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Heavy decline of the largest European Arctic Skua *Stercorarius parasiticus* colony: interacting effects of food shortage and predation

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ABSTRACT

Capsule: The number of breeding pairs of Europe's largest Arctic Skua *Stercorarius parasiticus* colony at Slettnes, Norway, showed a dramatic decline of at least 50% over two decades, with food shortage in four years and increasing predation by Red Fox *Vulpes vulpes* leading to total breeding failure in five out of six recent study years.

Aims: To document the decline of Europe's largest Arctic Skua colony and quantify bottom-up and top-down effects on reproduction.

Methods: We compared nest counts between 1997–1998 and 2014–2019 and collected data on egg size, clutch size and nest success for all years, and adult body mass, nest attendance, at-sea activity, aggressive nest defence, Red Fox *Vulpes vulpes* encounters, daily nest survival and adult survival for 2014–2019. We deployed nest cameras to identify predators in 2018–2019. In addition, we developed a demographic model to estimate the fecundity required for a stable population.

Results: A higher proportion of time spent at sea, small eggs, low adult female body mass and indirect assessment of foraging fish availability suggested food shortages in four of six recent study years. At the same time, nest predation by Red Foxes, the likely predator involved, increased during the six-year study. The combined effects of food shortage and nest predation led to total breeding failures in 2017–2019.

Conclusion: We provide evidence of both bottom-up (food shortage) and top-down (predation) effects on reproductive investment and hatching success in this colony. The reproductive output in recent years is far too low to sustain a stable population. The severe decline of the Arctic Skua colony at Slettnes fits reported trends for this species across most of its European breeding range, as well as for its important host species, the Arctic Tern *Sterna paradisaea* and the Black-legged Kittiwake *Rissa tridactyla*.

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Stercorarius parasiticus; Arctic Skua; Red Fox; colony; bottom-up; top-down

Seabirds are amongst the most threatened groups of birds, with approximately 28% of all species threatened globally (Croxall *et al.* 2012). In Europe, many seabird populations have declined substantially over the past decades (Mitchell *et al.* 2004, Barret *et al.* 2006, Frederiksen 2010), including that of the Arctic Skua *Stercorarius parasiticus* (Perkins *et al.* 2018). Arctic Skua populations around the Baltic Sea have been stable at least since the 1980s (Valkama *et al.* 2011, Ottosson *et al.* 2012), but substantial declines are reported from all other areas where reliable population estimates are available (Frederiksen 2010). For example, the species declined by approximately 80% over the last 25 years in Scotland (Eaton *et al.* 2015, Perkins *et al.* 2018). Although no trend is known for the large population in Iceland (Skarphéðinsson *et al.* 2016) or the supposedly very large population of Arctic Skuas across the Russian Arctic and Nearctic, the species is listed as 'least concern' on the International Union for Nature Conservation (IUCN) Red List of threatened bird species (BirdLife-International 2016). In Europe,

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however, the Arctic Skua is listed as 'endangered' in the EU27 Red List (BirdLife-International 2015). Arctic Skua populations are also in decline along the mainland coast of Norway and this population is consequently categorized as 'near threatened' on the Norwegian Red List (Henriksen & Hilmo 2015). The population appears stable in Svalbard, where the species is still listed as 'least concern' (Henriksen & Hilmo 2015).

Causes of Arctic Skua population declines have been studied in Scotland where reduced reproductive success was the main driver (Phillips *et al.* 1996, Perkins *et al.* 2018). As kleptoparasites, Arctic Skuas rely on host species for their food provisioning and the breeding success of both skuas and their hosts is often linked (Furness 1987, Phillips *et al.* 1996). Indeed, in Scotland, reproductive success of Arctic Skuas was positively linked to the breeding success of Black-legged Kittiwakes *Rissa tridactyla*, Arctic Terns *Sterna paradisaea* and auks (Perkins *et al.* 2018). Reproductive success of these host species was strongly impacted by the declining availability of pelagic forage fish, in particular Lesser Sandeels *Ammodytes marinus* (Phillips *et al.* 1996, Miles *et al.* 2015). Reproductive success of Arctic Skuas in Scotland was also negatively correlated to the abundance of Great Skuas *Stercorarius skua*, a competitor for nest sites and a predator of Arctic Skua eggs and chicks (Dawson *et al.* 2011). The relative contribution of these bottom-up and top-down effects differed as a function of the colony size of host species, with bottom-up effects being more important at larger host colonies (Perkins *et al.* 2018). Outside Scotland, potential causes of the population declines of Arctic Skuas have not been extensively studied. The relative importance of bottom-up and top-down effects in other areas could be different from the Scottish situation due to differences in prey, host and predator communities. For instance, predation by foxes did not occur at any of the Scottish colonies, as these were on islands where foxes did not occur. Elsewhere, Arctic Foxes *Vulpes lagopus* are known predators of Long-tailed Skuas *Stercorarius longicaudus* and Pomarine Skuas *Stercorarius pomarinus* in East Greenland and northern Alaska (de Korte 1986, Maher 1974).

Here, we report on the population development over the past 20 years in the largest Arctic Skua colony in Europe, located at Slettnes in northern Norway, and the contribution of both bottom-up and top-down effects to the strong population decline. We compare recent population estimates to an earlier survey in the late 1990s. For the recent period, we use clutch size, egg size, adult body mass and time spent at sea during the incubation period to characterize reproductive investment as a proxy for food availability. Nest survival rates are used to evaluate top-down control and nest camera images to identify predators. Finally, we estimate adult survival rates using colour-ring readings and, using an age-structured demographic model, calculate whether the reproductive success during the study period was sufficient to sustain a stable population.

