# Factors influencing Whooper Swan *Cygnus cygnus* numbers on the Isle of Tiree, Argyll, Scotland

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**Abstract**

Annual peak counts of Icelandic Whooper Swans *Cygnus cygnus* on the mesotrophic lochs of the Isle of Tiree in winters 2001/02–2020/21 varied between 106 and 502 birds in autumn and between 45 and 186 in January, with no significant trends over time. Swans were present in nationally important and sometimes internationally important numbers at Loch a' Phuill during 2001–2018 but counts dropped below the 1% threshold of nationally important numbers when this figure was revised upwards in 2019. Peak numbers of swans in both autumn and winter were significantly negatively correlated with recent rainfall. Periods of dry weather reduced loch levels by up to 0.5 m, which improved the swans' access to submerged macrophyte food supplies. A significant positive correlation between summer rainfall and peak autumn counts implied that autumn macrophyte food supplies were lower after dry summers, in which large parts of the lochs dried out completely. The annual proportion of cygnets recorded ranged from 5.6% to 29.9% and did not differ significantly from the rest of the UK. The proportion of cygnets did not correlate with peak swan numbers in either autumn or January, reinforcing the view that variation in swan numbers on the island was affected by external factors such as food supply, rather than annual variation in demographics.

**Key words:** autumn peak, Loch a' Phuill, loch levels, macrophytes, numbers, proportion of young, Tiree, Whooper Swan, wintering.

In common with many other Scottish sites, such as Loch of Wester in Caithness, Loch Eye in Highland Region, Loch of Lintrathen in Angus, Loch Park in Banffshire and the Insh Marshes in Strathspey (Robinson *et al.* 2004; Hewson 1963), Icelandic Whooper Swans *Cygnus cygnus* arriving in the autumn to the Isle of Tiree in the Inner Hebrides feed predominantly on natural vegetation. On Tiree, as at Loch of Wester, Loch Eye, Loch of Lintrathen and Loch Park (Robinson *et al.* 2004), this takes the form of submerged aquatic macrophytes and their tubers, which are accessed by the birds dip-feeding and upending from the surface of the lochs (often after a period of foot-paddling), whereas at the Insh Marshes the swans graze on natural floodplain vegetation

such as sedges *Carex* sp. On Tiree, this form of feeding continues to predominate throughout the winter, whereas at other Scottish sites swans move to adjacent stubble and arable fields as the winter progresses. This also contrasts with the situation elsewhere in Britain and Ireland, where most wintering Whooper Swans now feed on arable land and improved pastures during mid-winter (Hall *et al.* 2016; Brides *et al.* 2021).

Peak numbers of swans recorded on Tiree in autumn have fluctuated greatly, whereas January counts have been less variable. This study aims to identify factors influencing the number of swans using the Tiree lochs in autumn and in January. Although site fidelity in winter is relatively high (Black & Rees 1984), Whooper Swans can also be highly mobile, not only in relation to food supply (Rees *et al.* 1997) but possibly also in relation to the predominant wind direction during migration (McElwaine *et al.* 1995). Macrophyte food supply may be influenced by temperature and/or loch levels (hence rainfall) during the summer growing period (June–August), whilst the swans' ability to access this food could be affected by loch levels, both upon arrival in autumn (October–November) and in mid-winter (December–January). Frequency of westerly or easterly winds during the autumn migration period could also influence numbers, for example if more Tiree birds arrive via Ireland during autumns with predominantly easterly winds. The meteorological variables of summer temperature, summer rainfall, autumn rainfall, winter rainfall and frequency of westerly and easterly winds in autumn were all therefore investigated, to determine their impact on the number of swans on Tiree.

## Methods

### Study system

The Isle of Tiree in the Scottish Inner Hebrides has long been known to hold nationally important numbers of Whooper Swans in winter, with even larger numbers of birds visiting at times on passage, particularly in October/November and with a handful remaining each summer (*e.g.* Newton 1989; Bowler & Leitch 2020). Most Whooper Swans occur on the four main waterbodies on the island, all of which are shallow, naturally mesotrophic machair lochs (Fig. 1), with mostly sandy bottoms and extensive beds of submerged macrophytes, including no fewer than nine species of pondweed *Potamogeton* sp. and five species of stoneworts *Chara* sp. and *Tolypella* sp. (Pearman & Preston 2000). Largest numbers of swans typically occur on the largest waterbody, Loch a' Phuill, which is designated as a Special Area of Conservation for its naturally nutrient-rich waters and diverse pondweed assemblage (NatureScot 2021). This loch is part of the Tiree Wetlands and Coast Special Protection Area, although the Whooper Swan is not listed in citation for the latter, despite occurring regularly in numbers well above the threshold for national importance. Smaller numbers of swans occur on Lochs Bhasapol, an Eilein and Riaghain, whilst a handful occasionally utilise smaller lochs and floods elsewhere on the island (Fig. 1; see also Bowler & Hunter 2007).

