## Combined bottom-up and top-down pressures drive catastrophic population declines of Arctic skuas in Scotland

**Allan Perkins,1\* Norman Ratcliffe2, Dave Suddaby3, Brian Ribbands4, Claire Smith5, Pete Ellis6, Eric Meek7 and Mark Bolton8**

*1RSPB Centre for Conservation Science, East Scotland Office, 10 Albyn Terrace, Aberdeen, AB10 1YP, UK; 2British Antarctic Survey, High Cross, Cambridge, CB3 0ET, UK; 3BirdWatch Ireland, Head Office, Unit 20 Block D, Bullford Business Campus, Kilcoole, Greystones, Co. Wicklow, Ireland; 4Queenamidda, Rendall, Orkney, KW17 2PA; 5Handa Island Skua Project, Dunkeld, Perthshire, PH8 0EP, UK; 6RSPB Scotland, Shetland Office, Sumburgh Head Lighthouse, Virkie, Shetland, ZE3 9JN, UK; 7RSPB Scotland, East Scotland Office, 10 Albyn Terrace, Aberdeen, AB10 1YP; 8RSPB Centre for Conservation Science, UK Headquarters, The Lodge, Sandy, Beds., SG19 2DL, UK*

**Dedication:** The authors wish to dedicate this article to the memory of our co-author Eric Meek, in recognition of his tireless efforts to monitor and conserve seabirds on Orkney. Sadly, he passed away during the write-up of this manuscript, but his legacy includes many research papers and the wealth of knowledge and enthusiasm for ornithology, botany and wildlife conservation that he instilled in those fortunate enough to have worked with him.

\*Corresponding author. Email: allan.perkins@rspb.org.uk

**Running head:** Drivers of Arctic skua declines

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**Summary**

**1.** Understanding drivers of population change is critical for effective species conservation. In the northeast Atlantic Ocean, recent changes amongst seabird communities are linked to human and climate change impacts on foodwebs. Many species have declined severely, with food shortages and increased predation reducing productivity. Arctic skua *Stercorarius* *parasiticus*, a kleptoparasite of other seabirds, is one such species.

**2.** The aim of the study was to determine relative effects of bottom-up and top-down pressures on Arctic skuas across multiple colonies in a rapidly declining national population.

**3.** Long-term monitoring data were used to quantify changes in population size and productivity of Arctic skuas, their hosts (black-legged kittiwake *Rissa tridactyla*, common guillemot *Uria aalge,* Atlantic puffin *Fratercula arctica*, Arctic tern *Sterna paradisaea*), and an apex predator (great skua *Stercorarius skua*) over 24 years (1992–2015) in Scotland. We used digital mapping and statistical models to determine relative effects of bottom-up (host productivity) and top-down (great skua density) pressures on Arctic skuas across 33 colonies, and assess variation between three colony types classified by host abundance.

**4.** Arctic skuas declined by 81% and their hosts by 42–92%, whereas at most colonies great skuas increased. Annual productivity declined in Arctic skuas and their hosts, and reduced Arctic skua breeding success was a driver of the species’ population decline. Arctic skua productivity was positively associated with annual breeding success of hosts, and negatively with great skua density. Inter-colony variation suggested Arctic skua trends and productivity were most sensitive to top-down pressures at smaller colonies of host species where great skuas had increased most, whereas bottom-up pressures dominated at large colonies of host species.

**5.** Scotland’s Arctic skua population is declining rapidly, with bottom-up and top-down pressures simultaneously reducing breeding success to unsustainably low levels. Marine food web alterations, strongly influenced by fisheries management and climate change, are driving the decline, and this study demonstrates severe vulnerability of seabirds to rapid change in human-modified ecosystems. Potential but untested conservation solutions for Arctic skuas include Marine Protected Areas, supplementary feeding within colonies, and management of great skuas.

**Introduction**

Food availability and predation exert bottom-up and top-down control over animal populations, and quantifying their strength helps determine drivers of population change. Human activities often influence these pressures, profoundly altering food webs and predator-prey dynamics: fishing exerts top-down pressure on commercially harvested species, relaxing or augmenting top-down regulation at lower trophic levels depending on response of other predators (Baum & Worm, 2009). Conversely, anthropogenic increases in food availability can relieve bottom-up constraints, allowing population growth which may impact other species through increased competition or predation (e.g. Bicknell *et al*., 2013; Pasanen-Mortensen *et al*., 2017).

In marine ecosystems, seabirds are often considered top predators with populations regulated by bottom-up control of their fish and plankton prey (Frederiksen *et al*., 2006). However, many species also receive top-down pressure, including predation at breeding colonies (Hipfner *et al*., 2012; Horswill *et al*., 2014). Top-down and bottom-up controls may interact, with food shortage causing some seabirds to increasingly prey upon other seabirds (Regehr & Montevecchi, 1997). Such behaviour may arise especially in heavily fished seas where human-modified food webs benefit some seabirds over others. In the northeast Atlantic Ocean, great skua *Stercorarius skua* is a scavenger whose exploitation of anthropogenic food (fish discarded from fishing vessels) and reduced persecution helped fuel recent population growth (Furness, 1977; Votier *et al*., 2008; Jones *et al*., 2008). Increasingly since the 1980s, it is also a major predator of seabirds (Hamer, Furness, & Caldow 1991; Votier *et al*., 2004; Miles *et al*., 2015). By contrast, at Scottish colonies, the smaller Arctic skua *Stercorarius* *parasiticus* eats mostly fish kleptoparasitised from terns (e.g. Arctic tern *Sterna paradisaea*), small gulls (e.g. black-legged kittiwake *Rissa tridactyla*) and auks (e.g. common guillemot *Uria aalgae* and Atlantic puffin *Fratercula arctica*) (Furness, 1977; Phillips, Caldow, & Furness 1996; Jones 2002). However, some populations prey upon invertebrates, birds, eggs and rodents (Enquist, 1983; Ruffino *et al*, 2016).