Methods

Colony size

Fieldwork was carried out at the Arctic Skua colony of Slettnes (71°08'N 28°21'E, Figure 1(a)) near Gamvik, northern Norway, in two projects run nearly two decades apart. The first project (1997–1998) focused on the ecology and evolution of plumage colour morphs (Janssen *et al.* 2006, Janssen & Mundy 2013), whereas migration ecology was the primary subject of the second project (van Bemmelen 2019). Neither study aimed to find all nests and in 2016–2019 most effort was spent in the central part of the study area. To compare the number of nests between time periods, we used nest counts of both the colony at large and within the main study area that has been intensively studied in all years (Figure 1(b)). In addition, whole-colony censuses were carried out in 2016–2019, by systematically covering the entire study area and mapping the positions of all territorial pairs and single birds, as well as non-settled birds in 'clubs' (Furness 1987). The censuses took 2–4 days and were carried out within a 5–6-day period: 1–6 July 2016 (during the late incubation phase), 4–9 June 2017 and 5–11 June 2018 (both during the clutch initiation phase).

Reproductive investment and nest survival

Nests were located in all study years and upon first encounter nest positions were recorded on a topographic map (1997–1998) or using a handheld GPS (2014–2019). At each nest, the number of eggs was noted, and length and width of eggs were measured (to the nearest 0.1 mm) using callipers. In 1997–1998, hatching dates were recorded by direct observations. In 2014–2019, eggs were placed in lukewarm water and the angle at which they settled or the height at which they floated was used to estimate hatching date to within two days (Liebezeit *et al.* 2007) which could be further refined by observations

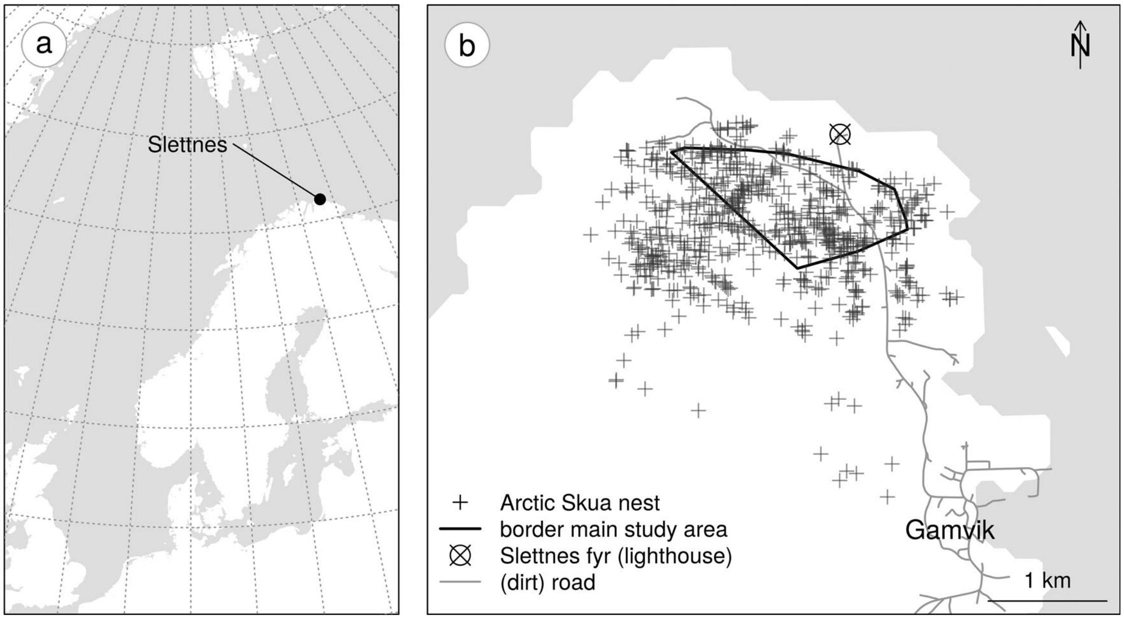

Figure 1. The study area; (a) its position in Norway and (b) distribution of all nests in 1997–1998 and 2014–2019 and the delineation of the main study area, the position of the lighthouse and the dirt road running from the village of Gamvik to the lighthouse.

of cracks or holes in the eggs. Egg length and width were measured (to the nearest 0.1 mm) using callipers and egg volume (mm^3) was calculated using the formula by Hoyt (1979): $V = 0.507 \times \mathrm{L} \times \mathrm{W}^2$. Difference in egg size between years was tested using ANOVAs for the largest egg in a 2-egg clutch, the smallest egg in a 2-egg clutch, and for single-egg clutches. As variation in egg size may be largely attributable to individual-level effects (Christians 2002), we also ran Linear Mixed-effects Models (LMEs) with random intercepts for individual females. The identity and sex of individual females was only known for a small subset of the nests and years, therefore, we only used the LMEs as a qualitative check of the ANOVA results for the years 2014–2018. Nests were monitored at 3–5-day intervals to register status (incubated, hatched, predated). Using these outcomes and length of intervals between two nest visits, daily nest survival rates were estimated for each year using a logistic-exposure model (Shaffer 2004). We fitted a model with only year as a fixed effect and one with year and day-of-year as fixed effects, to investigate whether predation rates changed during the season. We assessed the effect of day-of-year using Akaike Information Criterion (AIC). After hatching, chicks become mobile and hide upon approach, rendering it time-consuming to follow them throughout the chick period. As our primary research goals lay elsewhere, we put dedicated effort into ringing and finding chicks until late in the fledging period only in 2014, although any chicks encountered out of the nest in other years were ringed as well. As a consequence, our assessment of reproductive success is based primarily on nest success, but note that this was so low in several years that chick survival became almost irrelevant as a contributing factor (see Results). During each nest visit in 2014–2019, the level of aggressive nest defence by the adults was scored on a scale from 0 to 5, recording whether adults were absent (0), present without alarming or attacking or even left the territory (1), circled above the researcher, but did not swoop (‘dive-bomb’) at him/her (2), dive-swooped the researcher, but rarely or never hit (3), dive-bombed frequently and hit occasionally (4) or dive-bombed frequently and hit on most swoops (5) (Furness 1987). Assuming that aggressive nest defence carries a cost (through risk of injury and/or energy expenditure) we interpret its intensity as a form of reproductive investment, in which factors like physical condition or the ‘perceived’ probability of breeding success may influence the trade-off. To test differences between years in aggressiveness of nest defence, we modelled aggression score as an ordinal response variable in a Cumulative Link Mixed Model (CLMM) using the ‘ordinal’ package in R (Christensen 2019), with year as a fixed effect and nest identity as a random effect. In addition, date (centred around the mean date) was included as a fixed effect to account for potential seasonal changes (including a potential habituation effect) in the level of aggressive nest defence. Finally, the probabilities of aggression score > 2 during a nest visit at the mean observation date were taken as the overall aggressiveness in nest defence.