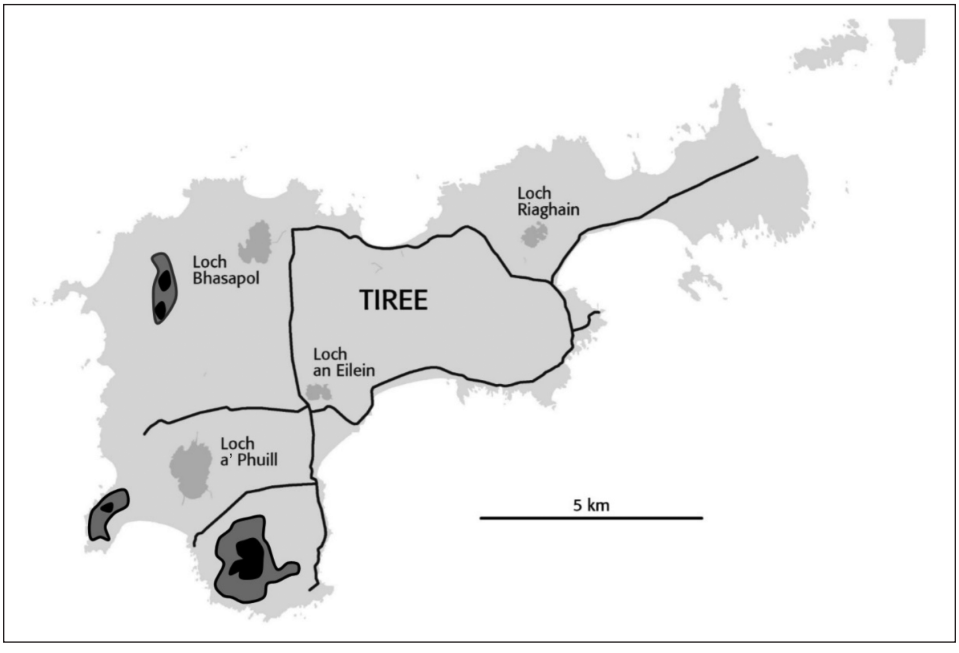


**Figure 1.** Map showing the location of the four main lochs used by feeding Whooper Swans on the Isle of Tiree (pale grey) plus areas above 50 m altitude (mid-grey) and above 100 m altitude (black).

## Data collection

*Swan numbers*. Between autumn 2001 and spring 2021, the author made regular counts of Whooper Swans on Tiree. Monthly counts of the four main lochs made for the Wetland Bird Survey (WeBS) scheme (Fig. 1; Bowler & Leitch 2020) were bolstered by monthly all-island counts throughout the winter (October–March), including annual counts in January timed to coincide with UK age-assessment counts co-ordinated by the Wildfowl & Wetlands Trust (WWT 2020). Additional day-counts were made at times of large influxes of swans to obtain maximum counts of birds present each year, as peak arrivals rarely coincided with WeBS count dates (see Bowler & Leitch 2020), thus emphasising the value of additional counts (as per Brown 2017). Flocks passing over the island without stopping during passage periods were also noted but were not included in the totals. Numbers of cygnets and family sizes were recorded routinely on all counts.

*Rainfall*. Rainfall data were obtained from the Meteorological Office Integrated Data Archive System (MIDAS 2020) using the CEDA Web Processing Service (WPS). Rainfall data were very sparse from both the Tiree Met Station and the Arinagour Met Station on the adjacent island of Coll, so more complete rainfall data from the Torran Met Station on Iona (31 km southeast of Tiree, elevation 6 m) were used instead, with gaps in October 2001–January 2002 and December 2005–January 2006 filled using

 

data from Arinagour, Coll (15 km northeast of Tiree, elevation 34 m). No rainfall data from any adjacent meteorological station in the Inner Hebrides were available for January 2009, July–December 2015 and December 2020–January 2021.