In Scotland (UK), Arctic and great skuas breed sympatrically, usually beside large colonies of cliff-nesting seabirds. In 2000–02, a national census (Seabird 2000) reported 2136 and 9634 Apparently Occupied Territories (AOTs) of Arctic skuas and great skuas respectively, with *c.*90% in the Orkney and Shetland Islands (Furness & Ratcliffe, 2004). Since then, declines reported for both species include Orkney’s Arctic skua population almost halving (Meek *et al*., 2011). These declines are a major conservation concern, due to global importance of Scotland’s great skuas (57% of world population; BirdLife International, 2018) and extent of Arctic skua decline (Eaton *et al*., 2015). Since the late 1980s, seabirds in Orkney and Shetland have experienced frequent poor breeding success, leading to localised population declines (Mitchell *et al*., 2004; Miles *et al*., 2015). Similar seabird declines throughout the northeast Atlantic Ocean (Vigfusdottir, Gunnarsson, & Gill 2013; Fauchald *et al*., 2015) are closely linked to reduced availability of lesser sandeels *Ammodytes marinus* (Phillips *et al*., 1996; Oro *&* Furness, 2002; Miles *et al*., 2015). Consequently, within Europe several seabird hosts of Arctic skuas are Endangered (e.g. Atlantic puffin), Near-Threatened (common guillemot) or Vulnerable (black-legged kittiwake), and thus Arctic skua is Endangered within the European Union (BirdLife International, 2015). Arctic skuas also receive top-down pressures from great skuas, which prey upon their young and sometimes displace or kill adults during territory disputes (Furness, 1977; Phillips, Furness, & Stewart 1998; Jones *et al*., 2008). Predation by great skuas may also drive population declines of Arctic skua hosts, thus exacerbating bottom-up pressures (Phillips, Thompson, & Hamer 1999; Oro & Furness, 2002; Votier *et al*., 2004).

Here, we analyse temporal and inter-colony variation in population size and breeding success to quantify bottom-up and top-down pressures on Arctic skuas in their core Scottish breeding areas. Specifically, we aim to 1) model population and productivity trends for Arctic skua, great skua and their hosts since the 1990s; 2) test for differences in Arctic skua trends according to local great skua and host densities; 3) determine whether variation in breeding success is driving Arctic skua population trends; 4) quantify effects of host productivity (an index of food availability) and great skua density (predation pressure) on Arctic skua breeding success. If bottom-up pressures are driving Arctic skua declines, we predict steeper declines at colonies where host productivity is lowest, which is most likely where Arctic skuas are dependent entirely on terns for food, as these hosts are highly sensitive to localised food availability (Robertson *et al*. 2014). Large colonies of cliff-nesting hosts such as auks, whose diving ability, flexible time budgets and greater foraging ranges make them less vulnerable than ground-nesting terns to local food shortage, may buffer availability of food to Arctic skuas in years when terns fail to breed successfully (Furness & Tasker 2000). However, such colonies also attract great skuas, and if top-down pressures are strongest, we predict steeper declines at colonies exposed to many great skuas. Finally, we discuss potential conservation measures to alleviate bottom-up and top-down pressures on Arctic skuas.

**Materials and methods**

DATA COLLATION

Data sources comprised a skua/tern monitoring programme in Orkney and Shetland throughout the 1990s (RSPB unpubl. data); skua censuses in 1992 and 2010 (Meek, Sim, & Ribbands1994; Sears *et al*., 1995; Meek *et al*., 2011); ‘Seabird 2000’ census (Mitchell *et al*., 2004); UK Seabird Monitoring Programme database (SMP) (Joint Nature Conservation Committee, 2016). All data were from field surveys using standardised methods (Mitchell *et al*., 2004).

Counts of Apparently Occupied Territories (AOTs) and data on annual productivity (chicks fledged per pair) were collated for all Scottish Arctic skua colonies for 1992–2015. Few colonies had annual data, and only colonies with ≥ 5 years of AOT counts were retained for analysis (Fig. 1, and Supporting Information Table S1 for number of years per colony); these held 34% of the national population during Seabird 2000 (Furness & Ratcliffe, 2004). For great skua and four hosts (black-legged kittiwake, common guillemot, Atlantic puffin and Arctic tern), data were collated for all colonies in northern Scotland for 1992–2015. Those within 20 km of at least one selected Arctic skua colony (Fig. 1) were retained for analysing each species’ population and productivity trends, and further subset for specific analyses of localised pressures on Arctic skuas. Other hosts such as razorbill *Alca torda* and common tern *Sterna hirundo* were omitted because productivity data were sparse, abundance was generally low, and trends and breeding success tend to correlate with those of common guillemot and Arctic tern respectively.