In 2014–2019, adults (n females = 75, n males = 51) were captured on the nest using bow nets or snare traps. We never experienced nest abandonment after catching. Trapped individuals were fitted with a blue colour-ring with a two-letter code on one tarsus and a blue darvic ring with a light-level geolocator (weight 2.5 g, model C250, Migrate Technology Ltd, Cambridge, UK) on the other tarsus, under license provided by the Norwegian Food Safety Authority (FOTS ID 6328, 7421, 8538). Besides recording ambient light every 5 min (data used primarily to describe migration), geolocators also sampled submersion in saline water every 6 s and recorded the change of state from wet to dry or dry to wet. Upon recapture and downloading the data, the mean daily duration of 'wet periods' in June was calculated for each individual and used as an index of time spent swimming at sea. More time spent at sea means less time attending the territory; the latter has been shown in Arctic Skuas to be lower in years with low food availability (Phillips *et al.* 1996). Note that under permanent daylight, geolocators are not suitable to derive data on movements. The following biometrics were taken on trapped birds: body mass (±1 g), wing length (±1 mm), bill length (±0.1 mm), head plus bill length (±0.1 mm), tarsus length (±0.1 mm) and projection of the elongated central tail feathers (t1) beyond the adjacent tail feather (t2; ±1 mm). Birds were sexed using DNA extracted from blood samples (Fridolfsson & Ellegren 1999). Differences between years in body mass were tested using LMEs, where we allowed random intercepts for individuals, considering body mass may be largely attributable to individual quality. In 2014–2019, colour-ringed birds were identified whenever possible during our daily field visits, using binoculars, a telescope or camera. In the main study period (early June-mid July), every part of the study area was visited at least every three days.

Predator activity and identification

As an index of Red Fox *Vulpes vulpes* activity in the area, the daily number of fox encounters per observer was recorded by two independent observers (BG and HR) studying Dunlins *Calidris alpina* across our study area. When active Red Fox dens were encountered, they were mapped. To identify nest predators, we deployed nest cameras (Bushnell Trophy Cam Essential E3) at nine and 13 nests respectively in 2018 and 2019, for a total of 46 and 34 recording-days throughout the breeding period. Cameras were set to take three pictures at a trigger event, followed by another three after 10 s. When active Red Fox dens were encountered, they were subsequently mapped and monitored to determine activity and the presence of cubs. In the same way as daily nest survival rates were estimated based on nest visits, daily nest survival rates were also estimated for 2018 and 2019 based on camera observations, using the outcome (incubated/hatched or predated) and duration of camera deployments in a logistic-exposure model (Shaffer 2004).

Adult survival and demographic model

Based on encounter histories of 78 adults individually marked in 2014–2018, adult apparent survival φ_a and resighting probability p were estimated using Cormack–Jolly–Seber (CJS) models for live encounter data in the 'Rmark' package in R (Laake 2013), an interface to the program MARK (White & Burnham 1999). Considering that survival rates of seabirds are generally high with low annual variability and that it is common to forego breeding (Weimerskirch 2002), we fitted a model with a time-constant value of φ_a while allowing p to vary with year.

Estimates of adult apparent survival were used in an age-structured demographic model to estimate: (1) whether reproduction during the study years was sufficient to maintain a stable population and (2) the annual reproductive output and number of reproductive years required to maintain a stable population. The demographic model sums the expected reproductive contribution over all ages for a female individual that starts to breed at an age of four years (O'Donald 1983). This leads to the expected lifetime reproductive output (R_0), which depends on annual survival probabilities, annual fecundity and the total number of reproductive years. We assume that annual survival increases linearly from φ_j during the first year of life to φ_a at an age of four years, after which it remains constant. From the expression of lifetime reproductive output (Appendix A), the fecundity f_a that is required for a stable population ($R_0 = 1$) is given by Equation (1):

$$f_a = S_j^{-1} \cdot \left(\frac{1-\varphi_a}{1-\varphi_a^m}\right) \qquad (1)$$

where S_j depends on both φ_j and φ_a and equals the cumulative survival during the first 4 (non-breeding) years of life, m is the number of reproductive years (with an upper limit set by φ_a) and annual fecundity f_a is expressed as number of female chicks per pair. Considerable uncertainty exists in φ_j, as most immatures only start to return to the breeding grounds in their 3rd calendar-year (Furness 1987). Therefore, we varied the value of φ_j between 0.5 and 0.9 and m between 1 and 20, while retaining φ_a as estimated for the Slettnes population.

Results

We were able to compare the two study periods (1997–1998 and 2014–2019) on the basis of the number of nests found, clutch size, egg volume and fraction clutches lost (Figure 2). Adult body mass, intensity of nest defence, and the fraction of time spent at sea were compared between years of the recent study period (Figure 3).