*Temperature*. Complete temperature data from the Tiree Airport Met Station (elevation 9 m) were available via MIDAS for all years, and the yearly means of the daily summer maximum and minimum temperatures were calculated using data from 1 June–31 August inclusive.

*Windspeed and wind direction*. These measures were recorded daily on Tiree by the author in 2004–2020, using the Beaufort Scale, measured by eye, and assigning wind direction in relation to 16 compass directions. To assess the frequency of westerly and easterly winds during autumn migration, the number of days in October and November were tallied in which the wind was either in the west (SSW to NNW, 192°–348°) or in the east (NNE to SSE, 11°–169°) and expressed as a percentage of the days in the two month period (see Table 1).

*Water levels*. No long-term water level measures were available for this study, so the effects of the depth of water in the lochs on the swans' use of sites on Tiree could not be analysed directly. Water levels recorded by data loggers at 15 min intervals at Loch a' Phuill from March–November 2007 and at Loch Bhasapol from June–November 2007 (from Johnson 2008) are however presented for illustrative purposes.

### Analyses

Successive annual counts of long-lived waterbird species, including swans, may show strong patterns of temporal autocorrelation (*e.g.* Wood *et al.* 2019). If unaccounted for, such autocorrelation can violate the assumptions regarding the independence of data points in a regression analysis (Crawley 2013). However, initial exploration of linear regression residuals of temporal trends in the autumn and January count data, fitted using the nlme package in R (Pinheiro *et al.* 2020; R Core Team 2020), showed no consistent patterns of statistically significant residual temporal autocorrelation across years. No autocorrelation structures therefore were included in subsequent analyses for either data set. Trends in swan numbers over time and comparisons of the weather variables with count data were tested using Spearman's rank correlations (two-tailed tests), calculated as per Fowler and Cohen (1996), because the data were not normally distributed. A paired sample t-test was used in Excel to compare the annual proportion of cygnets recorded on Tiree with that from the rest of the UK (WWT 2020).

## Results

### Autumn counts

Whooper Swan arrivals were noted from the end of September until late November and all were recorded feeding on the machair lochs, except for very occasional groups of 1–6 birds on flooded pasture (< 1% of all counts). Peak autumn counts ranged between 106 (in 2001) and 502 (in 2015), with a mean of 238 (Fig. 2). There was no significant trend in numbers over the study period ($r_s = –0.179$, $n = 20$, $P > 0.1$, n.s.), although peaks in 2017–2020 were lower

**Table 1.** Rainfall, temperature and wind direction for selected months in 2001–2021: June–August (summer pondweed growing period), October–November (autumn Whooper Swan passage period) and December–January (Whooper Swan mid-wintering period). Rainfall data are from the Torran, Iona Met Station with gaps (*) filled from the Arinagour, Coll Met Station; mean daily maximum and minimum temperature data are from the Tiree Airport Met Station; frequency of westerly and easterly wind directions = % days on Tiree with wind in the SSW–NNW (192°–348°) and NNE–SSE (11°–169°); nd = no local data available.

| Winter | Rainfall (mm) | Rainfall (mm) | Rainfall (mm) | Mean max Temp (°C) | Mean min Temp (°C) | Wind (% days in W) | Wind (% days in E) |
|---|---|---|---|---|---|---|---|
| | Jun–Aug | Oct–Nov | Dec–Jan | Jun–Aug | Jun–Aug | Oct–Nov | Oct–Nov |
| 2001/02 | 142.3 | 606.6* | 301.8* | 14.4 | 10.9 | nd | nd |
| 2002/03 | 259.6 | 349.5 | 163.8 | 14.5 | 11.5 | nd | nd |
| 2003/04 | 261.1 | 373.8 | 378.6 | 15.9 | 12.4 | nd | nd |
| 2004/05 | 338.2 | 344.6 | 414.0 | 15.6 | 12.0 | 41.0 | 26.2 |
| 2005/06 | 443.5 | 300.2 | 242.8* | 15.2 | 11.8 | 31.1 | 26.2 |
| 2006/07 | 223.7 | 289.4 | 402.1 | 15.4 | 12.1 | 37.7 | 24.6 |
| 2007/08 | 250.0 | 404.8 | 380.7 | 15.0 | 11.5 | 52.5 | 19.7 |
| 2008/09 | 314.4 | 295.9 | nd | 15.2 | 11.6 | 26.2 | 3.3 |
| 2009/10 | 416.1 | 397.2 | 320.7 | 15.4 | 11.9 | 37.7 | 24.6 |
| 2010/11 | 343.4 | 499.6 | 206.0 | 15.1 | 11.6 | 27.9 | 41.0 |
| 2011/12 | 356.3 | 735.2 | 875.5 | 14.4 | 10.7 | 34.4 | 29.5 |
| 2012/13 | 253.9 | 243.8 | 383.4 | 14.7 | 11.2 | 47.5 | 19.7 |
| 2013/14 | 297.6 | 313.8 | 564.8 | 15.4 | 11.6 | 55.7 | 26.2 |
| 2014/15 | 297.4 | 370.4 | 351.1 | 15.6 | 12.2 | 31.1 | 42.6 |
| 2015/16 | 507.0 | nd | 424.6 | 13.9 | 10.5 | 50.8 | 11.5 |
| 2016/17 | 259.5 | 173.9 | 258.9 | 15.2 | 12.0 | 16.4 | 39.3 |
| 2017/18 | 305.3 | 537.4 | 345.6 | 15.0 | 11.7 | 65.6 | 13.1 |
| 2018/19 | 238.5 | 495.9 | 230.1 | 16.4 | 11.9 | 45.9 | 13.1 |
| 2019/20 | 350.7 | 255.6 | 466.7 | 15.5 | 12.3 | 23.0 | 45.9 |
| 2020/21 | 297.5 | 415.6 | nd | 15.1 | 11.6 | 47.5 | 31.1 |

