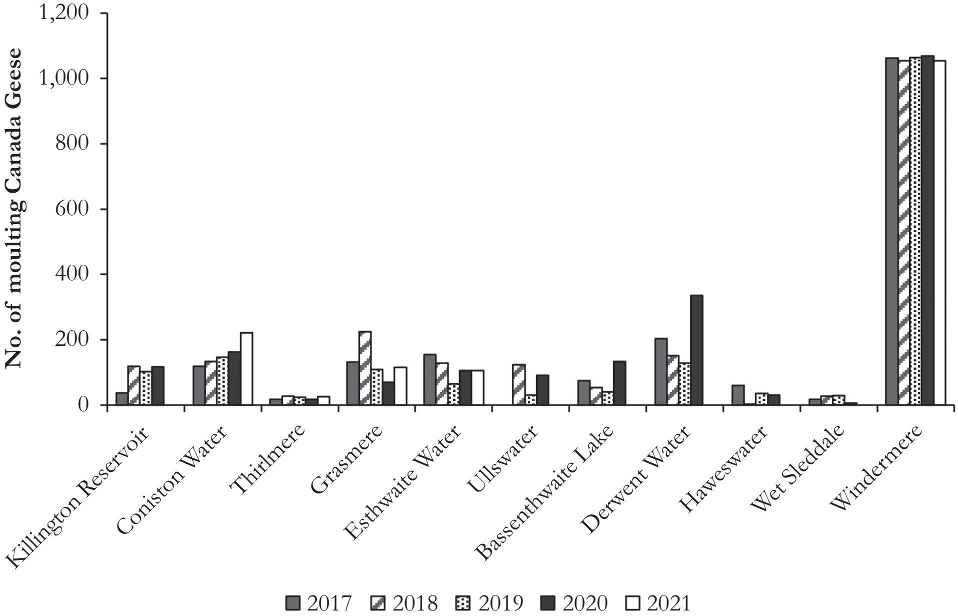

Figure 2. Coordinated counts of moulting Canada Geese at various waterbodies in Cumbria during the third week of June in years 2017–2021.

addition to the weekly counts made in 2017, single-day coordinated counts took place, using the same counting method, in the third week of June (the mean period when peak numbers of geese were present) each year from 2017–2021 inclusive, to produce annual counts of geese moulting on Windermere (Fig. 2).

For methods used during the Greylag Goose study, for comparison with the results of the present study, please refer to Brides *et al.* (2019).

Individual movements

Sightings of colour-ringed birds were collected by bird watchers and the authors, whilst wildfowlers reported the ring numbers of harvested birds. All re-encounters were computerised using the BTO's Integrated Population Monitoring Reporter (IPMR) database and movements were calculated in kilometres, based on the locations of ringing and finding. Distances were grouped based on sightings outside (August–May) and within the June–July moulting period.

We assessed whether the dispersal of ringed Canada Geese away from Windermere differed from a random pattern of equal dispersal probabilities for all directions. If dispersal showed no spatial pattern, we would expect approximately equal proportions of re-encounters in all directions, as the birds would have an equal probability of dispersing in each direction. For our analysis, we divided the area surrounding Windermere into eight equal segments corresponding to north, northeast, east, southeast, south, southwest, west and northwest (Fig. 1). Each re-encounter was assigned to one of these directional segments, and the proportion of the total number of re-encounters recorded in each segment was calculated. For each directional segment, we used a two-sample binomial test for equality of proportions in R (R Core Team 2022) to assess whether the proportion of re-encounters in that segment differed statistically from the proportion that would be expected if no spatial pattern existed (*i.e.* a proportion of 0.125, given that there were eight segments). Proportions were considered to differ from random where $P < 0.05$, following the adjustment of the P values via Holm-Bonferroni corrections to account for the multiple tests that we carried out (Holm 1979).

Survival analysis

The annual survival probability between successive summer moult periods from 2013/14–2020/21 was estimated using Barker joint live–dead models (Barker 1997), run using Program MARK version 10.0 (White & Burnham 1999). Based on the capture dates, May to the following April was considered the time between successive moult periods. Our analysis was based on 600 adult individuals (assigned EURING age codes 4 or 6 on capture, denoting adults of unknown age) that were marked with leg rings from July 2013 onwards; the models were informed by a data set of 211 live recaptures during the moult period, together with 1,579 live resightings and 90 recoveries of dead individuals outside of the moult period (Table 1). The Barker models estimated a total of seven parameters: the annual true survival probability between moult periods (S), the probability that a live individual within the study area would be recaptured during the moult period (P), the probability of a dead individual being recovered and reported between moult periods (r), the probability that an individual would be resighted alive between moult periods (R), the probability of a live resighting within the same interval as being recovered dead (R'), the probability of fidelity, *i.e.* remaining within the study area between capture occasions (F), and the probability of an individual that had previously left the study area returning and thus becoming available for capture again (F'). We tested whether each of the seven parameters was constant (.) or varied between years (t).