Colony size

In 1997 and 1998, respectively 187 and 172 nests were found. Not all nests were located; the estimated number of breeding pairs in the entire colony was about 250. In recent years (2014–2019), excluding known relays, the numbers of nests found were less than half of that level and tended to show a further decline, with only 37 nests found in 2019. The decline is also evident when restricting the nest count to the main study area (Figure 2(a)). The whole-colony census in 2016 recorded 70 attendant pairs in early July, of which only a part had a nest (though some pairs that were unsuccessful in breeding had probably already left the colony). Censuses in early June recorded 65 attendant pairs in 2017, 91 in 2018 and 112 in 2019.

Reproductive investment and adult body mass

In 1997 and 1998, respectively, 84% and 94% of the pairs that laid eggs produced two eggs, others laid one. This percentage decreased to 72–75% in 2014–2016 and 11–29% in 2017–2019 (Figure 2(b)). In 2018, 12 pairs laid a second clutch after predation of the first; nine (82%) of the first clutches and eight (75%) of the second clutches were one-egg clutches. In 2019, one pair laid a second clutch after predation of the first. Both were one-egg clutches. Egg size differed significantly between years, irrespective of clutch size (largest egg in a two-egg clutch: $F = 5.2$, $P < 0.001$; smallest egg in a two-egg clutch: $F = 5.5$, $P < 0.001$; one-egg clutches: $F = 3.2$, $P = 0.003$), but due to large

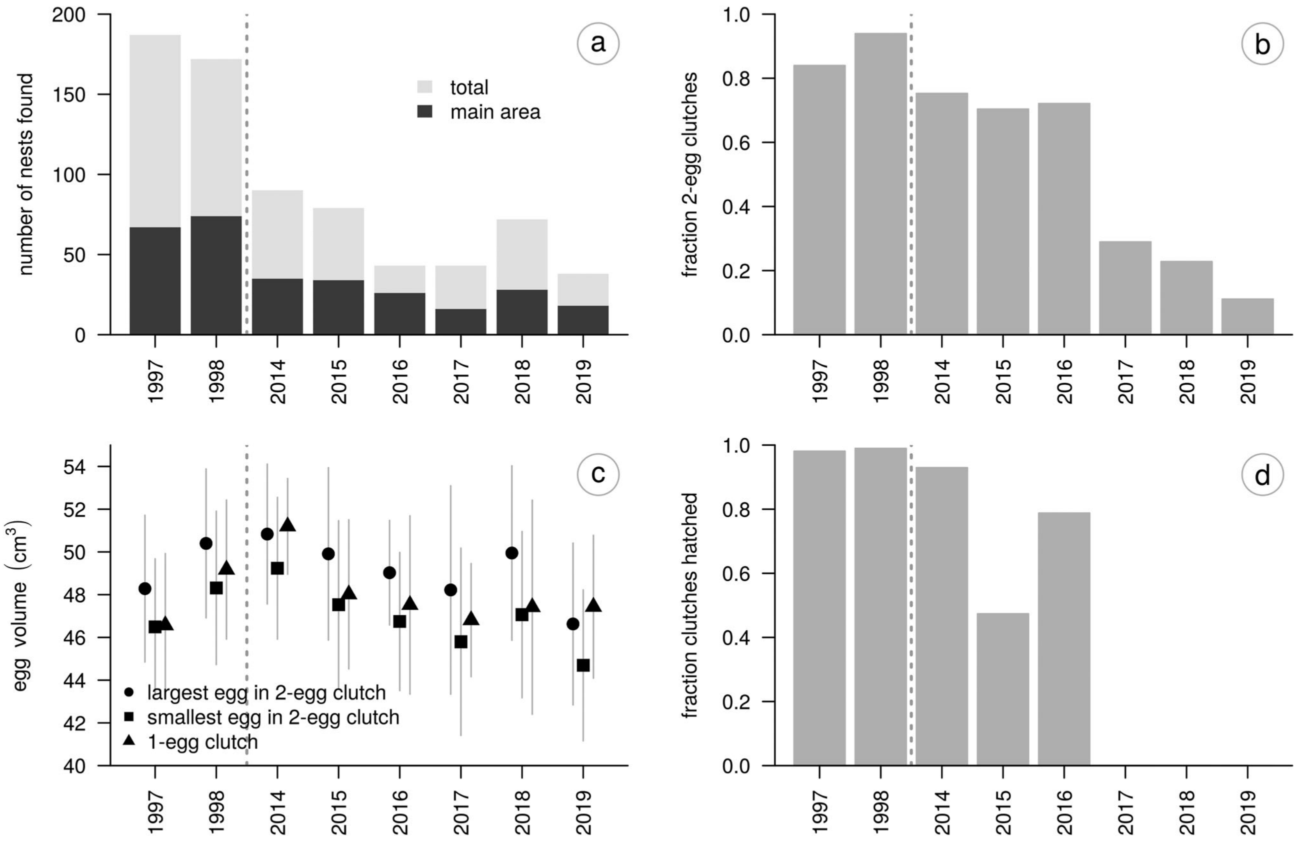

Figure 2. Breeding parameters of Arctic Skuas at Slettness measured in both study periods 1997–1998 and 2014–2019: (a) number of nests found; (b) fraction of clutches with two eggs versus with one egg; (c) egg size; (d) (raw) fraction of clutches that hatched (bars).