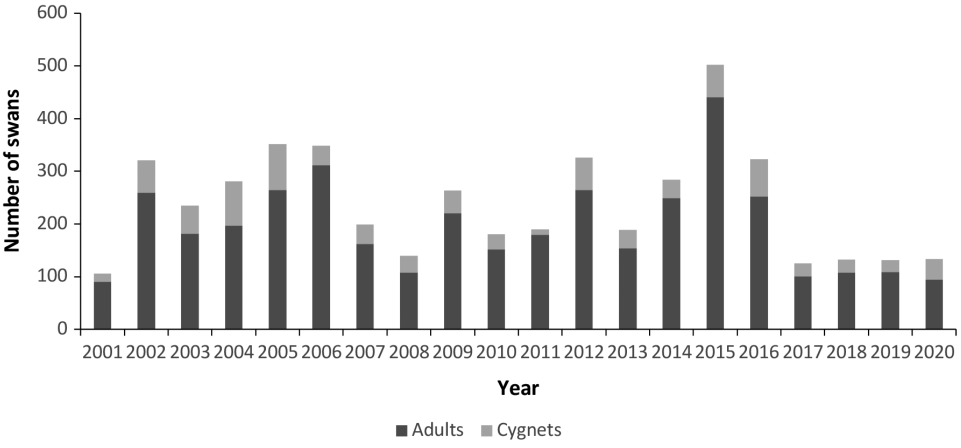


**Figure 2.** Peak autumn (October–November) counts of Whooper Swans on Tiree in 2001–2020 (dark grey bar = adults; pale grey bar = cygnets).

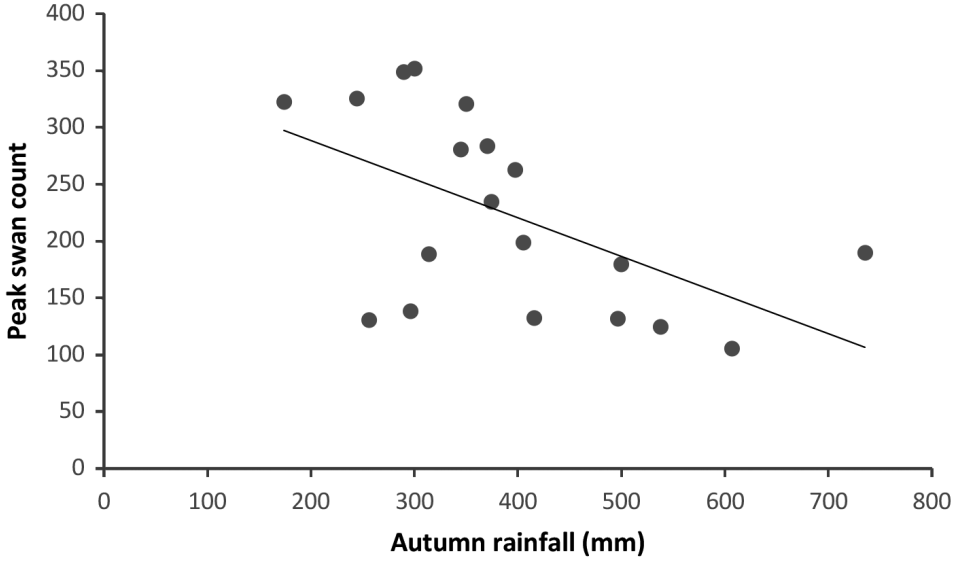


**Figure 3.** Peak autumn (October–November) counts of Whooper Swans on Tiree in 2001–2020 plotted against autumn (October–November) rainfall ($r_S$ = –0.551, $n$ = 19, $P$ < 0.02, with trendline added). Note: there were no rainfall data available for autumn 2015.