Prior to running our survival models, we first assessed the goodness-of-fit of the data to our global model ($S_{(t)},P_{(t)},r_{(t)},R_{(t)},R'_{(t)},F_{(t)},F'_{(t)}$), using the median $\hat{c}$ method that is recommended for joint live–dead models (Cooch & White 2019). The lower bound of $\hat{c}$ was set to 1.00 (*i.e.* perfect goodness-of-fit) whilst the upper bound was set to 6.90 (set above the value for observed deviance/ degrees of freedom for our global model of 6.84). The median (± s.e.) $\hat{c}$ value was estimated as 1.52 ± 0.06 (95% CI = 1.44–1.60), within the limit of 3.00 recommended by Lebreton *et al.* (1992) for reliable survival modelling.

The relative performance of all candidate models was compared using second-order Akaike Information Criteria (AIC_c) (Burnham *et al.* 2011), adjusted for the minor observed lack-of-fit as overdispersion using the $\hat{c}$ value of 1.52 (hereafter $QAIC_c$). Models were ranked by $QAIC_c$ value, with all candidate models with $\Delta QAIC_c$ values < 6.0 considered competitive (Richards 2008); however, to avoid uninformative parameters (*sensu* Arnold 2010), models were considered competitive only if the $QAIC_c$ value of a more complex model was lower than a simpler version containing fewer estimated parameters (Arnold 2010). Where multiple competitive models were identified, Program MARK can report parameter estimates that are averaged across all competitive models, weighted by the $QAIC_c$ weight score associated with each model (White *et al.* 2001). The mean annual survival rate S was used to estimate the mean expected life span (L, no. years) of individuals, where $L = -1/\ln(S)$, with the lower and upper 95% confidence intervals associated with L estimated by substituting S for the lower and upper 95% CIs of S, respectively (Ricklefs 2010).

Results

Individual movements

Overall, 1,033 full-grown geese (EURING age codes 4 and 6), five juveniles (EURING age code 3) and four goslings (EURING age code 1) were fitted with engraved plastic leg rings at Windermere during the study. Since ringing, 60.3% of birds (n = 628) were subsequently re-encountered, either recaptured at Windermere or resighted, with 27.5% (n = 287) individuals being seen away from Windermere and 8.6% (n = 90) being reported dead. A further 37 birds were not recorded again after ringing.

Subsequent resightings away from Windermere, between August and May, show that marked birds were found in 34 counties within the UK, with 46.9% (n = 254 individuals) seen in Cumbria, 16.1% (n = 87) in Lancashire and 9% (n = 49) seen in Cheshire (Table 2, Fig. 1). Forty-eight individuals were seen in two or more counties, whilst 442 individuals were only ever recorded in one county.

All movements combined show that birds ranged between 1 and 375 km from Windermere during the non-moulting period (Figs. 1 & 3) and between 1 and 296 km during the moulting period, having switched to moult at a different location, away from Windermere, in a subsequent year (Fig. 4). The mean (± 95% CI) dispersal distances for all ringing locations was 146.3 km (± 15.0 km) (median = 127 km), with the equivalent data for the five individual ringing locations being 153.8 km for Ambleside (± 27.6 km) (median = 137 km), 141.7 km for Rayrigg Hall (± 18.5 km) (median = 123.5 km), 130.8 km for Bowness-on-Windermere (± 43.0 km) (median = 122 km), 75.2 km for Fell Foot (± 22.3 km) (median = 48 km) and 38.4 km for the five breeding colonies on Windermere, combined (±69.396) (median = 4 km). To assess whether the mean dispersal distance away from Windermere of 146.3 km was being biased by a small number of individuals moving far and being resighted often, the mean dispersal distance for each individual was also calculated, producing a mean of 76 km (± 14.2 km) (median = 110.5 km) overall across all individuals.

Between June 2014 and 2020, 354 individuals (34%) were recorded moulting in a subsequent year back at Windermere. Of these, 244 (68.9%) were seen in one year after the initial capture, 67 in two

Table 2. The number of individual colour-marked Canada Geese and total number of sightings generated by county from August to May 2014–2020. The equivalent results for the number of Greylag individuals and sightings are given in parentheses.

County	Number of individuals		Number of sightings	
Cumbria	254	(93)	817	(185)
Lancashire	87	(111)	110	(747)
Cheshire	49	(5)	57	(6)
Shropshire	29	(6)	43	(32)
Herefordshire	24		131	
Merseyside	18	(7)	36	(36)
Gloucestershire	14	(1)	57	(2)
Greater Manchester	7	(1)	7	(1)
Glamorgan	7		12	
Flintshire	5		5	
Staffordshire	7	(3)	7	(3)
Worcestershire	4		7	
Dumfries & Galloway	4	(1)	5	(1)
Powys	4		5	
Highland	4		4	
Nottinghamshire	2	(4)	4	(1)
North Yorkshire	2	(104)	3	(396)
Clwyd	2		3	
Carmarthenshire	2		2	
South Yorkshire	2	(2)	2	(9)
West Yorkshire	2	(30)	2	(160)
Caerphilly	1		8	
Derbyshire	1	(4)	8	(19)
West Midlands	1		5	
Newport	1		4	
County Durham	1	(11)	3	(27)
Ceredigion	1		1	
Conway	1		1	
Denbighshire	1	(2)	1	(2)
Fife	1		1	
Monmouthshire	1		1	
Northumberland	1	(3)	1	(8)
Rutland	1		1	
Warwickshire	1		1	