*Local densities of hosts and great skuas at Arctic skua colonies*

For analysing effects of spatial variation in host and great skua densities on Arctic skua trends and productivity, we used digital mapping (MapInfo Professional v6) of Seabird 2000 and Orkney/Shetland skua census data. Each Arctic skua colony was categorised by abundance of cliff-nesting hosts (black-legged kittiwake, common guillemot and Atlantic puffin) breeding within foraging range (5 km, Thaxter *et al*., 2012) of its colony centroid. Thus, type 1 colonies had > 10 000 pairs of cliff-nesting hosts; type 2, 1000–10 000 pairs; type 3, < 1000 pairs. For Arctic tern, whose distribution fluctuated greatly, we instead used counts only from the same year as the Arctic skua AOT count. Great skua AOTs were estimated within the likely range of each Arctic skua colony centroid over which competitive and predatory interactions between the two species occur (1 km, Phillips *et al*., 1998). Great skua surveys were often frequent, allowing use of AOT counts from the same years as Arctic skua AOT counts. For years without great skua counts, we assumed linear rates of change between successive counts to impute missing great skua AOT values.

*Annual host productivity as an index of food availability at Arctic skua colonies*

For quantifying effects of food availability on Arctic skua productivity, we estimated local host breeding success as an index. Host productivity inside 5 km Arctic skua colony buffers was often unknown, so for black-legged kittiwake and common guillemot, data from annually monitored sites up to 30 km and 110 km away were used. This was justified by 120–135 km maximum foraging ranges amongst these hosts (Thaxter *et al*., 2012), with cliff-nesting seabird colonies tens of kilometres apart likely to experience similar foraging and breeding success. Small samples were pooled to give island or sub-region estimates. For Arctic tern, whose foraging range is much smaller, and breeding success more sensitive to local conditions (Robertson *et al*., 2014), we took a similar approach but restricted the radius to 20 km. For each Arctic skua colony, we then calculated annual indices of cliff-nesting host productivity (mean number of black-legged kittiwakes and common guillemots fledged per pair within that island or sub-region) and Arctic tern productivity (estimated Arctic terns fledged per Arctic skua AOT within the 5 km buffer). The latter involved multiplying Arctic tern AOTs within the 5 km buffer in that year by the local productivity estimate, then dividing by Arctic skua AOTs. This finer scale approach was not possible for cliff-nesting hosts due to sparsity and infrequency of AOT counts (hence categorisation of colony types by cliff-nester abundance during Seabird 2000).

STATISTICAL ANALYSIS

We used SAS GLIMMIX (SAS Institute, 2013) to fit generalized linear mixed models (GLMMs), with variances multiplied by observed overdispersion parameter (‘random residual’ option) to account for overdispersion, and using the Kenward-Roger method to calculate denominator degrees of freedom for testing fixed effects (Littell *et al*., 1996). In all GLMMs, *site* was fitted as a random categorical effect to account for non-independence of data (repeated measures per colony). Model validation involved visually inspecting residual plots (histograms, Q-Q plots, and normalized residuals against fitted values using the ‘PearsonPanel’ option), and all models presented met the assumptions of linearity and normality of residuals. Models for host population trends showed some deviation from homoscedasticity, with higher fitted values tending to have larger residuals. Collinearity was avoided by testing for pairwise correlations between predictors.

*Population and productivity trends*

Population trends for all six study species were modelled separately using GLMMs with a log-link function and Poisson error distribution, with number of AOTs or pairs as the response variable. *Year*, *year2* and the *Seabird 2000 count* (log-transformed) were fixed effect covariates. Due to missing counts for some colony-years, plots of inter-annual changes in AOTs used annual population estimates from a second set of models with *year* as a fixed categorical effect. Fitting the *Seabird 2000 count* gave annual indices relative to population size during the Seabird 2000 census. To test for geographical variation in trends, we repeated the first set of models but added *latitude* and *year\*latitude*. To test for variation in trends between Arctic skua colonies, categorised by cliff-nesting host abundance, we repeated both sets of models but added *colony type* (3 levels: type 1, > 10 000 cliff-nesting host pairs; type 2, 1000–10 000 pairs; type 3, < 1000 pairs), *year\*colony type* and *year2\*colony type* (the latter was removed if *P* > 0.05). *Latitude* was also fitted if previous models had shown significant geographical variation in trends (*year\*latitude* *P* < 0.05).

Following a similar approach, we analysed annual variation and trends in productivity using GLMMs with a binomial error distribution and logit link, with number of chicks fledged as the response variable and number of breeding adults or pairs as the denominator. Common guillemot and Atlantic puffin lay only one egg, so we used breeding pairs as the denominator. Arctic skua, great skua, black-legged kittiwake and Arctic tern lay 2–3 eggs but never fledged > 2 chicks per pair amongst the colony-years studied, so we used breeding adults as the denominator and multiplied each annual mean estimate by two to express productivity as number of chicks fledged per pair.