than in all other years except 2001. Autumn peak counts were significantly negatively correlated with autumn rainfall ($r_s$ = –0.551, $n$ = 19, $P$ < 0.02, Fig. 3). Highest numbers were recorded in the very dry autumn of 2015 (although no local rainfall data were available), when > 300 swans were present at Loch a' Phuill between 27 October and

7 November, peaking at 431 on 3 November 2015. A further 71 swans elsewhere on the island on the same day gave a record total of 502 for the whole of Tiree.

In wetter autumns, large numbers of swans merely passed over the island without stopping or stopped only briefly at night on the lochs. For example, 195 swans flew south in four flocks over Balephuil between 08:00–09:00 h on 22 October 2020, during a very wet autumn in which the peak count of swans on the island was of only 133 birds. It was not possible to determine the proportion of Whooper Swans that stayed to feed compared to those overflying the island because flocks passed overhead on a broad front at all hours of the day and also at night. Autumn peak counts were significantly positively correlated with summer rainfall ($r_s$ = 0.451, $n$ = 20, $P < 0.05$), but not with the mean maximum or mean minimum daily temperature in June–August, the frequency of westerly or easterly based winds in October–November, nor with the proportion of cygnets present in the flocks that year ($r_s < 0.322$, $n$ = 17–20, $P > 0.1$, n.s. in all cases).

## January counts

All-island counts in January ranged between 45 (in 2004) and 186 (in 2003), with a mean of 124 swans recorded (Fig. 4). January counts were of > 100 birds in all years except in 2004, 2005, 2012 and 2014. There was no significant trend in January counts over the study period ($r_s$ = 0.204, $n$ = 20, $P > 0.1$, n.s.), with particularly high counts of > 180 birds occurring every eight years in 2003, 2011 and 2019. January counts were significantly negatively correlated with mid-winter rainfall ($r_s$ = –0.594, $n$ = 18, $P < 0.02$, Fig. 5), but not with autumn peak counts in

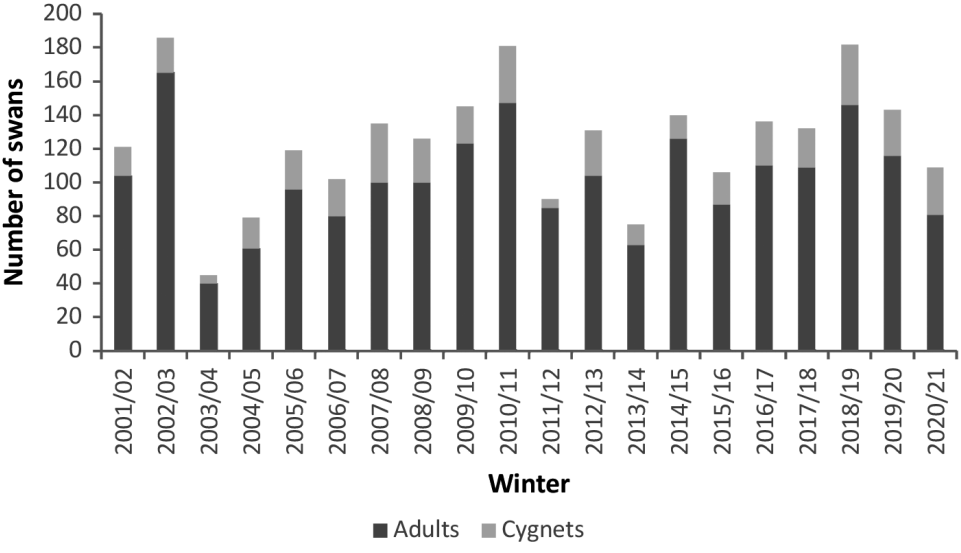


**Figure 4.** Maximum January counts of Whooper Swans on Tiree in winters 2001/02–2020/21 (dark grey bar = adults; pale grey bar = cygnets).

