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Effects of spring temperature and volcanic eruptions on wader productivity

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Key demographic parameters often show substantial annual variation that can have important consequences for rates of population growth. Since 2011 we have conducted annual estimates of the productivity of Icelandic Black-tailed Godwits *Limosa limosa islandica* over a large part of its breeding range. During this period, a volcanic eruption resulted in extensive dust deposition across the region. We show that Godwit productivity varies with spring temperatures but, in the year of the volcanic eruption, productivity was reduced to almost zero. This rare but extreme event is likely to

have had only a short-term influence, while ongoing warming of subarctic regions is potentially a more substantial driver of the continued growth of this population.

A major driver of population growth rates is the temporal variation in recruitment (Sæther et al. 2016). However, identifying temporal drivers of demography may require information collected over sufficiently large spatial scales to encompass the influence of variation in local factors such as habitat quality, density and predation rates, which can also influence demography (Jónsson et al. 2013, Stojanovic et al. 2014). In order to develop the population-wide demographic models needed in a rapidly changing world (Robinson et al. 2014), long-term, large-scale studies of temporal variation in demography are therefore needed. In particular, extreme but rare events may have important effects on demography, but are inevitably difficult to identify (Katrínardóttir et al. 2015, Senner et al. 2015).

Many populations of waders (Charadrii) breed in temperate or Arctic regions, undertake long migrations to their wintering grounds, and currently have declining global populations (Thomas et al. 2007, Delany et al. 2009, Sutherland et al. 2012). It is therefore necessary to identify drivers of variation in demographic rates of waders in order to manage their impacts. Migratory wader populations, particularly those breeding in Arctic latitudes, often show high levels of annual variation in productivity over large spatial scales. For example, the proportion of juveniles in flocks of high Arctic-nesting species on the non-breeding grounds has been shown to fluctuate annually, in association with population abundance cycles of lemmings (*Lemmus* spp., *Dicrostonyx* spp.) in the Arctic (Summers & Underhill 1987, Aharon-Rotman et al. 2015), and the proportion of juveniles in non-breeding wader flocks has also been shown to vary annually with weather conditions during the breeding season (Schekkerman et al. 1998, Beale et al. 2006).

Iceland hosts internationally important breeding populations of several wader species (Gunnarsson et al. 2006), including almost the entire population of the *islandica* subspecies of Black-tailed Godwit *Limosa limosa islandica* (Gunnarsson et al. 2005a). Godwits are restricted to breeding in lowland basins around the country, with the southern lowlands of Iceland containing the largest breeding area and hosting around half of the breeding population (Gunnarsson et al. 2006, Jóhannesdóttir et al. 2014). In 2011, a monitoring programme was initiated for Godwits (and for more species from 2012), in which brood counts are used to estimate annual variation in breeding success in the southern lowlands. In 2010 and 2011, two volcanoes erupted in Southern Iceland; Eyjafjallajökull (63° 38.0' N, 19° 37.0' W) in 2010 (14 April -23 May) and Grímsvötn (64° 25.12' N, 17° 19.48' W) in 2011 (21-28 May) (Sigmundsson et al. 2010, Petersen et al. 2012). Both these eruptions emitted large amounts of volcanic dust and, while much of the ash from Eyjafjallajökull went out to sea, Grimsvotn ash was widely distributed in southern Iceland (Gudmundsson et al. 2012). During the field season of 2011, volcanic ash was widespread in the study area but its daily prevalance was highly dependent on local weather conditions. On dry days, fieldworkers used face masks to protect their respiration as simply walking through vegetation disturbed large amounts of ash into the air. The ash was further redistributed by wind and often formed piles in depressions. A layer of ash was frequently observed covering pools in wetlands and traps for invertebrate sampling frequently became clogged with ash. Short-term negative effects of volcanic dust on birds have been reported previously, and are probably mediated through increased invertebrate mortality (Dalsgaard et al. 2007, Marske et al. 2007). For example, a pronounced reduction in breeding success of Icelandic Whimbrels *Numenius phaeopus* breeding closer to the eruption site was recorded in 2011 (Katrínardóttir et al. 2015). However, the duration of impact of the eruption on breeding waders and the spatial scale over which these effects may be apparent are unknown, as the opportunities to explore the effects of volcanic eruptions on bird demography are exceedingly rare. At high latitudes, timing of breeding and breeding success can also vary in relation to spring temperatures, probably as a consequence of temperature-driven variation in vegetation growth and invertebrate emergence and abundance (Tulp & Schekkerman 2008, Alves et al. in prep). The volcanic activity that coincided with our monitoring programme provided a unique opportunity to explore both the effects of spring temperature and of stochastic extreme events on large-scale productivity of a wader population on the sub-arctic breeding grounds. Here we quantify annual variation in Godwit productivity in order to assess whether productivity increases with spring temperatures but is negatively impacted by volcanic eruptions, and to assess the magnitude and duration of any effects of volcanic activity.