*Associations with Arctic skua population trends*

The extent to which Arctic skua productivity influenced population trend was assessed using a GLMM with a binomial error distribution and logit link to model inter-annual changes in AOT counts as a function of productivity in year *T-4* (fixed effect). We used *T-4* because Arctic skuas usually first breed in their fourth year (Davis, 1976). The response variable was the ratio of AOTs in year *T* to the sum of AOTs in years *T-1* and *T*. This gives a value between 0 (colony extinction) and 1 (colony establishment), where 0.5 represents no change. We then added two inter-correlated great skua variables in turn (*great skua AOTs*, and the *great:Arctic skua AOT ratio*, both log-transformed) to assess their effect on annual changes in Arctic skua population size. To compare amongst models, and with a ‘null’ model, the deviance explained, we re-fitted the GLMMs using a maximum likelihood framework (Laplace approximation, Bolker *et al*., 2009; SAS Institute, 2013). Goodness of fit was assessed using the Aikake Information Criterion corrected for small samples (AICC), which reduces the probability of overfitting. Finally, to test for overall association between Arctic skua population trend and great skuas, we used a GLMM with a log-link function and Poisson error distribution to model Arctic skua AOTs as a function of *great skua AOTs* (log-transformed) and *year\*great skua AOTs*, with *year*, *year2*, *latitude* and the Arctic skua *Seabird 2000 count* also fitted as fixed effect covariates.

*Associations with Arctic skua productivity*

For assessing effects of host breeding success and great skua abundance on variation in Arctic skua productivity, we used four separate GLMMs (Binomial error distribution and logit-link), fitting the fixed effect covariates: (i) *cliffnester productivity* and *cliffnester productivity2* (fledglings per cliff-nesting host pair); (ii) *Arctic tern productivity* (Arctic tern fledglings per Arctic skua AOT, log-transformed); (iii) *great:Arctic skua AOT ratio* (log-transformed), (iv) *great:Arctic skua AOT ratio* and *Arctic tern productivity*. Separate models were used instead of nested models or stepwise selection procedures to avoid collinearity amongst covariates (*cliffnester productivity* and *Arctic tern productivity,* R = 0.409; *cliffnester productivity* and *great:Arctic skua AOT ratio*, R = -0.299). Quadratic and logistic models were fitted because seabird breeding success responds non-linearly to food availability (Cury *et al*. 2011). *Colony type* and the *colony type*\*covariate interaction term were also fitted to test for differences between them. As before, to compare the deviance explained amongst models and with ‘null’ and ‘*year*’ models, we re-fitted GLMMs using Laplace approximation and used AICC to assess goodness of fit.

**Results**

OVERALL TRENDS

*Arctic skua*

Arctic skuas declined at almost all study colonies (Fig. 1), from 1061 AOTs overall in 1992 to approximately 200 in 2015 (Fig. 2a). Magnitude of decline between the 1992 and Seabird 2000 censuses closely matched that for all of Orkney, Shetland and Handa combined (-36%; Furness & Ratcliffe, 2004), suggesting our sample was representative, and that by 2015 just 554 AOTs (95CL: 422–728) remained; a 71% decline since 2000–02 and 81% since 1992. Annual productivity (chicks fledged per pair) also declined, from a 5-year mean of 0.91 in 1992–96 to 0.29 in 2011–15 (Fig. 2b). During 1992–2000, it fell below 0.5 fledged per pair just once (1998), whereas it reached this level only three times since (2006, 2014, 2015). Significant *year\*latitude* effects (F409.8 = 15.05, *P* = 0.0001 and F139.7 = 40.9, *P* < 0.0001) indicated larger declines in population size and productivity at more northerly colonies, with Handa (our most southerly study colony) maintaining relatively high productivity during the 2000s and 2010s.

*Great skua and hosts*

Great skuas increased at most sites (Fig. 3), including some very large increases (5–13 x) at smaller colonies (Table S1). However, a 24% decline at the largest colony (Foula) resulted in little overall change in AOTs across all colonies combined. Increases accelerated in later years, and were greatest at southerly colonies (*year\*latitude*: F224.8 = 8.78, *P* = 0.0034). Declines in Arctic skuas and increases in great skuas meant that great:Arctic skua AOT ratios increased. All four hosts declined (Fig. 3), with black-legged kittiwake and Arctic tern declines greatest further north (*year\*latitude*: F419 = 54.39, *P* < 0.0001 and F468.7 = 14.37, *P* = 0.0002, respectively). Annual productivity also declined in all five species (Fig. 3). More northerly colonies had lower black-legged kittiwake productivity (*latitude*: F14.05 = 31.98, *P* < 0.0001) and larger declines in common guillemot productivity (*year\*latitude*: F135.9 = 4.89, *P* = 0.0300). Strong inter-specific correlations in annual productivity among all six study species suggested large-scale drivers (Table S2).

*Variation with colony type*

Mean annual rates of Arctic skua population decline were greatest at type 2 colonies (1000–10 000 cliff-nesting host pairs within 5 km), whereas productivity declined most at type 1 and type 3 colonies (Table 1, Fig. S1). Larger annual rate of increase in great skua populations at type 2 colonies was of marginal significance (*P* = 0.0815; Table 1, Fig. S2). Throughout the study, great:Arctic skua AOT ratios were typically much larger at type 1 than types 2 and 3 colonies (Table 1). Black-legged kittiwake declines were marginally steeper at type 2 colonies, whilst Arctic tern declines were smallest at type 3 colonies (Table 1, Fig. S2). Productivity trends for great skuas and hosts did not vary with colony type.