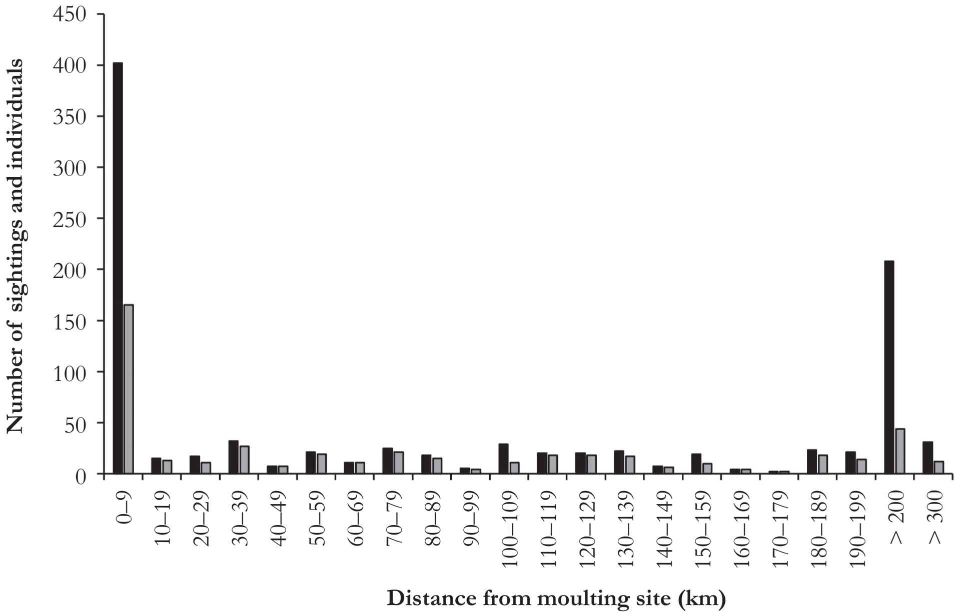

Figure 3. The number of sightings (black bars) and individuals (grey bars) and the distance dispersed away from Windermere during the non-moulting period (August–May 2014–2021) including resighting and ring recoveries from dead birds.

moulting seasons (18.9%), 30 in three seasons (8.5%), 11 in four seasons (3.1%), and two (0.6%) were seen during all six moulting seasons.

Results from the weekly counts that took place on Windermere in 2017 showed that numbers of Canada Geese started to build in early June, with 314 geese counted on 15 June, increasing to 454 on 18 June. Numbers peaked at 1,063 on 24 June (Fig. 2), with 581 present on 1 July and 456 on 14 July; by 21 July most geese had departed, with 148 remaining at Windermere.

The binomial tests indicated that the proportions of re-encounters recorded in each direction away from Windermere differed statistically from a random pattern for seven out of the eight directions tested (Table 3). Only the proportion of re-encounters documented in areas southeast of Windermere did not differ from the proportion expected at random (Table 3). The lowest proportion of re-encounters (0.012) was recorded for the areas west of Windermere, whilst the highest proportion (0.703) was found for areas to the south (Table 3).

Comparison with Greylag Geese

Canada Geese moulting at Windermere, on average, dispersed 76 km, compared with the 83.3 km found for Greylag Geese (Fig. 5). The principal counties receiving birds post-moult differed for each species, with 46.9% of Canada Geese sighted in Cumbria, 16.1% in Lancashire and 9%