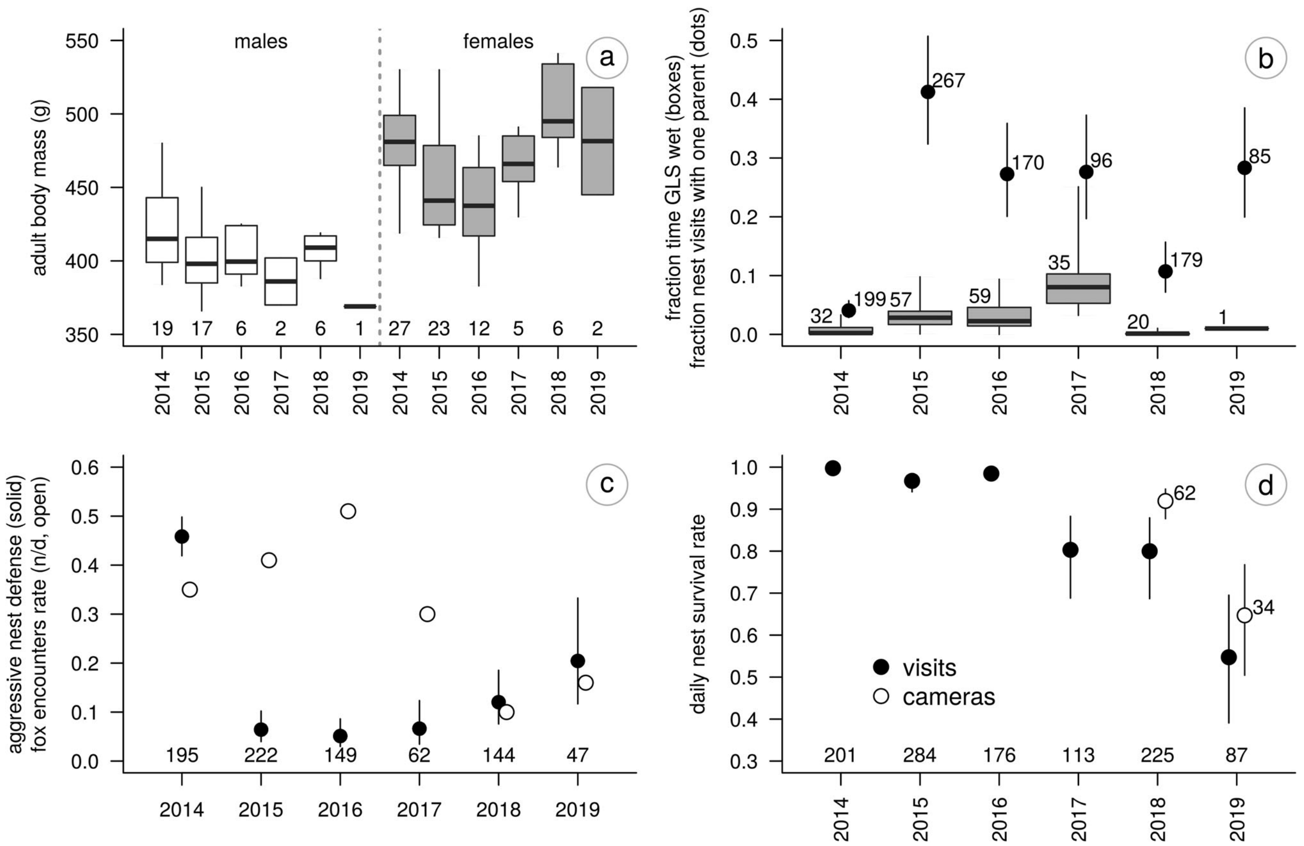

Figure 3. Breeding parameters of Arctic Skuas at Slettnes measured only in 2014–2019: (a) body mass during incubation of adult males (white) and females (grey); (b) indicators of time spent feeding at sea as fraction of time geolocators were submerged in saline water (boxplots), and fraction of nest visits by researchers during which only one parent was present in the breeding territory (dots); (c) fraction of nest visits with skua nest defence intensity exceeding 3, i.e. researchers hit by skuas (solid dots) and mean daily number of encounters with Red Foxes (open dots); (d) daily nest survival rate based on nest visits (solid dots) and on nest camera observations (open dots). In a and b, horizontal lines show medians, boxes delimit the 25% and 75% quantiles, and whiskers extend to the most extreme values. Error bars in b, c, and d represent standard error of model parameter estimates. Numbers above the x-axis or next to data points are sample sizes.

variation, only some between-year comparisons were statistically significant. In 1997, when breeding commenced late due to late snow melt, relatively small eggs were laid compared to 1998 (Figure 2(c)). Egg size diminished during 2014–2019 from a similar level as in 1998 to well below that level, although size of the largest egg in two-egg clutches increased again in 2018 to the level of 1998 and 2014. These differences between years in the period 2014–2018 remained when including individual-level random intercepts for females in LMEs.

Body mass differed between years in adult females ($F = 4.6$, $P = 0.001$), with significantly lower weights in 2015–2016 compared to 2014, 2017, 2018 and 2019 (posthoc Tukey test: $P < 0.01$). Between-year variation in body mass of adult males was not significant ($F = 2.2$, $P = 0.073$, Figure 3(a)). Mean daily time spent swimming at sea in June differed between years ($F = 38.2$, $P < 0.001$) and was low in 2014, 2018 and 2019, but higher in 2015–2016 and even more so in 2017. The proportion of nest visits by observers during which both pair members were present in the territory, i.e. not at sea, showed an approximately opposite pattern ($\chi^2 = 117.8$, $P < 0.001$; Figure 3(b)). Mean levels of aggressive nest defence were markedly higher in 2014 than in all subsequent years ($P < 0.001$ for 2015–2018 and $P < 0.01$ for 2019, Figure 3(c)).