ASSOCIATIONS WITH ARCTIC SKUA TRENDS

Arctic skua population change and mean annual productivity were positively correlated (Fig. 4), suggesting low breeding success was a driver of population declines. However, in a smaller subset with sufficient data (n = 129 colony-years), annual change in AOTs was unrelated to productivity four years previously (F127 = 0.10, *P* = 0.7526). Arctic skua productivity explained just 18% of variation in inter-annual changes in AOT counts four years later (model AICc = 729.55), and adding great skua AOTs and great:Arctic skua AOT ratios did not improve model fit or explanatory power (AICc = 730.90 and 731.40, respectively). Overall, Arctic skua population declines were steepest at sites with fewer great skuas (*year\*great skua AOTs*: F206.9 = 10.33, *P* = 0.0015), which although counterintuitive, accords with larger population declines at type 2 colonies where great skua densities were relatively low (Table 1).

DETERMINANTS OF ARCTIC SKUA PRODUCTIVITY

Host productivity (food availability) and relative density of great skuas (predation pressure) were both associated with Arctic skua breeding success (Table 2, Fig. 5). The best covariate model (*cliffnester productivity*) explained 95% of annual variation in Arctic skua productivity, whilst separate models fitting *Arctic tern productivity* and *great:Arctic skua AOT ratio* explained 53% and 50% of annual variation, respectively (Table 2). The model with both *Arctic tern productivity* and *great:Arctic skua AOT ratio* explained 75% of annual variation. A *year* model explained 44% of total variation in Arctic skua productivity.

Positive relationships between Arctic skua productivity and breeding success of cliff-nesting hosts (black-legged kittiwake and common guillemot) (Fig. 5a) and Arctic terns (Fig. 5b) contrasted with a negative great skua effect (Fig. 5c). Host productivity effects were strongest at colonies with the largest number of cliff-nesting seabirds (type 1), whilst great skua effects were strongest at colonies with moderate (type 2) or low (type 3) cliff-nesting seabird abundance (Figs. 5b,c).

Our model including both food and predation covariates predicted that in years with high host productivity, Arctic skuas nesting close to large colonies of cliff-nesting seabirds (type 1) would fledge ≥ 0.5 chicks per pair even at great skua densities > 50 AOTs per Arctic skua AOT (Fig. 6a). With moderate or low host productivity, such breeding success would only be maintained at great skua densities ≤ 25 or 3–4 AOTs per Arctic skua AOT respectively (Fig. 6a), or 2–4 AOTs per Arctic skua AOT (even with high host productivity) at colonies with fewer cliff-nesting hosts (types 2 and 3, Figs. 6b,c). By 2015, almost half of the 33 study colonies had great:Arctic skua AOT ratios > 3 (Table S2).

**Discussion**

Scotland’s Arctic skuas are declining rapidly, with bottom-up and top-down pressures simultaneously reducing breeding success to unsustainably low levels. Recent observed changes at all trophic levels in the northeast Atlantic Ocean indicate significant restructuring of foodwebs, driven by fisheries management and climate change acting in combination (Frederiksen *et al*., 2006; Carroll *et al*., 2017; Régnier, Gibb & Wright, 2017). Analogous examples in terrestrial ecosystems include interactions between humans, apex predators, land use and climate change affecting top-down and bottom-up pressures on mesopredators (Ritchie & Johnson, 2009; Newsome & Ripple, 2015; Pasanen-Mortensen *et al*., 2017).

BOTTOM-UP AND TOP-DOWN PRESSURES ON ARCTIC SKUAS

*Reductions in food availability*

Arctic skuas fledged more chicks when their main hosts also had high productivity. During the 1990s, skuas and cliff-nesting seabirds regularly fledged > 0.6 chicks per pair, and Arctic terns were more numerous and successful. However, since the early 2000s, poor breeding success and population declines amongst hosts has severely reduced food availability for Arctic skuas, with northerly colonies faring worst. Notably, skua and host productivity at Handa, our most southerly study colony, remained relatively high in years when severe food shortages were causing widespread breeding failure in Orkney and Shetland (Jones *et al*. 2008), indicating regional variation in bottom-up pressures on Scotland’s breeding seabirds. Unfortunately, lack of data prevented our inclusion of other skua colonies in western Scotland.

Driving seabird breeding failures in Orkney and Shetland have been shortages of post-larval sandeels during the chick-rearing period (Phillips *et al*., 1996; Oro & Furness, 2002; Miles *et al*., 2015). Sandeels are high energy prey for seabirds (Rindorf, Wanless, & Harris 2000; Wanless *et al*., 2005), and Shetland lacks suitable alternatives (Furness & Tasker, 2000). Juvenile age classes (0- and 1-group) are especially important because their smaller size, greater abundance and availability within surface waters than older sandeels gives access to a wider range of seabirds (Rindorf *et al*., 2000; Robertson *et al*., 2014). Recent sandeel scarcity around Shetland is attributed to low recruitment in most years since the mid-1980s, linked to hydro-climatic changes affecting hatching dates, survival and transport of larvae from major spawning areas north/west of Orkney (Wright & Bailey 1993; Poloczanska *et al*., 2004). Potentially, top-down pressures on sandeels also increased with population recovery of previously over-exploited predatory fish such as herring *Clupea harengus* and mackerel *Scomber scombrus* (Frederiksen, Furness, & Wanless 2007). Although human take impacts some North Sea sandeel stocks (Cook *et al*., 2014; Carroll *et al*., 2017), this is considered unlikely in the closely regulated small-scale Shetland fishery (Poloczanska *et al*., 2004). More significantly, environmental conditions for sandeels appear to be worsening, with sea temperature increases and oceanographic changes affecting their physiology, food supply, phenology and survival, leading to trophic mismatch and less food for seabirds (e.g. Frederiksen *et al*., 2006; Carroll *et al*., 2015; Régnier *et al*., 2017). The recent discovery that sandeels are cannibalistic, with such behaviour possibly driven by low prey availability or late hatching of larvae, may further explain low recruitment in some years (Eigaard *et al*., 2014).