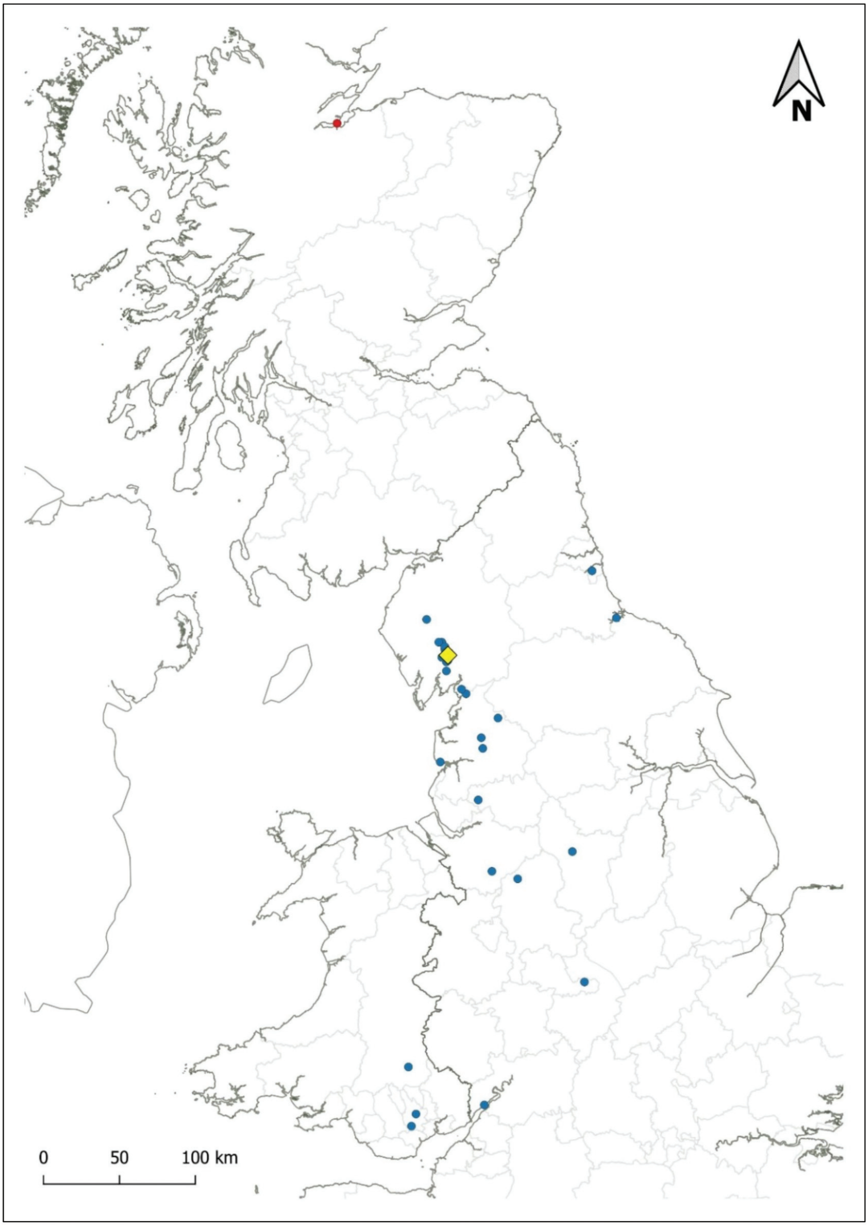

Figure 4. All re-encounters (blue, sightings; red, ring recoveries from dead birds) of colour-marked Canada Geese away from Windermere (yellow diamond) during June–July having switched to moult at a different location, away from Windermere, in a subsequent year, throughout the study. Sightings at other locations before or after moulting at Windermere in the same year are not mapped.

Table 3. The statistical significance of comparisons between the proportions of re-encounters in each direction and the proportion expected from a random spatial pattern in dispersal (*i.e.* 0.125). For all tests, d.f. = 1.

Direction	Proportion of re-encounters	χ^2	Adjusted *P* value
North	0.040	10.6	0.002
Northeast	0.016	20.8	< 0.001
East	0.024	16.8	< 0.001
Southeast	0.145	0.3	0.599
South	0.703	169.3	< 0.001
Southwest	0.024	16.8	< 0.001
West	0.012	23.0	< 0.001
Northwest	0.036	12.0	0.002

Cheshire, whereas Lancashire (31.8%), North Yorkshire (29.8%), Cumbria (26.6%) and West Yorkshire (8.6%) were predominately dispersed to by Greylag Geese. Although Canada Geese were sighted in more counties (n = 34) compared with Greylag Geese (n = 22), an obvious directional shift was detected for both species, with Canada Geese mostly appearing to make a north to south movement post-moult as far south as south Wales and through the west of central England, and Greylag Geese mostly migrating west to east through northern England (Figs. 1 & 5).

Survival

A comparison of all 128 candidate models indicated that eight of these models had $\Delta QAIC_c$ values < 6.0 (Table 4). The two models with the lowest $QAIC_c$ values, $S_{(t)},P_{(t)},r_{(t)},R_{(t)},R'_{(t)},F_{(.)},F'_{(.)}$ and $S_{(t)},P_{(t)},r_{(.)},R_{(t)},R'_{(t)},F_{(.)},F'_{(.)}$, had $\Delta QAIC_c$ values of $\leq$ 0.43, and together accounted for 78% of the $\Delta QAIC_c$ weights (Table 4). The remaining six models with $\Delta QAIC_c$ values < 6.0 were judged to contain uninformative parameters, based on the greater number of estimated parameters and higher $QAIC_c$ values compared with the first two models; these six models were therefore not considered further.