 

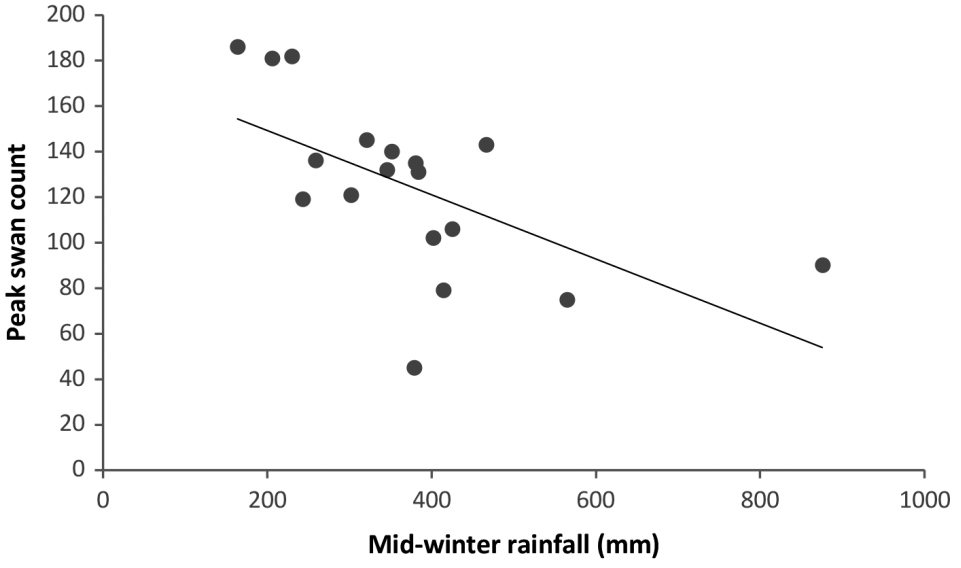


**Figure 5.** Maximum January counts of Whooper Swans on Tiree in winters 2001/02–2020/21 plotted against mid-winter (December–January) rainfall ($r_S$ = –0.594, $n$ = 18, $P$ < 0.02, with trendline added). Note: no rainfall data were available for 2008/09 or 2020/21.

the same winter or the proportion of cygnets present ($r_s$ < 0.27, $n$ = 20, $P$ > 0.1, n.s. in both cases), nor with the frequency of westerly or easterly based winds in October–November ($r_s$ < 0.256, $n$ = 17, $P$ > 0.1, n.s. in both cases).

## Spring counts

Numbers of wintering swans declined on the island in February and March (see Bowler & Leitch 2020) but were joined on occasion by additional passage flocks. Birds passed north through the islands between late February and May, with most recorded in March, peaking at 267 on 29 March 2006 and at 260 on 23 March 2021. Most swans simply passed over the island without stopping but occasional flocks were grounded by inclement weather such as strong head winds and poor visibility. Swans in such flocks mostly slept or preened at the loch-edges, with little feeding observed, and moved on quickly as conditions for onwards migration improved. Spring passage was generally erratic and short-lived on the island during the study period.

## Proportion of cygnets

The percentage of cygnets recorded on the autumn peak counts ranged between 5.8% (in 2011) and 29.9% (in 2004), with a mean of 18.3%, and was not correlated with the percentage of cygnets for the whole of the UK during winters 2004/05–2019/20 ($r_s$ = 0.220, $n$ = 16, $P$ > 0.1, n.s.) for which comparable data were available (WWT 2020). The percentage of cygnets recorded in January ranged between 5.6% in 2012 and 25.9% in 2008, with a mean of 17.6%. For winters 2004/05–2019/20, the January

mean on Tiree (18.1%) did not differ significantly from the percentage of cygnets recorded in flocks across the UK (15.4%, paired sample t-test: $t = 0.061$, d.f. = 16, $P > 0.1$, n.s.), and the two were not significantly correlated over time ($r_s = 0.147$, $n = 16$, $P > 0.1$, n.s.). The proportion of cygnets recorded in January on Tiree was however positively correlated with the proportion of cygnets recorded in the autumn peak of the same winter ($r_s = 0.549$, $n = 20$, $P < 0.01$). There was no significant correlation between year and the proportion of cygnets recorded in either autumn or January ($r_s < 0.22$, $n = 20$, $P > 0.1$, n.s. in both cases).

