Status and distribution of the Common Shelduck *Tadorna tadorna* in Iceland, with special reference to the core area in Borgarfjörður

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Abstract

The Common Shelduck *Tadorna tadorna* was first recorded as a breeding bird in Iceland in 1990. Since then, local monitoring programmes and casual observations suggest that the population has expanded in range and abundance, but a detailed overview of its breeding locations and the total number of birds recorded has not been compiled to date. We therefore investigated the size and distribution of the Icelandic population by collating information from published literature and from personal observations by the authors and birdwatchers (eBird, social media) reported between 1990 and 2019 inclusive. At the core breeding area in Borgarfjörður (western Iceland), low and rising tide surveys were conducted each week between 12 March and 25 October 2017 to investigate spring arrival times, overall numbers and site usage. The number of breeding pairs was estimated from the number of broods observed in June and July. The Icelandic population was estimated at 274 breeding pairs. Borgarfjörður continues to support the biggest aggregations, and the most breeding pairs (158 pairs, *c.* 60% of the Icelandic breeding population). The next most important areas are Breiðafjörður (northwest Iceland) and Melrakkaslétta (northeast Iceland) (*c.* 20 pairs each). The first arrivals in Borgarfjörður were recorded on 12 March. Birds were present throughout the survey period and 100 birds remained on the last survey on 25 October. A high count of 1,368 Shelducks was recorded on 26 June. The tidal state, subarea and week of the survey each had a significant effect on Shelduck numbers. This study shows that the population has grown exponentially and there has been a considerable expansion in breeding range.

A coordinated national survey is required to assess the population size and range more accurately. The relatively large numbers, and the proportion of the national population that occurs in Borgarfjörður, make it an attractive site for further research on these birds: on their wintering and moulting areas, productivity, diet and survival rates.

Keywords: breeding surveys, Iceland, population status, range, *Tadorna tadorna*.

The Common Shelduck *Tadorna tadorna* (hereafter Shelduck) has long been an irregular and rare vagrant to Iceland. The species was first recorded in the country in 1894 (Gröndal 1895), and by 1981 there were 21 records, totalling 25 individuals (Pétursson & Þráinsson 1999). During the past three decades, however, they have become regular breeders, with the first breeding pair reported at Eyjafjörður, northern Iceland, in 1990 (Snorrason 1992), and a second pair (with ducklings) at Borgarfjörður, west Iceland, in 1992 (Þráinsson *et al.* 1994). Since then the Shelduck's breeding distribution has expanded, and the population has increased substantially. Regional studies have been published on Shelduck nesting in Borgarfjörður during 2007–2008 (Jónsson 2011) and on the Melrakkaslétta Peninsula in northeast Iceland, during 2007–2009 (Kolbeinsson & Benediktsson 2013; Hjartarson 2016), but an overview of all breeding locations and bird numbers is required to describe changes in the numbers and distribution of Shelduck breeding in Iceland since the early 1990s.

Several waterfowl species, such as Northern Shoveler *Spatula clypeata*, Gadwall *Mareca strepera*, Common Pochard *Aythya farina* and Tufted Duck *Aythya fuligula*, have expanded their breeding range northwards into Iceland since the 1890s (Gudmundsson 1951). Species that breed in Iceland, such as Whooper Swan *Cygnus cygnus* (Hall *et al.* 2012), Pink-footed Goose *Anser brachyrhynchus* (Mitchell 2015) and Barnacle Goose *Branta leucopsis* (Mitchell & Hall 2020) have shown recent population increases. Barnacle Geese first nested in southeast Iceland in 1988 (Þorsteinsson *et al.* 1989), and have increased rapidly there since then (Jóhannesdóttir 2020).

The Shelduck population trend in Europe is increasing (BirdLife International 2015), with numbers rising throughout most of northwestern Europe in recent decades (Hagemeijer & Blair 1997). At similar latitudes to Iceland, Shelduck breeding populations have increased and their ranges have extended northwards in Norway (Størkersen 1994) and Sweden (HELCOM 2013). They recolonised Finland in 1968 (Cramp & Simmons 1977) and their distribution there is also expanding (Valkama *et al.* 2011). Climatic models predict that, by the end of the 21st century, much of Iceland will be suitable for breeding Shelduck (Huntly *et al.* 2007).

This paper aims to describe the breeding distribution and numbers of breeding pairs for Shelduck across Iceland during 2017–2018, with a view to describing its current status at the national level. Additionally, due to the considerable increase in numbers at the core area in Borgarfjörður in the ten

years since the last assessment (Jónsson 2011), we estimate the breeding population size in 2017. We include a statistical analysis on the data collected in Borgarfjörður to explore the factors that affect their patterns of abundance throughout the season.

Methods

Study area in Borgarfjörður

The study area in Borgarfjörður in western Iceland (64°33'N, 21°48'W) is the core breeding location for Shelduck in Iceland. The study area was chosen because it comprises the estuarine portion of the Andakíll Ramsar site, which is designated in part on account of the Shelduck numbers it supports (Ramsar 2013). The area is characterised by extensive intertidal mudflats and sandflats, surrounded by alluvial floodplains, marshes, managed hayfields and heathlands (Fig. 1). Fresh water comes mainly from two large rivers, Hvítá and Andakílsá, which flow in from the north east and east, respectively. The ingress and outflow of water is constrained by two causeways that extend into the fjord from the north and south, and water is channelled under a 500 m long road bridge.

Survey methodology

The intertidal zone and open water visible from land-based vantage points on the east and south of the fjord were surveyed by

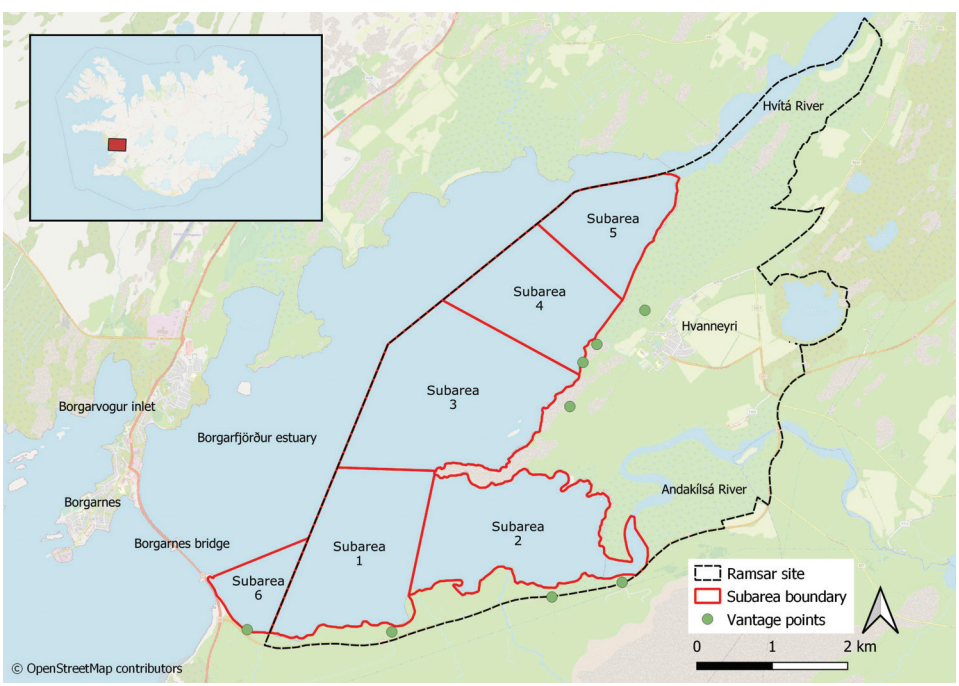

Figure 1. The study area in Borgarfjörður, western Iceland. The red lines show the site and subarea boundaries. The dots represent the vantage points used during surveys. The black dashed line shows the boundary of the Andakíll Ramsar site.

RAT and NT. In order to facilitate counting, the area was divided into six subareas, based on what could be surveyed from vantage points. The subareas were surveyed consecutively on each survey day.