METHODS

Estimating large-scale productivity

During the last ten days of June 2011-2016, road-based surveys were carried out over a large part of the lowlands of southern Iceland (Fig. 1). The car was driven at a maximum speed of 40 km/hr, with open windows. Surveying was only conducted in dry conditions and at windspeeds below 7 m/s. Along transects which totalled 198 km (Figure. 1), the presence of all alarming adult Godwits within 100 m of the car was recorded. All habitats along the transect were surveyed irrespective of their suitability for Godwits. Godwits (and many other waders) perform noisy and conspicuous alarm behaviour near their chicks (Gunnarsson et al. 2005b) and previous studies have shown that strongly alarming adults are a robust indicator of the presence of one or more chicks (Gunnarsson et al. 2005b). Each strongly alarming individual or pair was taken as presence of a brood. In each case the perpendicular distance from the road transect to the chicks (when seen) was recorded with a laser range finder to ensure only chicks within 100 m of the road were included, along with a GPS position of the car on the road. In those cases when chicks were not observed, the distance to the alarming adult or, for pairs, the midpoint between the two adults was recorded. The number of broods recorded along the transect was used as an estimate of annual productivity. The conspicuous alarming behaviour of adults means that detectability of broods is very unlikely to vary within 100 m of the vehicle.

Weather data

To assess the influence of spring temperature on large-scale productivity, we extracted the mean daily temperature during May of each year (2011-2016) from the weather station of the Icelandic Meteorological Institute (www.vedur.is) nearest to the transect (Eyrarbakki 63˚ 52’ N, 21˚ 09’ W). The relationship between spring temperature (mean May temperature) and annual Godwit productivity was assessed using a GLM with a normal error structure, with and without the year in which the volcanic eruption took place (2011).

Timing of laying

As part of long-term studies of Godwit breeding ecology in southern Iceland, the timing of egg laying has been monitored each year since 2001 (Alves *et al*. in prep) by locating as many nests as possible and floating the eggs to hindcast the date of laying of the first egg (Liebezeit et al. 2007). In each year of 2011-2016, between 14 and 28 Godwit nests (mean = 20.6 ± 5.5 SD) were monitored in the southern lowlands. As the surveys all took place in late June, the number of broods observed in each year could be influenced by the timing of egg laying. To assess whether our annual estimates of productivity varied in relation to timing of egg laying, a GLM with annual productivity as the dependent variable and mean nest initiation date as the predictor and a normal error structure was used.

Statistics were performed in R 3.2.2 (R Development Core Team 2008).

RESULTS

The mean number of broods recorded within 100 m along the 198-km transect between 2011 and 2016 was 17.8 (± 10.1 SD) but the variation between years was extremely high (range 2-31 broods per year; Fig. 2a).

The number of broods along the transect was strongly, positively related to mean May temperature in each year between 2012 and 2016 but not when 2011 was included (Fig. 2b). In 2011, when the region was largely covered by volcanic ash, only 2 broods were recorded along the transect. This number of broods is only 7.5% of the value (26.7 broods) that would be predicted by the relationship with mean May temperature for non-eruption years (7.2 °C, the second highest May temperature in 2011-2016) (Fig. 2b).

The overall mean start of laying in 2011-2016 was 26 May (range 21-28 May), and the mean timing of nest initiation in each year was not significantly related to the number of broods present in late June (R^2 = 0.399, P = 0.18).