Individual family sizes varied from 1–7 cygnets on Tiree, with mean brood sizes for the island ranging from 1.73 in January 2016 ($n = 11$ families) to 3.32 in autumn 2005 ($n = 22$ families). The overall annual mean was of 2.45 cygnets/family in autumn ($n = 20$ years) and 2.18 in January ($n = 20$ years) for the 2001/02–2020/21 study period.

### Environmental variables

*Weather data*. Some years might be expected to be wetter overall than others, but there was no significant correlation between summer rainfall and autumn rainfall or between autumn rainfall and mid-winter rainfall ($r_s < 0.353$, $n = 17$–$20$, $P > 0.1$, n.s. in both cases). Equally there was no evidence of any trends in rainfall or temperature over time, with no significant correlations between year and rainfall in summer, autumn or mid-winter ($r_s < 0.281$, $n = 18$–$20$, $P > 0.1$, n.s. in all cases), or between year and mean maximum and mean minimum summer temperature ($r_s < 0.148$, $n = 20$, $P > 0.1$, n.s. in both cases).

*Loch levels*. Water levels in 2007, a year of below average summer rainfall and above average autumn rainfall (see Table 1), varied by up to 0.5 m at Loch a' Phuill and by up to 0.4 m at Loch Bhasapol, with lowest levels in June–July and highest levels in October–November (from Johnson 2008). Summer loch levels were sustained in 2007 despite dry spells in June because of frequent rainfall events in late summer and responded rapidly (within a day or two) to heavy rainfall events, whilst loch levels dropped on average by 0.137 m per month during dry weather (from Johnson 2008), with a significant portion (> 30%) of Loch a' Phuill drying out completely during very dry summers such as 2006 and 2012.

## Discussion

The Icelandic Whooper Swan population increased by 155% between 1995 and 2015, including a 16% increase between 2010 and 2015 (Hall *et al.* 2016), with a consequent increase in 2019 in the threshold level (1% of the total population) used to determine sites of national and international importance for the species. In contrast, there were no significant trends in the peak autumn and January counts on Tiree between 2001 and 2020, which fits with the pattern of a declining proportion of swans wintering in Scotland (Hall *et al.* 2016). Peak swan numbers in autumn on Tiree, based largely at Loch a' Phuill, exceeded the 1% threshold for international significance in the fifteen years between 2002 and 2016, but were well below this threshold in 2017–2020 and indeed dropped below the revised 1%

 

threshold for national significance after 2018/19. While there was justification for adding Whooper Swan interest to the designation citation for the Tiree coast and wetlands SPA during 2002–2016, this is no longer the case.

There was a significant negative correlation between autumn rainfall and the peak autumn count, with largest numbers occurring in autumns with below average rainfall and lowest numbers occurring in very wet autumns. The record count of 502 swans on 3 November 2015 occurred after the driest October on record in the Outer Hebrides (Rabbits 2019). Drier autumns resulted in lower water levels in the Tiree lochs, particularly Loch a' Phuill, which would likely allow up-ending swans to access more easily a larger proportion of the submerged macrophytes in the water and their tubers in the substrate, and indeed swans were observed feeding over a much wider part of the loch than normal in autumn 2015. This accords with the situation at Loch of Lintrathen, where large flocks of Whooper Swans were recorded feeding on pondweeds exposed when water levels were low (Robinson *et al.* 2004). In wetter autumns, loch levels on Tiree rose by as much as 0.5 m above typical mid-summer levels (Johnson 2008), and swans were forced to confine their feeding to the shallower fringes of the lochs as the central portions were too deep for them to reach easily the submerged macrophytes and tubers. This situation is analogous to salt-water feeding, where Whooper Swans feed mostly at low tide as feeding is harder in deeper water during high tide (Brazil 2003). This also concurs with the findings of Klaassen & Nolet (2007), who found that Bewick's Swans *Cygnus columbianus bewickii* feeding on *Potamogeton* tubers in the Netherlands preferred intermediate water depths, where the water was deep enough to uproot the tubers out of the sediment by trampling, but also shallow enough for swans to reach the uprooted tubers on the bottom with their beaks.