Surveys took place between 12 March and 25 October 2017. Initially (until 24 April), five subareas were surveyed, but thereafter the study area was enlarged by including subarea 6 (Fig. 1), which lies outside the Andakíll Ramsar site boundary. In order to capture the birds' use of the area at low tide and high tide, one low tide and one rising tide survey was undertaken each week, with the exception of two weeks in August. Low tide surveys commenced two hours before low tide and were completed within four hours. Rising tide surveys commenced three hours before high tide and were completed by high tide. The available feeding area during rising tide surveys was approximately 20% of what was available during low tide surveys. The tidal inundation pattern is that the subareas in the southwest of the site are submerged first, and those in the northeast last. The subareas were surveyed in the same order during all surveys; the surveyors moved northeastwards with the tide, as the fjord filled on rising tide surveys. The total number of Shelducks was recorded in each subarea on each survey. Prior to 6 August, fully-grown birds were counted separately to juveniles. Thereafter, when well-grown juveniles were independent of the adults and more widely dispersed in flocks, adults and juveniles were not differentiated routinely, so the counts included both adults and juveniles.

The age-profile of the flock was assessed by inspecting a proportion of the flocks and recording the ratio of adults and juveniles. Five such counts took place between 6 August and 2 October 2017. Between 35–60% of the flocks were assessed on each occasion. As the flocks were well mixed by this time in the season, the proportion of adults and juveniles was extrapolated to the total number of birds counted on that day. Juveniles were distinguished from adults by their whitish facial plumage, their grey-brown crown and hind-neck (as opposed to dark green to black in adults) and the absence of a brown chest-band or black belly stripe (Cramp & Simmons 1977).

An additional survey of suitable estuarine foraging habitat within 12 km of the study area was conducted on 5 August 2017 to determine if the survey area adequately accounted for the local Shelduck population. The area surveyed comprised: the northern shore of the Borgarfjörður estuary from the mouth of the River Hvítá to Borgarfjörður bridge; the intertidal areas west of the Borgarfjörður bridge surrounding the town of Borgarnes; the Borgarnes inlet; and the Langárós estuary, west of Borgarnes.

Estimating the number of breeding pairs

From 5 June onwards, when ducklings were first present on the estuary, the number and size of family groups and crèches was counted. As the flocks may have contained breeding adults, failed breeders, immature birds, and mature non-breeders, the number of breeding pairs had to be estimated based on the number of broods recorded. However, as Shelduck broods amalgamate into crèches comprising ducklings from two or more broods, the total number of

broods had to be estimated, based on the average brood size counted on a given day. A group of ducklings with an adult or adults was considered a "brood" if it contained ≤ 12 ducklings, and "crèche" if it contained 13 ducklings or more. This upper limit of 12 ducklings was chosen as it is likely that broods comprising more than this are the result of more than a single pair (Hori 1969; Patterson 1982).

To estimate the number of broods within a crèche, the number of ducklings in each crèche was divided by the average brood size calculated on that day, and the resulting number was rounded up to the nearest whole number. The estimated number of broods from all crèches was added to the number of individual broods counted, to give the total estimated number of broods on each survey between mid-June and the end of July. The estimated number of successful breeding pairs was then calculated from the estimated number of broods. In a 13-year study, Patterson (1982) found that the average number of pairs that successfully took ducklings to water was 40.5% (range: 25–55%), so the total number of breeding pairs was estimated on the basis of this level of nesting success. Birds frequenting the Borgarfjörður estuary and mudflats are presumed to nest in the vicinity of the mudflats used for feeding, and when their chicks hatch, they are led by their parents to the feeding areas, but in most cases the nest locations are not known.

Statistical analysis

Exploratory analysis and knowledge of the ecology of the system led to the following decisions around model structure. A Poisson or negative binomial error structure was required for the response variable, *i.e.* the Shelduck counts across Borgarfjörður. Tide and subarea were included as fixed explanatory variables to allow inference of their effects on the count data. The area of each subarea was included as an offset. There are a number of advantages of using an offset as opposed to analysing densities (Zuur *et al.* 2007). A frequency plot indicated large numbers of zeros. These were classified as "true" zeros, *i.e.* the zeros are the result of a real ecological effect (Martin *et al.* 2005; Zuur *et al.* 2007); therefore, a zero-inflated mixture model was required. Scatterplots indicated a non-linear pattern of Shelduck counts over time, so a general additive model (GAM) was used to account for this when making inference about other variables.

Zero-inflated Poisson GAMs were fitted by using the "gam" function of the "mgcv" package (Wood 2017) in RStudio v 1.2.5019 (R Core Team 2019). This smoothed the counts using regression splines. The minimum adequate model was selected by backward selection using the Akaike information criterion (AIC). The model with the lowest AIC was validated graphically using deviance residuals (Zuur *et al.* 2007) (Supporting Materials Table S1, Fig. S1).

Population size and distribution in Iceland

Information on the number of breeding pairs reported across Iceland in 2017–2018 was extracted from the literature (*e.g.* the annual rare bird reports published in the Icelandic ornithological journal *Blikt*), personal observations (by A.P., Þ.B. and

Y.K.), communications with local or other observers, and open source bird databases (*e.g.* eBird), to describe the breeding distribution for the species nationally. Information on the locations of breeding birds also includes some records for 2019; the population size estimate is based primarily on 2017 data, when we undertook the Borgarfjörður surveys, acknowledging that not all Icelandic sites were counted in the same year. Information for certain areas was obtainable only for 2018, and in some cases only older data (pre 2017) were available.

Results

Borgarfjörður surveys

Total numbers throughout the season

Shelduck were present during all surveys between 12 March and 25 October 2017. Fourteen birds were recorded during the first survey (on 12 March) and numbers then increased rapidly until 3 April, when 253 birds were counted. There were 200–250 birds present during April, and numbers rose again during May and June to a peak of 1,368 (fully-grown) birds on 26 June. Numbers declined considerably during July. Despite some high counts during August and September, numbers gradually declined until the last survey on 25 October (Fig. 2). There was a significant association between the week of the survey and the number of Shelducks in the study area (Supporting Materials Table S2). Modelled counts peaked in early July, followed by a second, smaller peak in early September (Supporting Materials Fig. S2). This pattern fits the data most clearly for subarea 2, the subarea for which there were the most observations (Fig. 3).

While outside the designated study

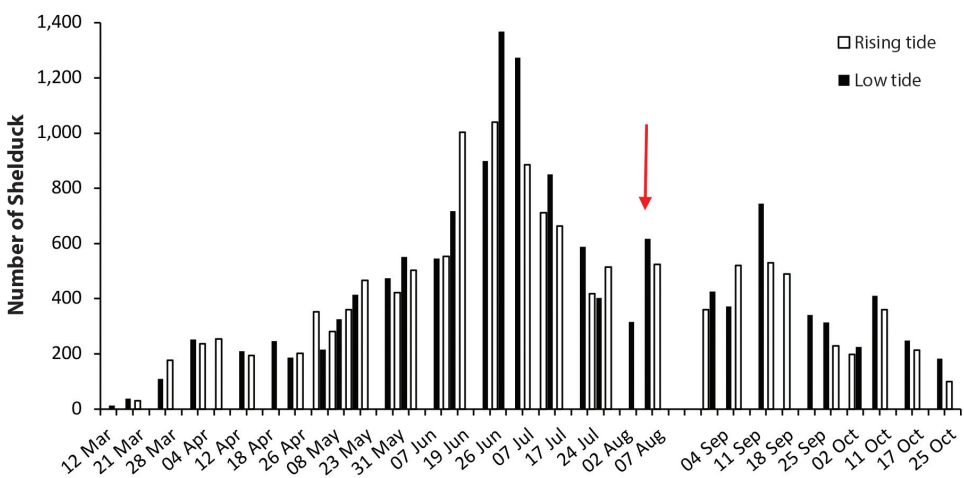

Figure 2. Numbers of Shelduck recorded in the Borgarfjörður study area during weekly low tide and rising tide surveys from 12 March–25 October 2017. Prior to 6 August (arrow), counts included only adult birds. Thereafter adults and juveniles were not differentiated routinely, so the counts from 6 August onwards include both adults and juveniles.

area, the north-western shores of the Borgarfjörður estuary were visible during each survey, and Shelduck were never observed there. The survey of the wider area, conducted on 5 August, resulted in no Shelduck being recorded in the areas surveyed within 12 km of the study area.