Reproductive success and predation

No cases of nest desertion were observed in either study period; all losses were due to predation. In 1997–1998, predation of complete clutches was recorded in just 1–2% of the clutches found (Figure 2(d)). In 2014, 7% of the clutches were predated, increasing to 21–53% in 2015 and 2016. In 2017–2019, not a single egg hatched within our study area (Figure 2(d)). In 2018, median time between laying of the first egg and predation was

5 days (range 2–21, $n = 46$) and at least 12 pairs initiated a second clutch. Consistent with this, daily nest survival rate decreased from 0.99 in 2014 to 0.97, 0.98, 0.80, 0.80 and 0.55 in 2015–2019 (Figure 2(d)). Including day-of-year as a covariate in the logistic-exposure model decreased the model fit ($\Delta\text{AIC} = 1.9$), indicating no strong seasonal effect on predation rates. Our data on chick survival and overall reproductive success are less than complete, but indicated that, out of the six recent study years, 2014 was the only year with a reproductive success clearly above zero. In 2014, 109 chicks were ringed at ages of 7–39 days (fledging). In a total of 35 nests within the main study area, 35 chicks were ringed. Of these 35 chicks, 29 were encountered with a body mass of more than 250 g, corresponding to an age of about two weeks (Maher 1974). Of these 29 chicks, nine were pairs of siblings and 11 were single chicks that either came from a one-egg clutch, or whose sibling died or was not found. Considering that some of these 29 chicks may not have fledged (although the majority probably did), but that on the other hand we may not have found all large chicks present, we estimate the fecundity at around 0.4 (female offspring per pair) in 2014. In 2015 and 2016 only two and one chick(s), respectively, were found at an age of about two weeks; in 2017–2019 no chicks hatched in the entire study area.

We found no active Red Fox dens in 2016 and 2019, one in 2014, 2017 and 2018, and three in 2015. A different pattern was found in the number of Red Fox encounters per observer-day, which was highest in 2016 and low in 2018 and 2019 (Figure 3(c)). In 1997–1998, no Red Foxes were seen. During nest camera deployments at nine nests in 2018, six nests were predated and in four cases the predator was photographed and identified as a Red Fox (online Figure S1). In two cases the predator was not photographed. In 2019, cameras were deployed at 13 nests of which 12 were lost. For 10 predated nests, the predator could be identified with certainty from the photographs: nine as Red Foxes and one as Reindeer *Rangifer tarandus*. Based on the camera trap deployments, the estimate of daily nest survival rate was 0.92 in 2018 and 0.65 in 2019 (Figure 3(d)). Through a comparison of fur colouration and patterns caused by moult or damage, two individual Red Foxes were identified in nest camera photos from 2018, and again two in 2019.

Two instances of suspected predation on adult Arctic Skuas were documented. On 9 July 2015, the remains of an adult light morph female were found, 150 m from its nest. Primary feather shafts were bitten, indicating predation by a mammal. On 24 May 2017, a Red Fox was photographed with a dark morph adult Arctic Skua (with geolocator) in its mouth (Jan Erik Røer *pers comm*).

Demography

Mean annual adult apparent survival rate (φ_a) was estimated at 0.89 (95% CI = 0.84–0.93) and the resighting probability p, was estimated at 0.58 for 2015 and 0.81–0.87 in 2016–2019 (Figure 4(a)). We estimated a dispersion coefficient with the Bootstrap goodness of fit function in MARK, and obtained $\hat{c} = 1.0$. The combinations of number of reproductive years and first-year survival probability (φ_j) that lead to a stable population are depicted in Figure 4(b). Assuming $\varphi_j = 0.7$ (cf O'Donald 1983), the estimated fecundity of 2014 (0.41 female chicks fledged per pair) would be sufficient to maintain a stable population if the number of reproductive years is approximately 11 years or more. However, the expected mean lifespan after reaching adulthood ($-1/\log(\varphi_a)$) is only 8 years, which requires an annual fecundity of 0.48 female chicks fledged per pair to maintain a stable population. Fecundity was almost zero in 2015–2019. In case 4 out of 8 potential reproductive years fail, and again assuming $\varphi_j = 0.7$, fecundity in the remaining 4 years needs to be raised from 0.48 to 0.77 female chicks fledged per pair to maintain a stable population (Figure 4(b)).

Discussion

With approximately 250 breeding pairs in the late 1990s, the Arctic Skua colony at Slettnes was the largest in Europe (Anker-Nilssen *et al.* 2000, Mitchell *et al.* 2004). Over the two decades since then, the colony more than halved in size. This decline is far greater than can be explained by differences in census methods used in the two periods or variation in timing of the survey within the second period. It is in line with declines reported elsewhere from the European breeding range of the Arctic Skua (Eaton *et al.* 2015, Perkins *et al.* 2018). In Norway, declines in Arctic Skua populations have been reported in particular from the southern and western parts of the country (Henriksen & Hilmo 2015). Population changes from the northern regions of Norway have not been documented in any detail (Henriksen & Hilmo 2015), so our study fills an important knowledge gap by showing a heavy decline in the largest Arctic Skua colony of Europe.

In our study, we found indications for both bottom-up (food availability) and top-down (predation) effects