DISCUSSION

During a six-year period in which spring temperatures varied greatly and a major volcanic eruption took place in southern Iceland, we recorded substantial variation in the productivity of Godwits. The variation in productivity between 2012 and 2016 was very closely and positively related to mean May temperatures. However, during a relatively warm spring (2011) when a volcanic eruption impacted the study area, productivity of the Godwit population fell to almost nothing. The study provides a rare example of the magnitude of impact that extreme events such as a volcanic eruption may possibly have on bird productivity but also highlights the likely short-term duration of such an event. Godwits are long-lived (median lifespan c. 10 years; Gill et al. 2001) and events of this type are rare in comparison to their typical lifespan. A large part of the Icelandic Godwit population winters on the estuaries of Britain, and annual censuses on these areas have shown sustained increases in the Godwit population (Frost et al. 2016). Intriguingly, the population index for 2011/12 (immediately following the eruption) decreased slightly before increasing quite substantially the following winter (Frost et al. 2016), potentially reflecting the reduction and subsequent increase in productivity recorded in our surveys on the breeding grounds.

The rapid recovery of productivity in the year following the volcanic eruption (2012) indicates that the negative effects of the volcanic eruption seem to be short in duration. A similar effect has been observed in Whimbrels in the same region where large-scale breeding success was temporarily negatively impacted during the 2011 eruption (Katrínardóttir et al. 2015). In the long-term, the effects of volcanism on waders in Iceland are most likely to be positive, as volcanic dust recharges vegetated land with nutrients, buffers pH, and densities of waders across Iceland are generally higher where volcanic dust inputs are higher (Gunnarsson et al. 2015). The negative short-term effects of volcanic eruptions are likely to be due to the effects of the high volume of volcanic dust on invertebrate prey populations. Previous studies have suggested that the brittle volcanic dust can cause mortality of invertebrates through blocking of the spiracles and increased rates of abrasion and desiccation (Marske et al. 2007, Elizalde 2015). Volcanic eruptions may also influence water and air quality (Horwell & Baxter 2006, Stewart et al. 2006), and the presence of large amounts of ash covering the ground could encourage adults to defer breeding attempts in that year.

The process by which higher spring temperatures promote higher productivity is not yet fully understood but is likely to be a combination of factors. It is worth noting that even though May and June temperatures were not correlated for the set of years considered here, temperature in these months is correlated in longer time series (Alves et al. in prep.) so temperature links with productivity may well operate over longer or different periods than for the May correlate explored here. The timing of emergence of the invertebrate prey of waders can vary strongly with temperature (Tulp & Schekkerman 2008, Pearce-Higgins et al. 2010), and the resulting variation in food abundance can potentially affect both adult body condition and the growth and survival of young (Schekkerman et al. 1998a, Pearce-Higgins et al. 2010). The timing of laying of Godwits in Iceland is earlier in warmer springs (Gill et al. 2014, Alves et al. in prep) and thus variation in the number of broods counted in late June could result from differences in hatch dates (with fewer broods having hatched by late June in colder years). However, the annual variation in productivity that we recorded was unrelated to timing of laying in these years. Another potential driver of a relationship between spring weather and productivity in waders is the proportion of adults which defer breeding attempts or do not renest upon early failure each year but this may be more common in colder springs when adults are in poorer body condition. Our relationship with pre-breeding tempearature (May) may point to the potential of this process to influence large-scale productivity. However, little is known about how common deferral of breeding may be in these species.

This study shows how annual variation in productivity of a wild bird population over large areas can vary greatly in response to both rare, extreme events and moderate but persistent effects of temperature on environmental conditions. As expected for a long lived species, effects of a single year of very low productivity were short in duration and probably had a limited effect on population growth rate. The pronounced effect that spring temperature has on annual variation in productivity is, however, likely to be crucial for the future population trajectory of Godwits and related species, given the ongoing and rapid warming of Arctic and Sub-arctic regions.

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Figure 1. Map of Iceland and the location of the 198-km road transect along which Godwit broods were surveyed in late June 2011-2016.