Distribution of Shelduck across the study area

Shelduck were distributed throughout the study area (Fig. 4), especially in the early part of the survey period. In most surveys, the highest numbers were in subarea 2, on the mudflats at the outflow of the River Andakílsá (Figs. 3 & 4). The average density in subarea 2 throughout the survey period was 87 birds/km^2. This increased to 190 birds/km^2 in the period when the highest numbers were present (12 June–10 July). Subareas 1 and 3 were used in the first half of the season, and almost not at all subsequently (Fig. 3). Subarea 4 was mainly used during the middle part of the season, between 8 May and the end of July. Unfortunately, there was insufficient statistical power to test whether these seasonal variations were significant. However, there was a highly significant effect of subarea and tide on counts and a significant interaction between the two variables (Supporting Materials Table S2). The curves of the modelled count reflect differences in magnitudes caused by subarea and tide (Supporting Materials Fig. S2).

There were several regularly used high tide roosts, both on the water and above the high tide line. These were mostly in subarea 2, but also in subareas 1 and 3.

Estimate of breeding pairs

The first two broods appeared on the estuary on 5 June, and there was an overall

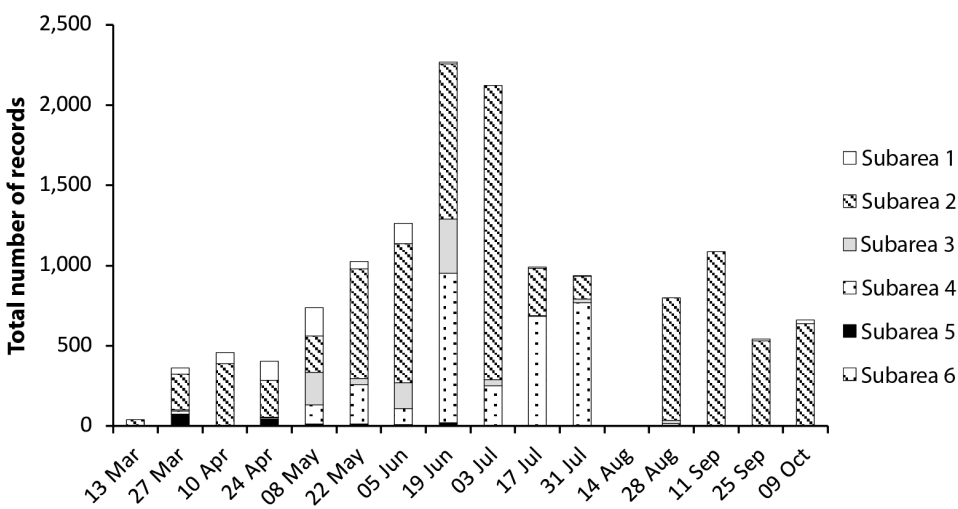

Figure 3. Number of Shelduck records in each subarea at the Borgarfjörður study site during low tide surveys in two-week periods from 12 March–23 October 2017. No surveys were conducted from 14–27 August inclusive.

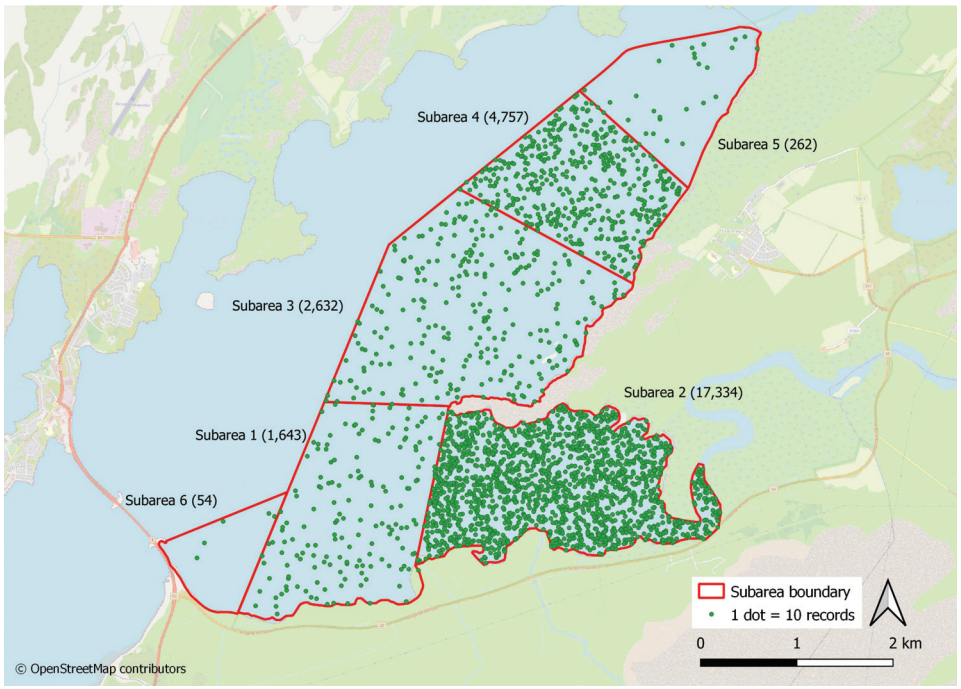

Figure 4. Relative abundance of Shelducks during weekly low tide and rising tide surveys in the Borgarfjörður study area from 12 March–25 October 2017. Each dot represents the presence of 10 birds in that subarea, not the specific location of birds. The numbers in brackets refer to the total number of bird-records in each subarea throughout the survey period.

increase in the number of broods until 31 July (Fig. 5). Visibility was impaired during the surveys on 10 and 17 July, due to heat haze and choppy conditions, respectively. This may have resulted in ducklings being missed. Based on the number of broods and the number of ducklings in crèches, there was an estimated total of 64 broods on the estuary on 31 July. This date was chosen to estimate the local breeding population, as it included the birds that held territories on the mudflats and nested close to the study area, and also those that nested further afield, but took their ducklings to the study area. However, the size of this catchment is not known. Assuming 40.5% (range: 25–55%) of pairs that attempt to breed, nest successfully and take ducklings to water (see Patterson 1982), this indicates 158 (range: 116–256) breeding pairs.

Ratios of adults to juveniles

The total number of birds present during August, September and October was variable, ranging between 100–744 birds. There was a general decline from mid-September, then an increase in mid-October and a subsequent decline thereafter (Fig. 6). On each of the five surveys when the proportion of adults and juveniles was assessed, the flocks were

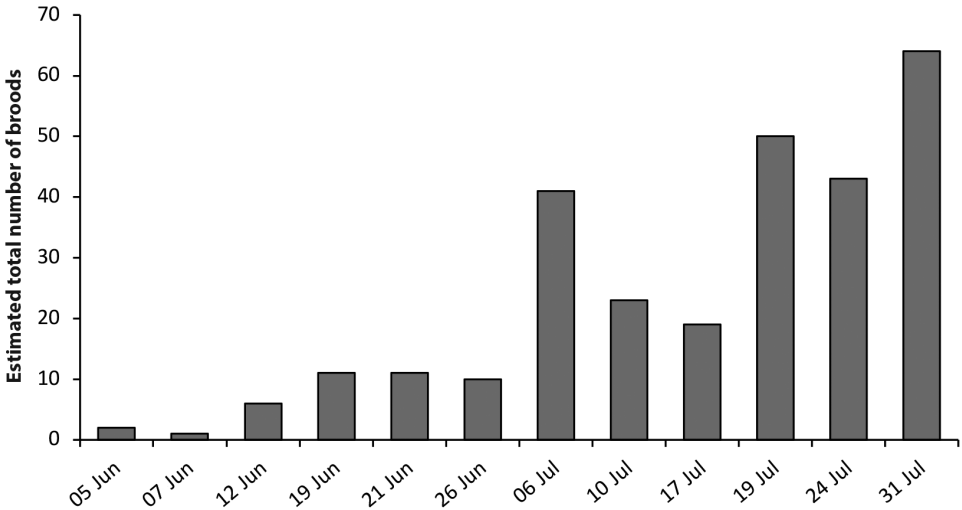

Figure 5. Total number of Shelduck broods estimated for the Borgarfjörður study area during 5 June–31 July 2017. Brood counts ceased on 31 July, because most of the juveniles were well-grown or were not associating in close family groups.