Averaged parameter estimates were obtained from the two models with the lowest $\Delta QAIC_c$ values (Table 5). Annual true survival rates (S) varied between years in both models, ranging from 0.510 in 2018–2019 up to 0.875 in 2013–2014, with a geometric mean ± standard error (s.e.) of 0.654 ± 0.199 (95% CI = 0.556–0.751). The mean survival rate corresponded to a mean life span of 2.4 years (95% CI = 1.7–3.5 years). Recapture probability (P) also varied between years in both models, ranging from 0.000 in 2020 to 0.456 in 2014 (Table 5). The

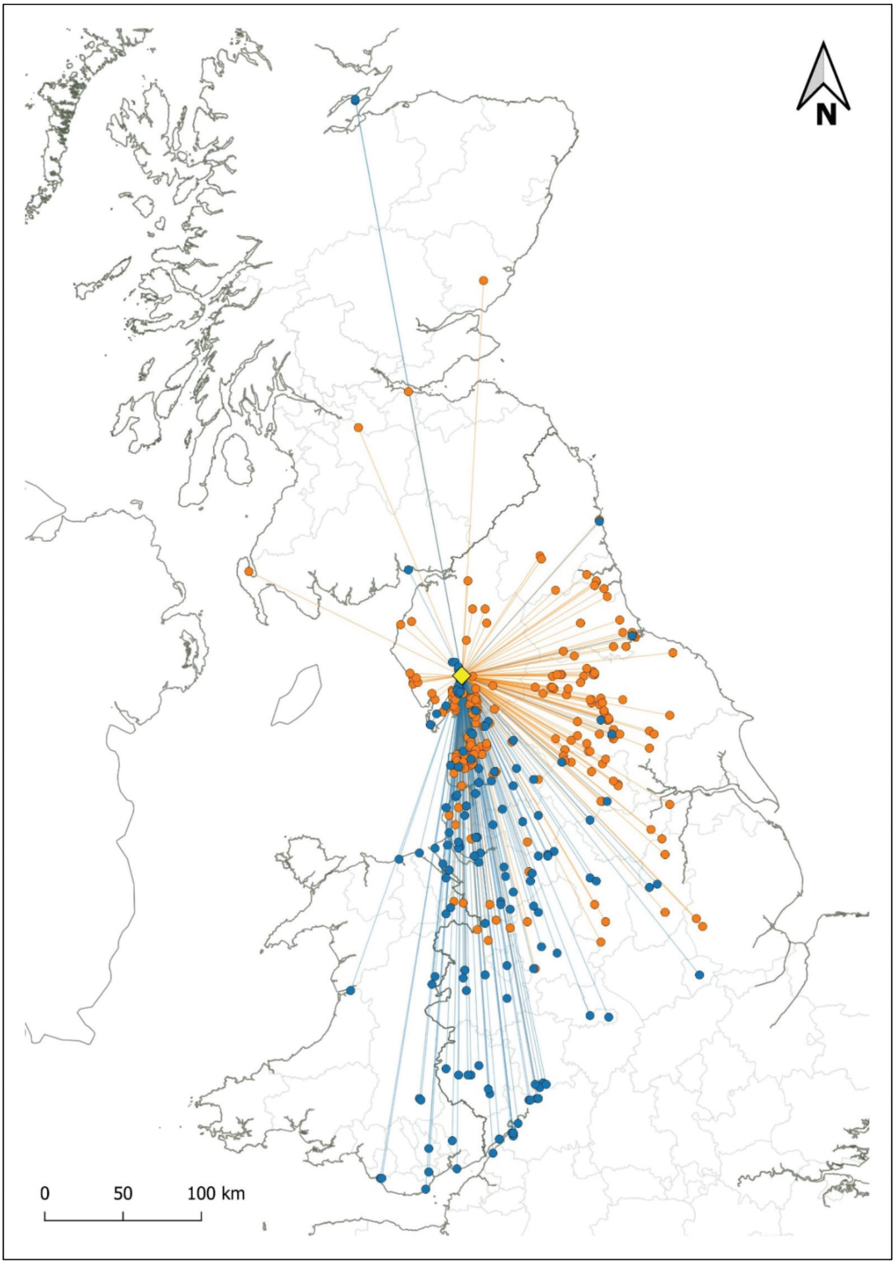

Figure 5. All re-encounters (sightings and ring recoveries from dead birds) of colour-marked Canada Geese (blue) and Greylag Geese (orange) away from Windermere (yellow diamond) during August–May.

Table 4. The relative support associated with the candidate models of Canada Goose true survival (*S*) with $QAIC_c$ weights ≥ 0.01. Our best-supported models are highlighted in bold. Here *k* indicates the number of estimated parameters within each model. See text for parameter definitions.

Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weights	Model likelihood	*k*	Q deviance
$S_{(t)},P_{(t)},r_{(t)},R_{(t)},R'_{(t)},F_{(.)},F'_{(.)}$	**3227.72**	**0.00**	**0.40**	**1.00**	**38**	**597.4**
$S_{(t)},P_{(t)},r_{(.)},R_{(t)},R'_{(t)},F_{(.)},F'_{(.)}$	**3228.15**	**0.43**	**0.32**	**0.81**	**33**	**608.3**
$S_{(t)},P_{(.)},r_{(t)},R_{(t)},R'_{(t)},F_{(t)},F'_{(t)}$	3231.99	4.27	0.05	0.12	43	591.1
$S_{(t)},P_{(t)},r_{(t)},R_{(t)},R'_{(t)},F_{(.)},F'_{(t)}$	3232.14	4.42	0.04	0.11	42	593.4
$S_{(t)},P_{(.)},r_{(.)},R_{(t)},R'_{(t)},F_{(t)},F'_{(t)}$	3232.24	4.51	0.04	0.10	38	601.9
$S_{(t)},P_{(t)},r_{(t)},R_{(t)},R'_{(t)},F_{(t)},F'_{(.)}$	3232.25	4.53	0.04	0.10	43	591.3
$S_{(t)},P_{(t)},r_{(.)},R_{(t)},R'_{(t)},F_{(.)},F'_{(t)}$	3232.45	4.73	0.04	0.09	37	604.2
$S_{(t)},P_{(t)},r_{(.)},R_{(t)},R'_{(t)},F_{(t)},F'_{(.)}$	3232.50	4.78	0.04	0.09	38	602.2
$S_{(.)},P_{(t)},r_{(.)},R_{(t)},R'_{(t)},F_{(.)},F'_{(.)}$	3233.73	6.01	0.02	0.05	25	630.6
$S_{(t)},P_{(.)},r_{(.)},R_{(t)},R'_{(t)},F_{(t)},F'_{(.)}$	3236.08	8.35	0.01	0.02	33	616.3

recovery probability for dead individuals *r* varied between years in only one of the two models, with a mean (± s.e.) probability of 0.170 ± 0.167 (Table 5). The *R'* parameter varied between years in both models, whereas resighting probability *R* only varied between years in one of the two models, with a mean (± s.e.) probability of 0.395 ± 0.121 (Table 5). Both of the fidelity parameters (*F* and *F'*) were time-invariant in both models; site fidelity *F* was particularly high, with a mean ± s.e. probability of 0.959 ± 0.139 (Table 5).

Discussion

Salomonsen (1968) reports that the two main objectives of a moult migration are for birds to move to areas that have sufficient food and offer safety from predation during the vulnerable flightless period, and for immature, non- or failed-breeding birds to free up food resources, thus reducing competition with pairs with goslings. Results from our study identify a previously unknown moult migration for Canada Geese in the UK. Earlier research on the moult migrations undertaken by the UK's Canada Geese (*e.g.* the well-documented Yorkshire and East Midlands to the Beauly Firth, Highland route) involved the ringing of birds undertaken > 40 years ago (Dennis 1964; Walker 1970; Austin *et al.* 2002), so movement patterns may have changed, but it should be noted that observations during June and July in recent years on various Firths in the Highlands of Scotland indicate

Table 5. The averaged parameter values estimated from the two best-supported models. See text for parameter definitions.

Parameter	Mean	SE	Lower 95% CL	Upper 95% CL
$S_{(2013–2014)}$	0.875	0.041	0.771	0.935
$S_{(2014–2015)}$	0.813	0.043	0.705	0.887
$S_{(2015–2016)}$	0.688	0.043	0.592	0.770
$S_{(2016–2017)}$	0.775	0.033	0.667	0.856
$S_{(2017–2018)}$	0.566	0.051	0.399	0.720
$S_{(2018–2019)}$	0.510	0.063	0.370	0.649
$S_{(2019–2020)}$	0.546	11.320	0.000	1.000
$S_{(2020–2021)}$	0.557	27.228	0.000	1.000
$P_{(2014)}$	0.456	0.092	0.289	0.634
$P_{(2015)}$	0.269	0.062	0.165	0.406
$P_{(2016)}$	0.049	0.022	0.020	0.115
$P_{(2017)}$	0.004	0.004	0.000	0.012
$P_{(2018)}$	0.007	0.009	0.000	0.023
$P_{(2019)}$	0.119	0.084	0.027	0.395
$P_{(2020)}$	0.000	0.000	0.000	0.000
$r_{(2013–2014)}$	0.145	0.071	0.042	0.395
$r_{(2014–2015)}$	0.220	0.062	0.088	0.452
$r_{(2015–2016)}$	0.125	0.029	0.066	0.227
$r_{(2016–2017)}$	0.248	0.048	0.103	0.485
$r_{(2017–2018)}$	0.111	0.023	0.047	0.237
$r_{(2018–2019)}$	0.173	0.040	0.099	0.284
$r_{(2019–2020)}$	0.116	2.071	0.000	1.000
$r_{(2020–2021)}$	0.313	52.405	0.000	1.000
$R_{(2013–2014)}$	0.185	0.050	0.106	0.302
$R_{(2014–2015)}$	0.332	0.039	0.261	0.412
$R_{(2015–2016)}$	0.393	0.040	0.318	0.473
$R_{(2016–2017)}$	0.348	0.035	0.283	0.418
$R_{(2017–2018)}$	0.588	0.048	0.492	0.677
$R_{(2018–2019)}$	0.600	0.066	0.468	0.719
$R_{(2019–2020)}$	0.246	0.076	0.128	0.422
$R_{(2020–2021)}$	0.814	73.538	0.000	1.000
$R'_{(2013–2014)}$	1.000	0.000	1.000	1.000
$R'_{(2014–2015)}$	0.472	0.130	0.240	0.717
$R'_{(2015–2016)}$	0.454	0.082	0.296	0.621
$R'_{(2016–2017)}$	0.888	0.048	0.319	0.993
$R'_{(2017–2018)}$	0.867	0.043	0.406	0.984
$R'_{(2018–2019)}$	0.860	0.079	0.204	0.993
$R'_{(2019–2020)}$	0.985	19.281	0.000	1.000
$R'_{(2020–2021)}$	0.674	78.733	0.000	1.000
F	0.959	0.139	0.021	1.000
F'	0.000	0.000	0.000	0.000

that this moult migration is still active today (B. Swann, pers. comm.).