*Increases in great skuas*

Great skua AOTs increased by a colony average of 75%, including much larger increases, but declines at the two largest colonies (Foula and Hoy) resulted in overall numbers remaining stable. Productivity declined less than in other seabirds because great skuas are not dependent on sandeels and can switch to scavenging behaviour or preying upon seabirds (Hamer *et al*., 1991; Ratcliffe, Furness, & Hamer 1998; Votier *et al*., 2008).

Arctic skua breeding success was negatively associated with the ratio of great skua to Arctic skua AOTs. Great skuas prey upon Arctic skua chicks, and although Arctic skuas can mount defence, territory attendance is lower when food scarcity demands greater foraging effort (Phillips *et al*., 1996; Caldow & Furness, 2000; Davis *et al*., 2005). For waders, aerial defence is more effective when compatriots combine forces (Elliot, 1985), and positive associations between Arctic skua hatching success, short-term post-fledging survival and territory density suggest similar effects for skuas (Phillips *et al*., 1998). Therefore, widespread food shortage combined with increases in great:Arctic skua AOT ratios have likely increased Arctic skua vulnerability to great skua predation. Observations at Handa support this, where co-operative defence declined and predation increased with falling Arctic skua numbers (Jones *et al*., 2008), and *vice versa* with increasing numbers in recent years (C Smith pers. obs.).

Top-down pressures may exceed our estimates, as great skuas frequently kill Arctic skua fledglings and occasionally adults (Phillips *et al*., 1998; Davis *et al*., 2005; Jones *et al*., 2008). Insufficient data also excluded consideration of potential effects of non-breeding great skuas, which gather in ‘clubs’ around colonies and sometimes outnumber territorial pairs (Furness, 1977; Klomp & Furness, 1992). Finally, great skuas exacerbate food shortages for Arctic skuas by killing auks and black-legged kittiwakes, thereby depleting fish-carrying host populations (Phillips *et al*., 1999; Oro & Furness, 2002; Votier *et al*., 2004). This may be exacerbated by the phased reduction in fish discards from trawlers, which will reduce scavenging opportunities available to great skuas and cause a switch to seabird predation (Votier *et al*., 2004; Bicknell *et al*., 2013).

VARIATION WITH COLONY TYPE

Population trends varied amongst colony types, but not entirely as predicted. We expected larger Arctic skua declines at colonies with few or no cliff-nesting seabirds and high dependency on terns (type 3 colonies). However, declines were largest at sites with moderate auk and black-legged kittiwake abundance (type 2 colonies), although these colonies also lost the most Arctic terns. Large colonies of cliff-nesting seabirds can buffer Arctic skuas against localised food shortage when terns are scarce or unsuccessful, but also attract many great skuas. Despite this, host productivity appears to be driving Arctic skua breeding success at type 1 colonies (> 10 000 cliff-nesting seabird pairs). By contrast, at type 2 colonies with fewer hosts and smaller but rapidly growing great skua populations, Arctic skua breeding success was most strongly associated with great:Arctic skua AOT ratio. At such colonies, less competition for territories allows adolescent great skuas to breed earlier, leading to rapid population growth (Furness, 2015), whilst less interference competition may result in higher adult fitness and per-capita predation of seabirds (Votier *et al*., 2007).

INTER-ANNUAL FLUCTUATIONS IN ARCTIC SKUA POPULATION SIZE

Productivity was unrelated to AOTs four years later, when Arctic skuas normally recruit into the breeding population (Davis, 1976). This suggested inter-annual variation in adult survival (Davis *et al*., 2005), immigration/emigration of young birds to/from non-natal colonies (Furness, 1977; Phillips *et al*., 1998), or widespread non-breeding in years with exceptionally low food availability (Phillips *et al*., 1996; Catry *et al*., 1998; Wanless *et al*., 2005). Annual monitoring is therefore essential to fully understand population changes.

POTENTIAL CONSERVATION SOLUTIONS

Marine policies that could reduce bottom-up pressures on Arctic skuas and their hosts include restrictions or complete closure of sandeel fisheries (Furness & Tasker, 2000; Cook *et al*., 2014; Carroll *et al*., 2017), and protecting sea areas from damaging activities (Thaxter *et al*., 2012). Recent proposals for marine Special Protection Areas (SPAs) and the designation of nature conservation Marine Protected Areas (MPAs) for sandeels in Scottish waters are good examples (Scottish Government, 2016; Scottish Natural Heritage, 2016), although climate change impacts on marine food-webs present major barriers to restoring food resources for seabirds (Carroll *et al*., 2015, 2017).