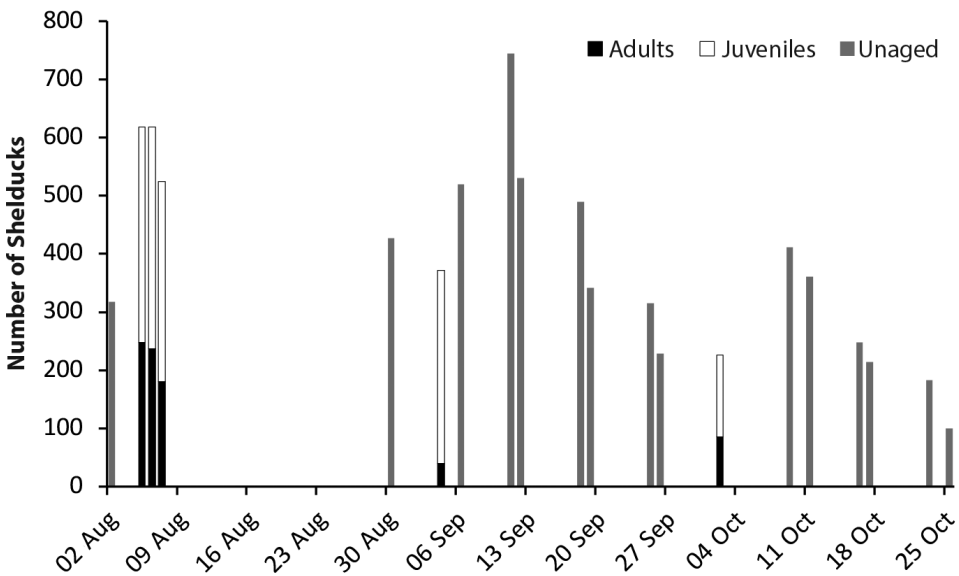

Figure 6. The number of Shelducks recorded in the Borgarfjörður study area from 2 August–25 October 2017. Bi-coloured bars represent surveys where the age ratio of a sample of the flock was assessed. The proportion of adults and juveniles from these samples was extrapolated to the total number of birds counted on that day. Grey bars refer to surveys when adults and juveniles were not distinguished.

composed of between 60–89% juveniles (mean = 68%, s.d. = 12%).

Breeding Shelducks at the national level

Shelducks breed sporadically around most of the Icelandic coastline where suitable habitats, such as mudflats, coastal marshes and lagoons, exist (Fig. 7).

The greatest number of breeding birds by far is in Borgarfjörður, with 158 pairs (this study), and breeding occurs in another eight 10 km squares in the region totalling 23 pairs. Much lower numbers occur on Melrakkaslétta (northeast Iceland) (*c.* 20 pairs in eight 10 km squares) and Breiðafjörður (northwest Iceland) (*c.* 20 pairs in eleven 10 km squares). There are fewer than ten pairs each at Eyjafjörður (northern Iceland), Strandir and Sigríðarstaðavatn (northwest Iceland), Vopnafjörður (northeast Iceland), Djúpivogur, Álftafjörður and Hornafjörður (southeast Iceland), and the Selfoss area (southern Iceland), while most other breeding sites hold single pairs. A pair with young was observed in Norðfjörður (east Iceland) in 2000 (Kolbeinsson *et al.* 2003), but is not included here as this was on

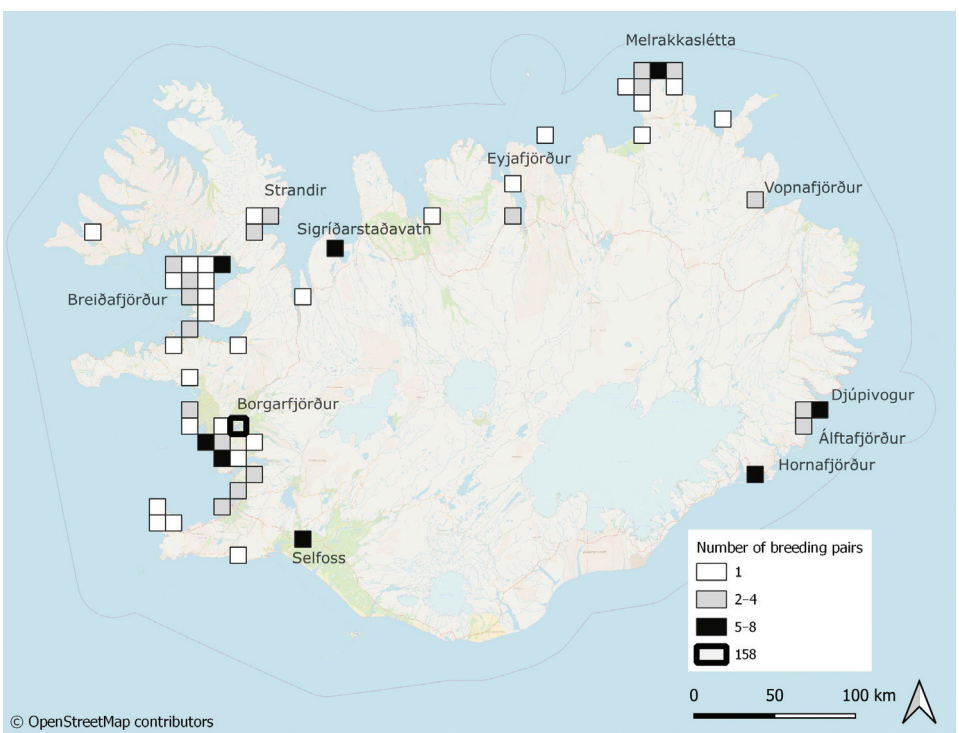

Figure 7. The known breeding locations of Shelducks in Iceland in 2017–2018. Squares represent 10 km squares where nests or broods of small ducklings have been seen. As a full census of the population has not been undertaken in a single year, older data was used for some locations, and information only for 2019 was used for others.

12 September, the young had fledged and may have come from elsewhere. Breeding Shelducks have not been recorded there since.

As breeding numbers have not been estimated at all locations in the same year, only a rough estimate can be made of the Icelandic-breeding population. However, the information that has been gathered indicates that the population is expanding exponentially (Fig. 8), and in 2017–2018 the Icelandic population was estimated at 274 breeding pairs.

The colonisation of the species across Iceland appears to have progressed from multiple centres, and not solely from the earliest settlement locations (Fig. 9). Breeding was recorded for the first time in four 10 km squares in the 1990s, 17 in the 2000s, and 34 in the 2010s. The range expansion appears to be greater in the west of the country, in Breiðafjörður and the Borgarfjörður region, than in other regions. In Eyjafjörður (where breeding was first recorded in Iceland in 1990), Hornafjörður (first breeding record in 2001) and