Elsewhere in Europe non-native Canada Goose populations are also known to undertake moult migrations with a high proportion of the Fennoscandian breeding population making a post-nuptial migration to southern Sweden, Denmark and northeast Germany, with smaller numbers possibly continuing to the Netherlands, Belgium and France (Andersson *et al.* 1999). Moult migrations undertaken by non-native Canada Geese in Europe mirror similar movements to birds in the species' native home range of North America, where Canada Geese are highly migratory, and many populations are known to undertake long distance journeys to find suitable wetlands to commence their annual moult.

The summer population of Canada Geese moulting at Windermere consists mainly of failed and non-breeding and second calendar year birds, which undertake moult migrations to the Lake from elsewhere. Canada Geese do breed at Windermere; however, breeding success remains very low due to egg-control effort being undertaken to help reduce numbers at the Lake. Whilst small numbers of goslings are seen (2% in 2019), it is thought that breeding output is not a major contributor to the numbers summering at the Lake. The flocks found at Ambleside, Bowness-on-Windermere and Rayrigg Hall mostly consist of incoming non- and failed-breeding birds, evident from the mean distance of travel away from Windermere post-moult. However, the flock found at Fell Foot is more likely to host small numbers of breeding pairs and their families, which do not disperse as far. Interestingly, shorter dispersal distances were also seen at Fell Foot by the Greylag Geese, compared with the other moulting locations on Windermere.

Interchange between years with other UK moulting congregations has been observed during this study. Geese marked at Windermere have subsequently been found moulting in other, better known, moult congregations, with three Windermere-ringed birds found at the Llangorse Lake, Powys (51°55'N, 3°16'W) moulting flock in Wales in 2013, 2015, 2016 and 2017 (Fig. 1, Table 2). Furthermore, two birds ringed at Llangorse Lake were found moulting at Windermere in 2013 and 2016. Confirmation of movement between Windermere and the Highlands of Scotland also occurred during this study, with three Windermere-ringed birds being found at Udale Bay and one each near Alness and North Kessock, between August and September 2013, 2014 and 2016, suggesting that they possibly moulted in Scotland during these years.

The proportions of re-encounters in each direction away from Windermere differed statistically from the pattern of random dispersal, for seven out of eight directions. Our findings suggest that there are clear trends in the dispersal of Canada Geese, in particular towards the south. Certain factors are likely influencing the direction of dispersal for Canada Geese moving away from Windermere; however, the identity of these factors has not yet been determined. Different areas available to the geese within the landscape surrounding Windermere likely differ in their suitability as Canada Goose habitat; *e.g.* in terms of the availability of feeding and roost sites, which might affect site selection by the geese (Dunton & Combs 2010; Dorak *et al.* 2017). Intrinsic variables such as age and sex may also influence Canada Goose dispersal behaviour (Lessells 1985; James & Krementz 2005). Future research which investigates the influence that landscape and intrinsic variables have on the dispersal direction and settlement probabilities of geese would help to address this knowledge gap.

The survival rate of Canada Geese (mean = 0.654, 95% CI = 0.556–0.751) was similar to the survival rate of Greylag Geese (mean = 0.680, 95% CI = 0.584–0.775) that also moult in the Windermere area. Our mean annual survival estimate of 0.654 was somewhat lower than the 0.755–0.900 estimated in an earlier study by Thomas (1977) for Canada Geese in Yorkshire, northern England. The true survival rates estimated from our models were, however, within the range of 0.463–0.958 reported by earlier studies of Canada Geese from their native range in North America (Hestbeck & Malecki 1989; Samuel *et al.* 1990; Rexstad 1992; Castelli & Trost 1996; Balkcom 2010; Shirkey *et al.* 2018). Balkcom (2010) showed that mean Canada Goose survival rates were higher among birds living in urban areas than those in rural areas (0.958 *vs.* 0.682), largely attributable to lower shooting pressure. Given that our study location is in a rural region, it is perhaps unsurprising that our estimates were closer to the value reported for the rural birds. Of the 90 birds found dead and where a cause of death was submitted with the finding details, over half had been recorded as shot dead.

Where individuals lose their leg rings or other markers, *e.g.* because they become damaged and fall off, this can cause survival rates to be underestimated (Wood *et al.* 2018; Allen *et al.* 2019). However, an earlier study of Canada Geese marked with neck collars found that the annual retention rate was 99.3% (Hestbeck & Malecki 1989). Another study which marked Canada Geese with both neck collars and leg rings between 1984 and 1993 reported that no recaptured individual with a neck collar was found to have lost its leg ring, and therefore the rate of leg ring loss was concluded to be negligible (Sheaffer *et al.* 2004). Moreover, as each of the individuals in our sample was also fitted with a metal leg ring, we would have been able to identify any recaptured individuals that had lost their colour ring, yet none of the birds marked in our study that were recaptured subsequently were found to have lost their colour markers. The rate of ring loss among our focal birds therefore was likely to have been negligible.