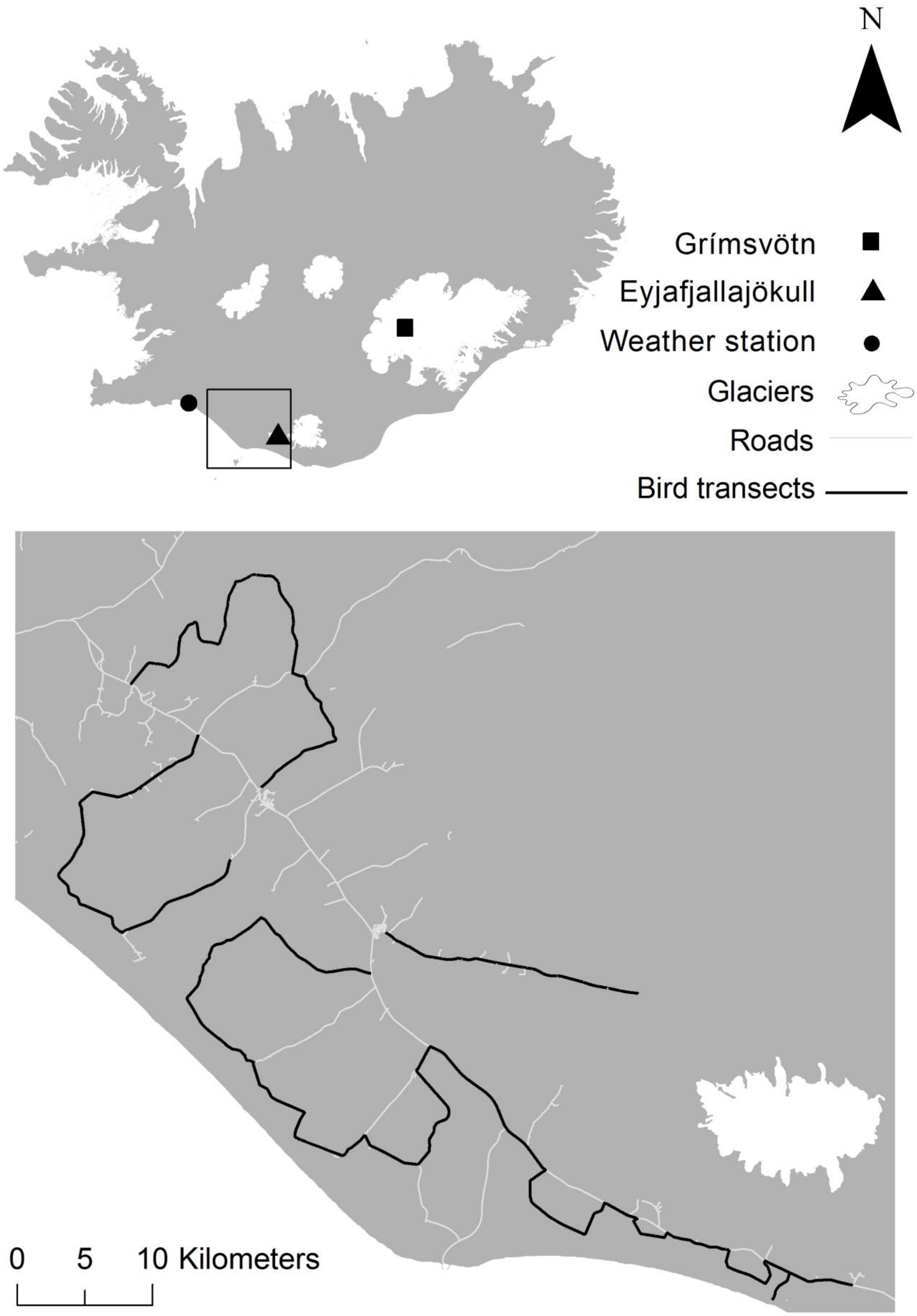

Figure 2. (a) Annual variation in productivity of Black-tailed Godwits and (b) the relationship between mean May temperature and large-scale productivity. Productivity is measured as the number of broods recorded along a fixed road transect in Southern Iceland each year. The line is fitted through years 2012-2016 but 2011, which was the only year with a volcanic eruption, is shown by an open circle. Linear model without eruption year: $R^2 = 0.94$, $P = 0.007$; Linear model including eruption year: $R^2 = 0.11$, $P = 0.53$).