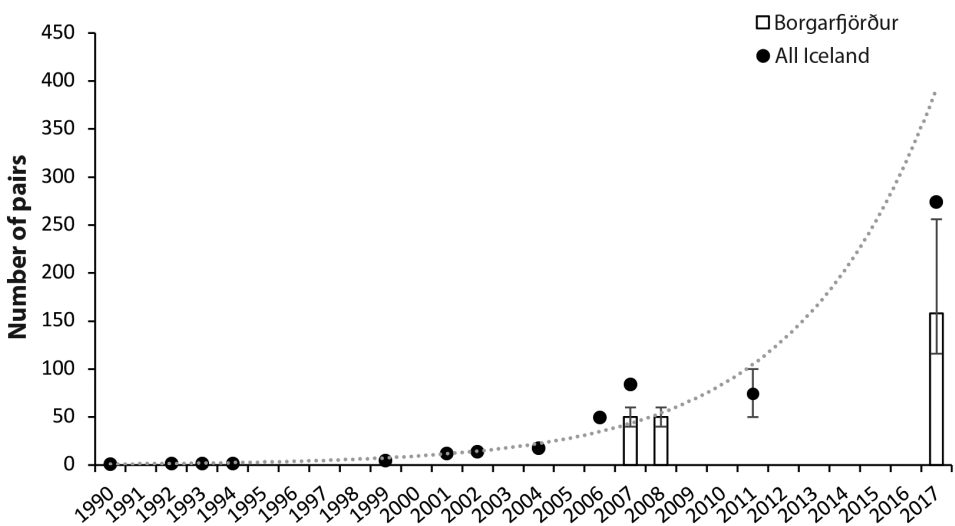

Figure 8. Number of Shelduck pairs in Iceland from 1990–2017. The dotted line represents the exponential trend; bars represent the number of pairs in Borgarfjörður in 2007 and 2008 (Jónsson 2011), and in 2017 (this study). The number of pairs for Borgarfjörður in 2017 is based on the assumption that 40.5% (range: 25–55%) of pairs that attempt to breed, nest successfully and take ducklings to water (see Patterson 1982). All figures are estimates because counts made in different parts of Iceland were not undertaken in the same year. Data sources for the counts in each year: 1990 (Snorrason 1992); 1992 (Þráinsson *et al.* 1994); 1993 (Þráinsson *et al.* 1995a); 1994 (Þráinsson *et al.* 1995b); 1999 (Anon [Hilmarsson & Einarsson] 2000; Kolbeinsson *et al.* 2003; Hilmarsson 1999); 2001 (Kolbeinsson *et al.* 2004); 2002 (Kolbeinsson *et al.* 2005); 2004 (Kolbeinsson *et al.* 2007); 2006 (Hreinsdóttir *et al.* 2006); 2007 (Þráinsson *et al.* 2011; Jónsson 2011); 2008 (Jónsson 2011); 2011 (Hilmarsson 2011); 2017 = present study.

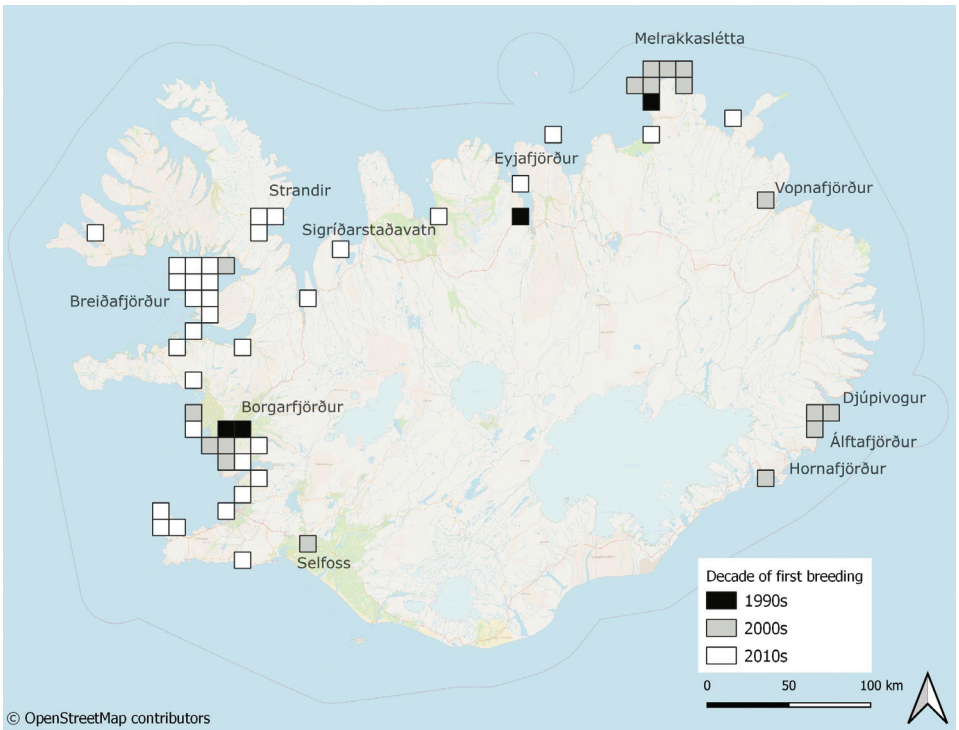

Figure 9. Known breeding locations for Shelducks in Iceland between 1990 (when breeding was first recorded) and 2019, showing the range expansion in 10-year periods. Squares represent 10 km squares where nests or broods of small ducklings have been seen.

Melrakkaslétta (1999), the populations appear to be increasing at a slower rate.

Discussion

The Borgarfjörður study area

Borgarfjörður continues to support the biggest aggregation of Shelducks, with *c.* 60% of the Icelandic breeding population. The importance of the Andakíll Ramsar site is highlighted, as Shelducks were heavily concentrated within the survey area. The weekly low tide and rising tide surveys showed that total numbers of Shelduck at the site and the number of breeding pairs estimated in 2017 far exceeded the estimate of 40–60 pairs from 2007 and 2008 (Jónsson 2011). The high survey frequency, which covered the entire breeding season, allowed a thorough assessment of how Shelducks use the Borgarfjörður mudflats and estuary, providing a description of their overall numbers, phases of arrival and departure, subarea usage, the timing of arrival of ducklings, and the proportions of adults and juveniles at the site.

Spring arrival

There were 14 Shelducks present on the first survey on 12 March, so the first arrival date

is not known. However, the main arrival occurred during March, with 38 recorded on 20 March and 177 on 28 March. This is earlier than in a previous study in Borgarfjörður, when three birds were first seen on 28 March 2007 and six pairs on 23 March 2008 (Jónsson 2011). At Melrakkaslétta (in northeast Iceland) the date of the first sighting each spring has advanced by over a month, from the last week in April to the last week in March, from 2001 to 2009 as the population has grown (Kolbeinsson & Benediktsson 2013). Barrett (2002) gives the earliest spring arrival date to Troms, northern Norway, at a similar latitude (69°N), as 21 March. While wintering Shelducks have been recorded in most years since 2007 (Icelandic Institute of Natural History 2020), the majority of the Icelandic population is migratory.

Overall numbers

The initial influx of birds and those present during April are likely to be the breeding adults (*i.e.* ≥ two years old), which arrive prior to immature, non-breeding birds (Patterson 1982). The additional birds present between May and early July are likely to include a combination of breeders, non-breeders and immature birds, in the early part of the period. And it is likely that these birds are then joined by failed breeders, local birds or from elsewhere, as the season progresses.

The provenance of the relatively high numbers of birds that were counted during late June and July is not known. However, as breeding was first recorded in 1992 (Þráinsson *et al.* 1994), and high numbers of birds have been recorded subsequently, in 2007 and 2008 (Jónsson 2011), Borgarfjörður is, and has been, the most important place for Shelducks in Iceland. This influx may reflect a traditional congregation, prior to onward migration. In the UK, conspicuous peaks in numbers have been noted before the moult period (Fox & Salmon 1994). It is likely that the high numbers, which peaked in late June and in the first week of July, include moult migrants from elsewhere in western and north-western Iceland gathering in Borgarfjörður before departing to their moulting sites. While other waterbirds moult in the study area, there was no evidence for moulting Shelducks, and it is still unknown where Icelandic Shelducks moult. The numbers of Greylag Geese *Anser anser* and Whooper Swans peaked in the study area (mainly in subarea 2) between late-June and August (N. Tierney & R. Tierney, unpubl. data), and moulted flight feathers from both species were abundant on the shoreline in this period. However, no Shelduck feathers were detected, and Shelducks were observed in flight throughout the summer.

Breeding

Shelducks have a complex social structure with males holding territories on mudflats during the breeding season, and non-breeding birds (and subsequently failed breeders) forming flocks in areas not defended by territorial birds (Hori 1969; Jenkins 1972; Patterson 1982; Kear 2005). During incubation, the male defends a feeding territory, but after hatching, the birds are less territorial and take their ducklings to nursery areas with other successful breeders (Hori 1969; Patterson 1982). As crèching and mixing of broods of

small ducklings often occurs, determining the number of breeding pairs, brood sizes, and therefore overall productivity, can be problematic.