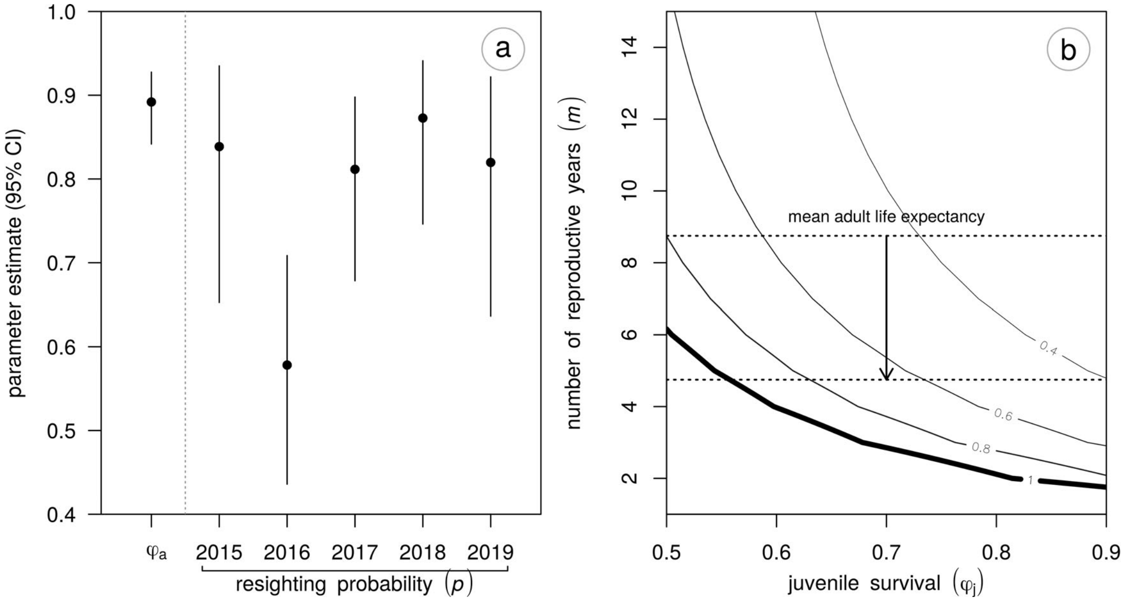

Figure 4. Demography of Arctic Skuas at Slettnes during 2014–2019: (a) mean annual survival (φ_a) and annual resighting probabilities (*p*) of adult Arctic Skuas (with 95% CL) and (b) required fecundity for a stable population (curved lines) as a function of juvenile survival (φ_j) and the number of reproductive years (*m*). Annual fecundity (f_a) is measured as the yearly mean number of female chicks per pair. The bold curve indicates a fecundity of 1, which is the maximum annual fecundity considering that Arctic Skuas lay at most two eggs and assuming an even sex ratio in eggs laid. The upper horizontal line shows the mean adult life expectancy based on our estimate of adult survival (thus the number of years after an age of four years, at which recruitment to the breeding population is assumed). The vertical arrow and lower horizontal line illustrate how four failed breeding years reduce the mean number of reproductive years, which leads to a considerably higher required fecundity in those years.

on the Slettnes Arctic Skua population. In three out of six recent study years (2015–2017), low body mass of adult females, small egg sizes and/or more time spent at sea and less on the territory suggest a poor local food situation for Arctic Skuas. We suggest that, after arriving at the breeding grounds with considerable body reserves (Belopol'skii 1961), the rate of body mass loss during the breeding season is largely a function of local food conditions. In addition, egg and clutch size should largely reflect local food conditions between arrival and clutch initiation, considering that Arctic Skuas produce eggs 84% from local resources (Hobson *et al.* 2000). Food availability seemed better in 2014 and 2018, when body mass of adult females was higher, eggs were larger and less time was spent at sea (Figures 2 and 3). The year 2019 takes an intermediate position, with fairly high body mass of adult females and less time spent at sea, but with clutch and egg sizes reaching an all-time low. The many relays following clutch predation in 2018 may also indicate that food was not limiting in that year. As recently as 2014, over 1000 pairs of Arctic Terns bred within the perimeter of the Arctic Skua colony, of which many successfully fledged chicks, and which must have led to an abundance of food-carrying hosts. In 2016–2019 breeding terns were absent but in 2018 we observed almost daily foraging associations of hundreds to thousands of Black-legged Kittiwakes and Herring Gulls *Larus argentatus* in the first few kilometres offshore of the colony, in which Arctic Skuas were frequently seen foraging as well. No or only very few such associations were seen in 2015–2017 and in 2019, despite daily seawatches from the Slettnes lighthouse. Another index of fish abundance in nearshore waters may be provided by sightings of feeding large cetaceans (Minke Whales *Balaenoptera acutorostrata,* Humpback whales *Megaptera novaeangliae,* Fin Whales *Balaenoptera physalus* and White-beaked Dolphins *Lagenorhynchus albirostris*) within visible range from the Slettnes shoreline, which were regular in both 2014 and 2018, but not in 2015–2017 and 2019. Finally, stock estimates for the Barents Sea of Capelin *Mallotus villosus*, a pelagic fish species of great importance to many seabirds, are consistent with this pattern; abundance was very low in 2015–2016, but higher in 2014, 2017 and 2018 and very low again in 2019 (ICES 2019). In 1997 and 1998, Capelin biomass was also very low, but was increasing towards a peak in 2000. However, these stock assessments cover a much larger area than the area likely to be covered by Arctic Skuas at Slettnes during the breeding season and are carried out in autumn (late

August till early October, ICES 2019), which is after the breeding season of Arctic Skuas, when the bulk of Capelin has moved north. These surveys indicate that Capelin distribution is moving progressively eastwards, possibly in response to climate change (Rose 2005).

Seemingly inconsistent with the above is the large proportion of one-egg clutches in 2018 despite the good food situation. However, this may at least partly be explained by predation during the laying process (about 3 days), if pairs lay only one more egg after predation of their first or if the nest was found after laying one egg and predated before our next visit. Even under 'normal' conditions, 10–20% of the pairs will lay just one egg (Furness 1987 and our data from 1997–1998), and in 2018 about 30% of all other clutches may have been predated before the second egg was laid (assuming 85% of clutches will get two eggs, a mean laying interval of 2 days and a daily nest survival probability of 0.8 (Figure 3), this proportion equals $0.85 \cdot [1{-}0.8^2]$).

Annual fluctuations in body mass of adult males were similar to those in females, but statistically not significant. Body mass of adult males may be less affected by local food conditions, considering that males incubate less than females and can therefore spend more time foraging at sea (Furness 1987). This allows males to prioritize their own condition above provisioning the female. Finally, patterns in clutch size and chick survival in Black-legged Kittiwakes and Common Guillemots *Uria aalge* during 2014–2017 at two localities in Finnmark, Hornøya and Hjelmsøya, both at approximately 130 km from Slettnes, do not align with the pattern observed in Arctic Skuas at Slettnes. For example, the very poor breeding year of Black-legged Kittiwakes at both sites in 2014 is in sharp contrast to the high reproductive success of Arctic Skuas at Slettnes, whereas Common Guillemots at Hornøya had fairly stable fledging success throughout this period (Barrett *et al.* 2015). These discrepancies suggest that food availability may vary substantially even at the restricted spatial scale of about 130 km.