Their large appearance, tendency to congregate in large flocks and often aggressive behaviour (particularly when nesting) have brought Canada Geese into conflict with humans (Hughes *et al.* 1999). They can cause considerable damage to crops, with birds often trampling and grazing on young shoots, so although it is difficult to quantify the damage being done, agricultural surveys suggest that in highly affected areas there is an economic loss for farmers (Radtke & Dieter 2011). Observational studies in the UK have documented that Canada Geese can show aggressive behaviour towards native waterbirds (Wood *et al.* 2020). Large-bodied goose species can also pose a threat to air safety due to their flocking behaviour and tendency to feed on maintained short grassland found around airports (Bradbeer *et al.* 2017). Faecal inputs of nutrients such as phosphorus and nitrogen have been shown to contribute to the eutrophication of lakes (*e.g.* Manny *et al.* 1975). Furthermore, in urban areas, the droppings of these birds have the possibility of containing pathogenic bacteria that can be harmful to humans (Feare *et al.* 1999). At Windermere, moulting goose populations have come into conflict with landowners and there have been calls for the reduction in population size. This has seen the formation of the Windermere Geese Management Group, which is coordinated by the Lake District National Park Authority (LDNPA) and shares resources to carry out research and practical interventions to manage Canada Goose numbers on Windermere and other waterbodies in the catchment area. In response to public opposition in 2012, the group decided not to use population culling as a management option.

Since October 2021, there has been an unprecedented outbreak of highly pathogenic avian influenza (HPAI) of the subtype H5N1 in wild birds, initially in wintering waterbirds and then in breeding seabirds and other species (Pearce-Higgins *et al.* 2023). There is now a greater need to better understand movements of non-native species, especially in relation to their role as vectors in spreading HPAI. Movements together with knowledge of the other species with which they congregate will need to be better understood, not only spatially and temporally but also at different stages of their life cycle when mass movement may occur (*e.g.* during moult migrations). Furthermore, having more accurate and up-to-date knowledge of the population size of Canada Geese in the United Kingdom would be advantageous. Previously, national surveys of Canada Geese have been carried out (Blurton-Jones 1956; Ogilvie 1969, 1977; Delany 1992, 1993; Austin *et al.* 2007) and, whilst the UK's Wetland Bird Survey (WeBS) includes non-native species, coverage is limited in the wider countryside away from wetland sites (Pearce-Higgins *et al.* 2023). It therefore would be beneficial to undertake more regular coordinated censuses, in order to derive population estimates for this non-native population such as those afforded to native wildfowl populations (*e.g.* Brides *et al.* 2021a, b).

To gain a better understanding of Canada Goose movements in relation to moult migrations, pooling of data from ringing undertaken at different, discrete moult locations, such as those on the Beauly Firth (Highland), Llangorse Lake (Powys), Chew Valley Lake (Avon) and various sites in London, would provide better insight both spatially and temporally. In particular, it would also allow interchange between moulting sites to be studied in greater detail.

Our study has generated new information identifying a previously unknown moult migration. Counts undertaken at Windermere confirmed that an increase of Canada Geese occurred annually at the Lake from early June onwards and that their presence at Windermere in great numbers lasted for just 4–6 weeks. Owing to the UK's large Canada Goose population size and their willingness to travel large distances to undertake their annual moult, the reduction of numbers at Windermere by lethal control is unlikely to be an effective method for reducing Canada Goose numbers locally. Our study showed that the number of marked individuals returning to moult at Windermere year on year reduced as time went on; however, the numbers moulting at Windermere annually remained consistent (Fig. 2). Earlier avian population modelling studies have found that the removal of individuals from a population can be offset by immigration from outside of the managed area, which reduces the effectiveness of culling (Wood *et al.* 2013; Grarock *et al.* 2014). Removing individuals therefore may simply create capacity for other birds to moult the following year. Fencing off recreational areas and continuation of egg-control (*e.g.* Baker *et al.* 1993) may be a more suitable option for managing goose and human conflict at Windermere.

The catching and ringing of goslings at Windermere would provide insight into natal recruitment to future moulting flocks, by permitting assessment of whether Windermere-hatched birds choose to stay and breed, and the extent to which they moult at Windermere or moult elsewhere. Telemetry studies would be invaluable, because the GPS data would allow the annual cycle of individual Canada Geese to be tracked, and would provide a greater insight into moult site choice, arrival and departure timings, duration of stay and the frequency of moult site switching at Windermere. With both non-native Canada and native Greylag Geese sharing Windermere as a moulting destination, the dynamic of the interspecific competition between the two species in terms of food and moult site availability would also be a beneficial focus for future study.

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Photograph: Canada Geese in flight, by Graham Catley.