These factors meant that a crude estimation of the number of breeding pairs was unavoidable. The number of successful breeding pairs was based on an estimation of the number of broods that were taken to water. Then, assuming only 40.5% of potential breeders breed successfully (see Patterson 1982), the total number of breeding pairs was estimated. Considering what little is known about Shelducks' usage of Borgarfjörður, it is a useful starting point. The high frequency of surveys and detailed spatial coverage within the study area will facilitate further work on this species. This can focus on key periods, such as arrival, hatching and departure.

Another way to estimate the number of breeding pairs is to examine arrival times. As younger birds (*i.e.* functional non-breeders) return to breeding areas later than adults (Patterson 1982), it is likely that birds present early in the season, in April, are prospective breeders and go on to nest in the area. The average number of birds recorded on the eight surveys in April was 223 birds. While some turnover is expected at this time, this could comprise *c.* 112 (223/2) breeding pairs. Given the uncertainties in estimating the number of breeding pairs from the number of broods observed, and the potential immigration of family groups/crèches from surrounding areas, this is broadly comparable to our estimate of 158 pairs (range: 116–256).

In much the same study area as in 2017, Jonsson (2011) estimated 40–60 breeding pairs in 2007 and 2008, with a total of 457 birds in August 2007 and 477 in August 2008. This suggests a threefold increase in the breeding population in ten years.

Emergence of ducklings

The first arrival of ducklings on the estuary on 5 June is later than recorded in the UK. The earliest brood seen on the Ythan River estuary, Aberdeenshire, from 1970–1979 was on 18 May (Patterson 1982). Hori (1969) saw broods on Sheppey Island, Kent, on 26 May, and Fox and Salmon (1994) reported first broods in Slimbridge, Gloucestershire, on 14 May in 1988. In Cheshire, broods appear from mid-May onwards (Norman 2009). On the Ythan estuary, most broods arrived on the water during June, and no new broods were observed after 15 July (Patterson 1982). In Borgarfjörður new broods arrived on the mudflats at least until the end of July. This late appearance of ducklings in the second half of July may constitute immigration into the estuary from neighbouring areas, birds that have laid later, or both.

Distribution and seasonal changes

In terms of numbers, the most important part of the study area was subarea 2, at the mouth of the River Andakílsá. The highest numbers of birds were found here for the majority of the season, and most of the ducklings were observed in this area. Shelducks were recorded in subarea 1 during all surveys until the beginning of June, and not subsequently. This suggests that the birds recorded here were territorial males that subsequently moved to other areas when the ducklings hatched.

While no benthic sampling was carried out within the study area as part of this study or previously, the birds' apparent preference for subarea 2 is most likely driven by prey availability. Subarea 2 has a higher proportion of muddier substrate than the other subareas and is the least exposed to wind and waves. Such conditions typically support high numbers of benthic invertebrates (Little 2000; McLusky & Elliot 2004; Fujii 2012), with sandier sediments supporting comparatively fewer invertebrates (Prater 1981). Furthermore, the River Andakílsá flows into subarea 2. This is a productive river and supports high levels of biodiversity (Ólafsson *et al.* 2006). The particulate organic carbon values for Andakílsá are among the highest recorded within Iceland, and much of this particulate matter is algae that flows from Lake Skorradalsvatn (*c.* 10 km inland) (Eiríksdóttir *et al.* 2010). When this enters the calm waters of the estuary, a large portion of it is deposited onto the estuarine mud, promoting the benthic invertebrate communities that are important for Shelducks. Subareas 3, 4 and 5 are sandier and comprise the outflow of the glacial River Hvítá, which is likely to carry fewer nutrients.

It is probable that small ducklings present early in the season are from pairs that nested close to the study area, and the increase in the number of broods during July is a result of immigration from the surrounding areas. The increased use of subarea 4 in late June and throughout July (Fig. 3, Supporting Materials Fig. S2) coincides with this influx, consistent with birds arriving from inland nesting sites in the River Hvítá catchment area. The reduced use of subarea 4 from late August and during September and October suggests these birds relocate to the more preferable part of the site (subarea 2) as the overall numbers decline.

Numbers nationally

There is no national monitoring programme for Shelducks in Iceland and published estimates for the Icelandic population vary in quality. While Shelducks are monitored annually at Eyjafjörður in north Iceland (S. Thorstensen, pers. comm.), and at Melrakkaslétta in northeast Iceland (Kolbeinsson *et al.* 2017, 2019; Guðmundur Ö. Benediktsson, pers. comm.), there have not been wider systematic surveys. Published figures were not available for some breeding sites in years 2017–2018, so local birdwatchers were contacted for unpublished information or best estimates. Nevertheless, the surveys at Borgarfjörður in 2017, and the nationwide collation of breeding records provides a timely estimate of this rapidly expanding population. Due to the rapid colonisation rate, especially in the last decade, and the paucity of recent data at some sites, numbers in 2017 may be higher than the 274 pairs estimated. Hilmarsson (2017) puts the population at 200–300 pairs. It is likely, too, that there are Shelduck breeding areas that have not been discovered.

The population has expanded unevenly, with massive increases in some places, and much more modest increases in others. However, the data is insufficient to conduct robust regional assessments of growth rate.

Most of the population occurs in three main hotspots. Aside from Borgarfjörður, there are two regions (Breiðafjörður and

Melrakkaslétta) with > 15 breeding pairs. While pairs are distributed all around the country's coastline, where suitable habitat exists, most of the breeding sites are on the west coast. This is broadly aligned with the distribution of littoral mudflats as mapped in Ottósson *et al.* (2016). It is not clear why some areas have been colonised and others have not, nor whether carrying capacities at particular sites have been reached. Many apparently suitable mudflat areas, such as at Rif and Bjarnarhöfn (western Iceland), Önundarfjörður (northwest Iceland), Siglufjörður (northern Iceland) and Lón (southeast Iceland), have not been colonised.

Some areas need to be surveyed in more detail. One such area is the outer Mýrar (western Iceland) where large numbers of Shelducks (100s) are seen near breeding locations in May (A. Petersen, pers. obs.). The Breiðafjörður region has around 3,000 islands, numerous nesting possibilities (including Atlantic Puffin *Fratercula arctica* burrows), and extensive intertidal mudflats. Hornafjörður would also benefit from survey attention. The most recent information for Hornafjörður is from 2007, when seven pairs were recorded (Þráinsson *et al.* 2011) and has probably increased since then (*cf.* Hjörvarsdóttir *et al.* 2016).

The Borgarfjörður mudflats are among the most extensive in the country, so it is not surprising that it is an important area for Shelducks. The density and availability of prey must play a pivotal role in this. However, there is currently no information on Shelduck diet in Iceland. Elsewhere their preferred food is the small gastropod *Hydrobia ulvae* (Buxton & Young 1981), but this is not found in Iceland (Óskarsson 1962; Óskarsson *et al.* 1977). A related species, the Spire Snail *Hydrobia ventrosa*, occurs in Iceland, but the distribution is restricted to the west and southwest of the country (Oskarsson *et al.* 1977; Skirnisson 1977; Ingolfsson 1994; Skirnisson & Galaktionov 2002). Another gastropod species, the Flat Skenea *Skeneopsis planorbis*, is very common in intertidal habitats (Óskarsson 1962) and may be an important food resource for Shelducks in Iceland.

Besides mudflats, Shelducks are also known to forage on coastal marshes and lagoons (del Hoyo *et al.* 1992; Balmer *et al.* 2013; Green *et al.* 2019). Iceland has an area of 408 km² of mudflats, *c.* 50 km² of coastal marshes, and *c.* 450 km² of lagoons (Ottósson *et al.* 2016). Based on the apparently suitable habitat that remains uncolonised, and the population growth to date, it is expected that it will expand further, in range and abundance, in the coming years.

Departure and overwintering

Icelandic Shelducks are mostly migratory and by November Shelducks have largely disappeared from Iceland (Hilmarsson 2017). In 2017, the last two surveys in the Borgarfjörður study area recorded 183 and 100 Shelducks, on 23 and 25 October, respectively (Fig. 2). In 2019, two additional surveys on 12 and 18 October resulted in totals of 1,176 and 1,025 birds, respectively (N. Tierney & R. Tierney, unpubl. data). These counts are unprecedented, both in scale and timing. This disparity in October numbers between 2017 and 2019 suggest considerable interannual differences in productivitiy and migratory behaviour.