Direct interventions such as supplementary feeding and predator control, used widely in terrestrial ecosystems, should also be considered. At Foula, experimental food provision for Arctic skuas during chick-rearing resulted in higher breeding success and adult survival, but lower chick growth rates (Davis *et al*., 2005). Further feeding trials would need to compare different supplementary food types and assess their nutritional quality, but logistical constraints may make supplementary feeding unviable on a large scale. Predator control is widely used in seabird conservation (Brooke *et al*., 2018), but great skuas are much rarer globally than Arctic skuas, and Scotland holds approximately 57% and 1% of their respective world populations (BirdLife International, 2018). A large scale cull of great skuas is therefore not justifiable from a global conservation perspective. Alternative approaches include selective removal of bird-eating specialists, used successfully to manage predatory gulls (e.g. Sanz-Aguilar *et al*., 2009), and targeting colonies with small but increasing great skua populations. Type 2 and type 3 colonies could respond to small-scale culls, and a great:Arctic skua AOT ratio < 1, and ideally < 0.5, may allow Arctic skua breeding success to exceed 0.5 fledged per pair in years with moderate/high food availability. Aside from political challenges, management risks include failure to reduce great skuas if new recruits replace those removed, and overall predation remaining high from large numbers of non-specialists (Votier *et al*., 2004). Non-lethal deterrents including deliberate disturbance to prevent great skuas from settling, and/or nest removal, may be less contentious and are currently used elsewhere in the UK to protect locally rare tern colonies from herring gulls *Larus argentatus argenteus* and lesser-black backed gulls *L. fuscus graellsii*, despite these UK gull populations having greater international conservation status than the terns (Eaton *et al*., 2015). These methods are untested on great skuas, but may technically be viable conservation responses given the species’ avoidance of nesting in areas with high human disturbance (Dawson *et al*., 2011). However, such interventions raise significant questions of conservation philosophy and long-term sustainability, but if recent trends continue, Arctic skuas could face extinction in Scotland as a breeding species.

**Author’s contributions**

NR conceived the ideas and designed the methodology; NR, DS, BR, CS, PE and EM collected the data; AP analysed the data; AP led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

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**Data Accessibility**

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.v056r5h

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**Supporting information**

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Arctic skua and great skua AOTs at each study colony in 1992 and 2007–15.

**Table S2.** Correlation matrix of annual productivity estimates for the six study species.

**Figure S1.** Arctic Skua population trends and productivity, by colony type.

**Figure S2.** Great skua, black-legged kittiwake and Arctic tern population trends, by colony type.

**Table 1.** Variation in skua and host numbers among the three Arctic skua colony types during the Seabird 2000 census (Mitchell *et al*. 2004), and differences in modelled estimates of population change and breeding success during 1992–2015. Note that data were insufficient for modelling common guillemot and Atlantic puffin trends by colony type.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | **Type 1 (n=7)** | **Type 2 (n=9)** | **Type 3 (n=17)** | |  |
| **AOTs/pairs in Seabird 2000 (mean ± 1 sd)** | | | | | |
| Arctic skua | 37 ± 33 | 24 ± 22 | 14 ± 17 | |  |
| great skua | 467 ± 818 | 17 ± 15 | 10 ± 10 | |  |
| great skua:Arctic skua AOT ratio | 13 ± 17 | 5 ± 12 | 1 ± 2 | |  |
| black-legged kittiwake | 8849 ± 11839 | 595 ± 791 | 14 ± 43 | |  |
| common guillemot | 33178 ± 20312 | 1345 ± 1181 | 31 ± 84 | |  |
| Atlantic puffin | 13397 ± 16533 | 1089 ± 1869 | 72 ± 105 | |  |
| Arctic tern | 723 ± 884 | 2042 ± 2952 | 174 ± 239 | |  |
| **Population trend (mean annual rate of change, 1992 to 2015)** | | | | ***P*-value** | |
| Arctic skua | –6.4% | –8.2% | –6.7% | 0.0016 | |
| great skua | +2.2% | +5.2% | +2.5% | 0.0815 | |
| black-legged kittiwake | –7.2% | –9.4% | –7.8% | 0.0352 | |
| Arctic tern | –10.3% | –11.3% | –3.7% | 0.0024 | |
| **Productivity (annual number of chicks fledged per pair, 5-year mean)** | | | | | |
| Arctic skua, 1992-96 | 1.05 | 0.80 | 0.93 | <0.0001 | |
| Arctic skua, 2011-15 | 0.29 | 0.29 | 0.71a |
| great skua, 1992-96 | 0.84 | 0.76 | 0.63 | 0.1320 | |
| great skua, 2011-15 | 0.38 | 0.83 | 0.20b |
| black-legged kittiwake, 1992-96 | 1.02 | 0.96 | 0.51 | 0.1370 | |
| black-legged kittiwake, 2011-15 | 0.46 | 0.39 | 0.11 |
| Arctic tern, 1992-96 | 0.49 | 0.27 | 0.48 | 0.1414 | |
| Arctic tern, 2011-15 | 0.16 | 0.02 | 0.01b |

*P*-values are for Wald F-tests of the *colony type\*year* interaction term.

a no data for 2013–14. b no data for 2014–15.