Thus, peak autumn numbers recorded feeding on Tiree would appear to be constrained by access to food supply in autumns with higher than average rainfall creating higher loch levels. This would account for the observations of large numbers of swans passing through without stopping or pausing only briefly in wetter autumns, possibly because individual returning birds could assess loch levels, and hence access to food supplies, from above. Peak autumn numbers at some other key Scottish sites also varied greatly over the same period with, for example, 797 at Loch Eye in October 2008 but only 4 birds there in autumn 2009, and 92 counted at Loch of Strathbeg in November 2007 increasing to 1,188 present in November 2019 and a record 1,599 in October 2018 (Holt *et al.* 2012; RSPB unpubl. data). These wide fluctuations have been put down to variation in the amount of pondweed forage available thought to result from increased growth during dry summers (*i.e.* lowered water levels) in these shallow eutrophic lochs (Cranswick *et al.* 1996). However, neither the effect of autumn water levels on subsequent access to the pondweeds and their tubers was considered, nor indeed access to adjacent flooded unharvested arable crops in very wet autumns. The

 

opposite was found to be the case on Tiree, where peak autumn swan numbers were significantly lower following unusually dry summers, possibly resulting from reduced macrophyte growth in large areas of Loch a' Phuill, which had dried out completely. In contrast, there was no correlation between water levels and swan numbers at Loch Insh in the Highlands region of Scotland (C. Mitchell pers. comm.), since swans there were grazing on floodplain sedges, as opposed to submerged macrophytes.

McElwaine *et al.* (1995) found some evidence to suggest that predominant wind direction during the autumn migratory months of October–November in Northern Ireland affected the number and subsequent movements of individually ringed swans between Ireland and Britain later in the same winter. Autumns in which easterly winds predominated over westerly winds resulted in significantly more birds moving from Ireland to Britain than expected, whilst the reverse was generally true when westerly winds predominated over easterly winds, suggesting that some swans had been diverted by the prevailing winds and not arrived where they would later go on to spend the winter (McElwaine *et al.* 1995). In the current study, however, the proportion of westerly and easterly winds in autumn on Tiree had no significant effect on peak autumn numbers, nor indeed on numbers recorded in January, suggesting that Tiree swans do not go to Ireland first.

January counts were above the 1% threshold for national significance in most winters between 2001/02 and 2018/19 but dropped below the 1% threshold figure when it was revised upwards from 110 to 160 in 2019 (Frost *et al.* 2020). Although the January count on Tiree was higher in 2010 than in 2015 and 2020, the overall proportion of birds wintering in Scotland was slightly higher in both 2015 and 2020 than in 2010 (Hall *et al.* 2016; Brides *et al.* 2021). However, the proportion of birds wintering in Scotland has declined generally since 1986 as the proportion has risen in England, resulting in a decline in the number of sites achieving national significance in Scotland, with seven of the nine British sites that did not maintain either internationally or nationally important numbers between the 2015 and 2020 Icelandic Whooper Swan census being in Scotland (Brides *et al.* 2021).

The significant negative relationship between mid-winter rainfall and January counts indicated that numbers of swans wintering on the island were likely also constrained by access to submerged food supplies in wetter winters. There was no correlation between autumn peak counts and January counts within the same winter, which might have been expected. However, equally there was no correlation between autumn and mid-winter rainfall within the same winter, suggesting that swan numbers in January were affected directly by mid-winter loch levels irrespective of the numbers that arrived and stayed to feed on the lochs in autumn.

The annual proportion of cygnets recorded on Tiree did not differ significantly from elsewhere in the UK. This contrasts with the findings of Hall *et al.* (2016) who showed that flocks in northern regions of Scotland and Ireland had significantly higher proportions of cygnets than those further

 

south in the British Isles, reflecting a tendency for Whooper Swan families to stay closer to their breeding grounds, with more non-breeding birds migrating further south (Rees *et al.* 1997). The fact that the proportion of young recorded each year on Tiree did not correlate with either peak autumn counts or January counts, reinforces the view that variation in swan numbers on the island was affected by external factors such as food supply, rather than annual variation in demographics. Age assessments conducted on single days in autumn are believed to be less reliable indicators of overall breeding success than those in January, as non-breeding birds and families may migrate at different times (Cranswick 1998). However, age assessments made during the autumn peak counts on Tiree were positively correlated with those made in January of the same winter. This suggests that age-counts taken at peak autumn migration on Tiree, and by inference maybe at other key Scottish sites, could be used as a reasonable substitute for age-counts in January. Presumably because of the larger sample sizes involved, and perhaps also because many non-breeders (which tend to be the first to migrate in autumn) had already passed through to more southerly wintering sites, so that those present during peak autumn migration were more representative of those remaining on Tiree in January.

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**Photograph:** Whooper Swans feeding on submerged macrophytes at Loch Eilein, Isle of Tiree, by John Bowler.