Wintering Shelducks have been recorded in Iceland during the so-called "Christmas Bird Counts" over the last 13 years. Between one and six birds were recorded each year from winters 2007/08–2011/12, and there were 70–209 birds recorded in each winter during 2016/17–2019/20 (Icelandic Institute of Natural History 2020). This increasing trend, albeit with variable numbers, could be as a result of the increased population size and/or generally milder winters. Individual birds may switch wintering areas depending on the harshness of winter, as do some other bird species such as Greylag Geese and Whooper Swans. As there has been little ringing of Shelducks in Iceland (the first birds were ringed in 2017; Þ. Björnsson, pers. comm.), and no geolocator or satellite-tracking work to date, the wintering grounds of the Icelandic Shelduck population are still not known.

Further studies and recommendations

Being recent colonists in Iceland, many principal life history traits such as wintering and moulting areas, productivity, diet and survival are unknown. A coordinated national breeding survey is the most pressing issue, to obtain more detailed information on abundance and breeding distribution. Many current breeding locations need to be surveyed more systematically than hitherto, as well as other potential breeding areas.

A colour-ringing programme would be important to discover the moulting and wintering areas. Yet, the use of geolocators or GPS devices would provide such information more rapidly, as well as determining arrival and departure dates, and the proportion of migratory and sedentary birds in the population. GPS devices would also allow fine-scale investigation of habitat use.

Benthic sampling of the intertidal mudflats used by Shelducks is needed to determine prey composition and abundance, seasonally and spatially. Investigating prey abundance at uncolonised estuaries and mudflats would be informative. Comparing bird densities at preferred habitats and the national availability of these habitats, would give an indication of the theoretical maximum population and its distribution.

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References

Anon [Hilmarsson, J.Ó. & Einarsson, Ó.] 2000. Brandendur í sókn. (Varp 1999). *Fuglaverndarfélag Íslands, Fréttabréf* 13: 10–11. [In Icelandic.]

Balmer, D.E., Gillings, S., Caffrey, B., Swann, R.L., Downie, I.S. & Fuller, R.J. 2013. *Bird Atlas 2007–11: the Breeding and Wintering Birds of Britain and Ireland*. British Trust for Ornithology, Thetford, UK.

Barrett, R.T. 2002. The phenology of spring bird migration to north Norway. *Bird Study* 49: 270–277.

BirdLife International. 2015. *European Red List of Birds*. Office for Official Publications of the European Communities, Luxembourg.

Buxton, N.E. & Young, C.M. 1981. The food of the Shelduck in north-east Scotland. *Bird Study* 28: 41–48.

Cramp, S. & Simmons, K.E.L. (eds.). 1977. *The Birds of the Western Palearctic. Vol. 1*. Oxford University Press, Oxford, UK.

del Hoyo, J., Elliot, A. & Sargatal, J. 1992. *Handbook of the Birds of the World, Vol. 1: Ostrich to Ducks*. Lynx Edicions, Barcelona, Spain.

Eiríksdóttir, E.S., Gíslason, S.R., Snorrason, A., Harðardóttir, J., Þorláksdóttir, S.B., &. Eyþórsdóttir, K.G. 2010. Efnasamsetning, rennsli og aurburður straumvatna á Vesturlandi IV. *Gagnagrunnur Raunvísindastofnunar og Orkustofnunar*. RH21-2010, 46 pp. Veðurstofa Íslands and Umhverfisstofnun. Reykjavík, Iceland. [In Icelandic.]

Fox, A.D. & Salmon, D.G. 1994. Breeding and moulting shelduck (*Tadorna tadorna*) of the Severn Estuary. *Biological Journal of the Linnean Society* 51: 237–245.

Fujii, T. 2012. Climate change, sea-level rise and implications for coastal and estuarine shoreline management with particular reference to the ecology of intertidal benthic macrofauna in NW Europe. *Biology* 1: 597–616.

Green, R.M.W., Burton, N.H.K. & Cook, A.S.C.P. 2019. Review of the migratory movements of Shelduck to inform understanding of potential interactions with offshore wind farms in the southern North Sea. BTO Research Report No. 718. British Trust for Ornithology, Thetford, UK.

Gröndal, B. 1895. Íslenzkt fuglatal (Aves Islandiae). *Skýrsla um hið íslenska náttúrufræðisfélag árið* 1894–95: 17–71. [In Icelandic with English summary.]

Gudmundsson, F. 1951. The effects of the recent climatic changes on the bird life of Iceland. *Proceedings of the International Ornithological Congress* 10: 502–514.

Hagemeijer, W.J.M. & Blair, M.J. (eds.) 1997. *The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance*. T. & A.D. Poyser. London, UK.

Hall, C., Glanville, J.R., Boland, H., Einarsson, Ó., McElwaine, G., Holt, C.A., Spray, C.J. & Rees, E.C. 2012. Population size and breeding success of Icelandic Whooper Swans *Cygnus cygnus*: results of the 2010 international census. *Wildfowl* 62: 73–96.

HELCOM. 2013. *HELCOM Red List Species Information Sheets (SIS) Birds*. Report for 2013. HELCOM Ministerial Meeting, Helsinki, Finland.

Hilmarsson, J.Ó. 1999. *Íslanskur Fuglavísir*. Iðunn, Reykjavík, Iceland. [In Icelandic.]

Hilmarsson, J.Ó. 2011. *Icelandic Bird Guide (2nd Edition)*. Mál og menning, Reykjavik, Iceland.

Hilmarsson, J.Ó. 2017. *Fuglavefur Námsgagnastofnunar*. Námsgagnastofnun, Reykjavík, Iceland. Available at https://fuglavefur.is/birdinfo.php?val=1&id=72 (last accessed 12 May 2020).

Hilmarsson, J.Ó. 2019. Varp sjaldgæfra varpfugla 2017–18. *Fuglar* 12: 14–17. [In Icelandic.]

Hjartarson G. 2016. Fuglalíf á Sléttu. (Dýralíf á Melrakkasléttu). *In* Níels Á. Lund (ed.), *Sléttunga I (Safn til sögu Melrakkasléttu. Náttúra og mannlíf)*, pp. 143–145. Skrudda, Reykjavík, Iceland.

Hjörvarsdóttir, H.Ó., Hermannsdóttir, K., Arnarson, B.G., Stefánsson, J.H. & Guðmundsson, S. 2016. Grunnrannsóknir lífríkis við Míganda í Skarðsfirði. Náttúrustofa Suðausturlands. Report No. NattSA 2016-01. Náttúrustofa Suðausturlands, Höfn, Iceland. [In Icelandic.]

Hori, N.J. 1969. Social and population studies in the shelduck. *Wildfowl* 20: 5–22.

Hreinsdóttir, R., Guðmundsson, G.A., Egilsson, K., & Guðjónsson, G. 2006. Gróður og fuglalíf á rannsóknasvæði fyrirhugaðrar vega- og brúargerðar við Hornafjarðarfljót. Náttúrufræðistofnun Íslands Report No. NÍ06015. Náttúrufræðistofnun Íslands, Reykjavik, Iceland. [In Icelandic.]

Huntley, B., Green, R.E., Collingham, Y.C. & Willis, S.G. 2007. *A Climatic Atlas of European Breeding Birds.* Durham University, RSPB and Lynx Edicions, Barcelona, Spain.

Icelandic Institute of Natural History. 2020. *Vetrarfuglatalningar*. Icelandic Institute of Natural History, Reykjavik, Iceland. Available at https://www.ni.is/media/vetrarfuglar/vet19/2019T0.htm (last accessed 12 May 2020).

Ingolfsson, A. 1994. Species assemblages in saltmarsh ponds in western Iceland in relation to environmental variables. *Estuarine, Coastal and Shelf Science* 38: 235–248.

Jenkins, D. 1972. The status of Shelducks in the Forth area. *Scottish Birds* 7: 183–201.