**Table 2.** GLMMs of covariates of Arctic skua productivity, including a comparison of model fit statistics with a *year* model (categorical effect) and a null model. All models include *site* as a random categorical effect.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Model Variables** | | ***P*-value** | **AICC** | **Δ AICC** | **Par** | **Dev** | **Marg R2**  **tot / ann** |
| 1 | *year* | <0.0001 | 2026.86 | 0.00 | 25 | 1969.51 | 0.44 / 1.00 |
|  |  |  |  |  |  |  |  |
| 2 | *cliffnester productivity* | <0.0001 | 2067.84 | 40.98 | 9 | 2051.10 | 0.42 / 0.95 |
|  | *cliffnester productivity2* | 0.0003 |  |  |  |  |  |
|  | *colony type* | 0.0184 |  |  |  |  |  |
|  | *colony type\*cliffnester productivity* | 0.0174 |  |  |  |  |  |
|  |  |  |  |  |  |  |  |
| 3 | *great:Arctic skua AOT ratio* | <0.0001 | 2374.38 | 347.52 | 9 | 2357.64 | 0.33 / 0.75 |
|  | *Arctic tern productivity* | <0.0001 |  |  |  |  |  |
|  | *colony type* | 0.0725 |  |  |  |  |  |
|  | *colony type\*Arctic tern productivity* | <0.0001 |  |  |  |  |  |
|  |  |  |  |  |  |  |  |
| 4 | *Arctic tern productivity* | <0.0001 | 2700.07 | 673.21 | 8 | 2685.50 | 0.23 / 0.53 |
|  | *colony type* | 0.9970 |  |  |  |  |  |
|  | *colony type\*Arctic tern productivity* | 0.0006 |  |  |  |  |  |
|  |  |  |  |  |  |  |  |
| 5 | *great:Arctic skua AOT ratio* | <0.0001 | 2748.96 | 722.10 | 8 | 2734.39 | 0.22 / 0.50 |
|  | *colony type* | 0.0569 |  |  |  |  |  |
|  | *colony type\*great:Arctic skua AOT ratio* | 0.0457 |  |  |  |  |  |
|  |  |  |  |  |  |  |  |
| 6 | Null model |  | 3501.22 | 1474.36 | 1 | 3497.16 |  |

*P*-values are for Wald F-tests of fixed effects. AICC = Akaike Information Criterion. Δ AICC = difference in AICC relative to the *year* model. Par = number of parameters estimated by the model. Model deviance = -2 log likelihood. Marginal R2 = proportion of total and annual variance in Arctic skua productivity explained by the fixed effect variables.

**Figure 1.** Locations of Arctic skua colonies used in analyses of population trend (n = 33 sites) and annual productivity (underlined, n = 20 sites). Dotted line = southernmost extent of Arctic skua breeding range during Seabird 2000. Overall percentage change in AOTs between the first and last year surveyed (1992 and 2008–2015) is given for each site (see Table S1 for further details). Symbol sizes are scaled to AOT counts in 1992 (four categories: 0–12, 16–26, 30–66, 101–159). Symbol shape denotes colony type, classified by cliff-nesting seabird host abundance within 5 km of colony during the Seabird 2000 census: squares = type 1 colonies (> 10 000 pairs), circles = type 2 colonies (1000–10 000 pairs), triangles = type 3 colonies (< 1000 pairs).



**Figure 2.** Arctic skua trend across study colonies during 1992–2015 for **(a)** population size, **(b)** productivity. Annual estimates (± 95% confidence intervals) from GLMMs with *year* as a categorical effect are shown. For population size (a), solid line = modelled trend from GLMM with *year* and *year2* as covariates (*P* values and overall predicted % change also shown); crosses = census counts across all 33 sites in 1992, 2000–2002, and 2008–2015 (for clarity, depicted as 1992, 2001 and 2012). See Table S1 for details on each colony’s contribution to these trends.

**a)**

**b)**

**Figure 3.** Trends in population size and productivity across Orkney, Shetland and Handa island during 1992–2015 for **(a)** great skua, **(b)** black-legged kittiwake, **(c)** Arctic tern, **(d)** common guillemot, **(e)** Atlantic puffin. Annual estimates (± 95% confidence intervals) from GLMMs with *year* as a categorical effect are shown. For population size, these are presented as indices relative to population size during the Seabird 2000 census; solid line = modelled trend from GLMM with *year* and *year2* as covariates (*P* values and overall predicted % change also shown).

**a)**

**b)**

**c)**

**d)**

**e)**

**Figure 4.** Overall change in Arctic skua population size plotted against mean annual Arctic skua productivity for 20 colonies during 1992–2015 (see Table S1 for colony identities and number of years).

**Figure 5.** Modelled relationships between Arctic skua productivity and **(a)** mean annual productivity of cliff-nesting hosts, **(b)** Arctic tern fledglings per Arctic skua AOT, **(c)** great skua to Arctic skua AOT ratio, from three univariate GLMMs with *colony type* and its interaction term also fitted. Bold sections of lines = interquartile range of observed values. Note that the x-axis in (b) and (c) is on a log scale. See Table S1 for colony identities and number of years.

**a)**

**c)**

**b)**

**Figure 6.** Modelled relationships between Arctic skua productivity and great:Arctic skua AOT ratio in years with high, medium and low food availability at **(a)** type 1 colonies, **(b)** type 2 colonies, **(c)** type 3 colonies, from GLMM with Arctic terns fledged per Arctic skua AOT and great:Arctic skua AOT ratio. High, medium and low food availability = 30, 1 and 0.05 Arctic terns fledged per Arctic skua AOT respectively, equating to cliff-nesting seabird productivity of approximately 0.8, 0.6 and 0.4 fledged per pair. Type 1, 2 and 3 colonies = > 10 000, 1000–10 000 and < 1000 cliff-nesting seabird host pairs, respectively. See Table S1 for colony identities and number of years.

**a)**

**b) c)**