Jóhannesdóttir, L., Hermannsdóttir, K. & Auhage, S.N.V. 2020. Varpútbreiðsla helsingja á Suðausturlandi 2019. Unnumbered report. Náttúrustofa Suðausturlands, Hornafjörður, Iceland. [In Icelandic.]

Jónsson, J.E. 2011. Brandendur í Borgarfirði 2007 og 2008. *Bliki* 31: 25–30. [In Icelandic with English summary.]

Kear, J. 2005. *Ducks, Geese and Swans. Volume 1*. Oxford University Press, Oxford, U.K.

Kolbeinsson, Y. & Benediktsson, G.Ö. 2013. Landnám brandandar á Melrakkasléttu. *Bliki* 32: 31–33. [In Icelandic with English summary.]

Kolbeinsson, Y., Þráinsson, G. & Pétursson, G. 2003. Sjaldgæfir fuglar á Íslandi 2000. *Bliki* 24: 25–52. [In Icelandic with English summary.]

Kolbeinsson, Y., Þráinsson, G. & Pétursson, G. 2004. Sjaldgæfir fuglar á Íslandi 2001. *Bliki* 25: 25–48. [In Icelandic with English summary.]

Kolbeinsson, Y., Þráinsson, G. & Pétursson, G. 2005. Sjaldgæfir fuglar á Íslandi 2002. *Bliki* 26: 21–46. [In Icelandic with English summary.]

Kolbeinsson, Y., Þráinsson, G. & Pétursson, G. 2007. Sjaldgæfir fuglar á Íslandi 2004. *Bliki* 28: 25–50. [In Icelandic.]

Kolbeinsson, Y., Snæþórsson, A.Ö. & Þórarinsson, Þ.L. 2017. Fuglavöktun í Þingeyjarsýslum 2016. Náttúrustofa Norðausturlands Report No. NNA-1703 Náttúrustofa Norðausturlands, Húsavík, Iceland. [In Icelandic.]

Kolbeinsson, Y., Einarsson, Á., Garðarsson, A., Snæþórsson, A.Ö. & Þórarinsson, Þ.L. 2019. Ástand fuglastofna í Þingeyjarsýslum árið 2018. Náttúrustofa Norðausturlands Report No. NNA-1902. Náttúrustofa Norðausturlands, Húsavík, Iceland. [In Icelandic.]

Little, C. 2000. *The Biology of Soft Shores and Estuaries.* Oxford University Press, Oxford, UK.

Martin, T.G., Wintle, B.A., Rhodes, J.R., Kuhnert, P.M., Field, S.A., Low-Choy, S.J., Tyre, A.J. & Possingham, H.P. 2005. Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. *Ecology Letters* 8: 1235–1246.

McLusky, D.S. & Elliott, M. 2004. *The Estuarine Ecosystem: Ecology, Threats and Management, 3rd edition*. Oxford University Press, Oxford, UK.

Mitchell, C. 2015. Status and distribution of Icelandic-breeding geese: results of the 2014 international census. Wildfowl & Wetlands Trust Report, Slimbridge, UK.

Mitchell, C. & Hall, C. 2020. Greenland barnacle geese *Branta leucopsis* in Britain and Ireland: results of the International census, spring 2018. Scottish Natural Heritage Research Report No. 1154. SNH, Dingwall, Scotland.

Norman, D. 2009. *Birds in Cheshire and Wirral: a Breeding and Wintering Atlas*. Liverpool University Press, Liverpool, UK.

Ólafsson, J., Aðalsteinsson, H. & Gíslason, G. 2006. Vistfræði vatnsfalla á Íslandi, flokkun með tilliti til rykmýs. *Orkuþing*: 218–223. [In Icelandic.]

Óskarsson, I. 1962. *Skeldýrafána Íslands. II. Sæsniglar með skel (Gastropoda, Prosobranchia & Tectibranchia)*. Prentsmiðjan Leiftur H.F., Reykjavík, Iceland. [In Icelandic.]

Óskarsson, I., Ingólfsson, A. & Garðarsson, A. 1977. Stranddoppa (*Hydrobia ventrosa*) á Íslandi. *Náttúrufræðingurinn* 47: 8–15. [In Icelandic with English summary.]

Ottósson, J.G., Sveinsdóttir, A. & Harðardóttir, M. (eds.). 2016. *Vistgerðir á Íslandi*. Fjölrit Náttúrufræðistofnunar Report No. 54. Náttúrufræðistofnun Íslands, Reykjavik, Iceland. [In Icelandic with English summary.]

Patterson, I.J. 1982. *The Shelduck. A Study in Behavioural Ecology*. Cambridge University Press, Cambridge, UK.

Pétursson, G. & Þráinsson, G. 1999. Sjaldgæfir fuglar á Íslandi fyrir 1981. *Fjölrit Náttúrufræðistofnunar* No. 37. Náttúrufræðistofnun Íslands, Reykjavik, Iceland. [In Icelandic with English summary.]

Pétursson, G., Þráinsson, G. & Ólafsson, E. 1993. Sjaldgæfir fuglar á Íslandi 1991. *Bliki* 13: 11–44. [In Icelandic with English summary.]

Prater, A.J. 1981. *Estuary Birds of Britain and Ireland*. T. & A.D. Poyser, London, U.K.

Ramsar. 2013. Information Sheet on Ramsar Wetlands. Ramsar Convention Secretariat, Gland, Switzerland. Available at https://rsis.ramsar.org/RISapp/files/RISrep/IS2129RIS.pdf (last accessed 12 April 2020).

R Core Team. 2019. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. Vienna, Austria. Available at https://www.R-project.org/ (last accessed April 2020).

Skirnisson, K. 1977. Athuganir á lífríki Melabakka í Hnappadalssýslu. B.Sc. dissertation. University of Iceland, Reykjavík, Iceland. [In Icelandic.]

Skirnisson, K. & Galaktionov, K.V. 2002. Life cycles and transmission patterns of seabird digeneans in SW Iceland. *Sarsia* 87: 144–151.

Snorrason, Þ. 1992. Brandendur í Eyjafirði 1990. *Bliki* 12: 9–10. [In Icelandic with English summary.]

Størkersen, Ø.R. 1994. Gravand *Tadorna tadorna*. *In* J.O. Gjershaug, P.G. Thingstad, S. Eldøy & S. Byrkeland (eds.), *Norsk Fugleatlas*, pp. 70–71. Norsk Ornitologisk Forening, Klæbu, Norway. [In Norwegian.]

Þorsteinsson, B., Pálsdóttir, E. & Arnarson, B. 1989. Nýjar helsingjavarpstöðvar á Suðausturlandi. *Bliki* 8: 7–8. [In Icelandic.]

Þráinsson, G., Kolbeinsson, Y. & Pétursson, G. 2011. Sjaldgæfir fuglar á Íslandi 2007. *Bliki* 31: 41–64. [In Icelandic with English summary.]

Þráinsson, G., Pétursson, G. & Ólafsson, E. 1994. Sjaldgæfir fuglar á Íslandi 1992. *Bliki* 14: 17–48. [In Icelandic with English summary.]

Þráinsson, G., Pétursson, G. & Ólafsson, E. 1995a. Sjaldgæfir fuglar á Íslandi 1993. *Bliki* 15: 21–51. [In Icelandic with English summary.]

Þráinsson, G., Pétursson, G. & Ólafsson, E. 1995b. Sjaldgæfir fuglar á Íslandi 1994. *Bliki* 16: 11–45. [In Icelandic with English summary.]

Valkama, J., Vepsäläinen, V., & Lehikoinen, A. 2011. *The Third Finnish Breeding Bird Atlas.* Finnish Museum of Natural History and Ministry of Environment, Helsinki, Finland. Available at http://atlas3.lintuatlas.fi (last accessed 30 August 2020).

Wood, S.N. 2017. *Generalized Additive Models: an Introduction with R (2nd edition).* Chapman and Hall/CRC, Boca Raton, USA.

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. 2007. *Mixed Effects Models and Extensions in Ecology with R.* Springer Science + Business Media, Berlin, Germany.

Photograph: Shelducks in Iceland, by Sigurjón Einarsson.