Beside the bottom-up effects, top-down effects also likely played a role in the decline of the Arctic Skua colony at Slettnes. In the absence of Red Foxes in 1997–1998, almost no nests were lost in those years. In contrast, predation caused almost total reproductive failure in five consecutive years (2015–2019). For 2018 and 2019, we have direct evidence from nest cameras that Red Foxes was the main predator of eggs. However, we are confident that Red Foxes were also responsible for nest predation in 2015–2017, as this was the only potential predator species regularly observed making foraging forays in the colony area. Although Arctic Foxes are known predators of Long-tailed, Pomarine and Arctic Skuas (de Korte 1986, Maher 1974, Underhill *et al.* 1993), we know of no published records of predation by Red Foxes on Arctic Skuas elsewhere.

Possibly, the high predation rates may have been indirectly caused by a poor food situation, resulting in a less dense colony (due to lower breeding propensity) and less aggressive nest defence, thus facilitating access to the colony for foxes. However, predation rates were also high in 2018, when the food situation was clearly better, but breeding numbers and intensity of nest defence still low. A potential explanation for the contrast between 2018 and 2014, when the food situation was also good and the predation rate was very low, is that individual Red Foxes at Slettnes specialized in preying on Arctic Skua eggs (Rodgers Jr 1987, Panzacchi *et al.* 2008). An observation consistent with individual specialization is the absence of a clear relation between daily nest survival rates and the number of active Red Fox dens or daily encounter rates of Red Foxes. Also, the fact that only two individual Red Foxes were recorded by our camera traps in both 2018 and 2019 is in line with this hypothesis but is based on only a small number of predation events and does not exclude the possibility that other foxes or other mammals were responsible for the predation of other nests. Although we occasionally observed Stoats *Mustela erminea* in the area and a pair of Ravens *Corvus corax* nested on the lighthouse and were regularly observed roaming the area, they were never recorded by our cameras.

In 2014–2019, reproductive success has been too low to sustain the Arctic Skua population at Slettnes. With an adult survival rate of 0.89, a mean of 8 reproductive years and assuming a juvenile survival rate after fledging of 0.70 (O'Donald 1983), the mean annual fecundity should be at least 0.48 female chicks per pair to maintain a stable population. In 2014–2019, fecundity only approached this level in 2014, while near-total breeding failures occurred in the other five years. It seems unlikely that this period of failed breeding years can be compensated for within the lifetime of the current population of birds breeding at Slettnes, given the regular occurrence of years with poor feeding conditions, the negative (indirect) impact of increasing sea temperatures on Capelin distribution and abundance (Stige *et al.* 2010), and the continuing presence of Red Foxes. The number of Red Foxes has increased over recent decades in northern Norway (Killengreen *et al.* 2011).

Winter survival and/or reproduction of Red Foxes may be especially high at Slettnes, as they can feed on marine resources along the coast (Roth 2003), fishery offal in the harbour of Gamvik, and are reportedly being fed by people in Gamvik during the winter months.

Obviously, uncertainty exists in several of the model parameters. The largest uncertainty exists in apparent juvenile survival, as there is neither data to estimate this for the Slettnes colony, nor values reported in the literature for other areas. O'Donald (1983) reasoned that juvenile survival should be around 0.70, if the Fair Isle colony were to be stable in his study years. Moreover, we assumed high natal philopatry, whereas recruiting immatures may disperse to other breeding sites, as has been documented in Great Skuas (Furness 1987). Less uncertainty exists in our estimates of adult apparent survival, which is similar to the 0.886 reported from 1973–1975 at Fair Isle, Scotland (O'Donald 1983) and 0.89 in 1992–1999 at Foula, Scotland (Phillips 2001). These adult survival rates appear slightly low for a seabird, which usually have survival rates of 0.90–0.95 (Weimerskirch 2002), and it should be noted that Arctic Skuas were already declining in Scotland in general in the 1990s (Phillips *et al.* 1996, Perkins *et al.* 2018). The two observations of adult Arctic Skuas apparently killed by Red Foxes may also have meaning in this respect. However, survival rates and longevity records for skuas and gulls are typically lower than for other seabirds such as auks, Fulmars *Fulmarus glacialis* and shearwaters (Weimerskirch 2002).

The estimate of apparent survival is the product of true survival and emigration. Adult Arctic Skuas show high site fidelity (O'Donald 1983, Furness 1987), rendering substantial emigration to other breeding sites unlikely. Even if adult survival rates were higher than our data suggest, our conclusion that reproductive success in the Slettnes colony has been too low during 2014–2019 to sustain a stable population, will remain unchanged (e.g. $\varphi_a = 0.95$ would lead to a required mean annual fecundity of 0.33 female offspring). A higher adult survival estimate would however permit one or two more failed breeding years before the required fecundity exceeds the maximum of one female chick per pair.

In conclusion, we documented a severe decline of the Arctic Skua colony at Slettnes, that is in line with trends observed in other seabirds along the Norwegian coast, including the Arctic Tern and the Black-legged Kittiwake, both important host species for Arctic Skuas (www.seapop.no, Fauchald *et al.* 2015). The decline in these hosts is mainly attributed to low forage fish stocks, with predation by avian and mammalian predators potentially contributing to population declines (Fauchald *et al.* 2015). At Slettnes, mammalian predation poses an important threat to the Arctic Skua colony that may prohibit skuas to reproduce even when food is abundant. Given the ongoing expansion of the Red Fox and increase in population size (Killengreen *et al.* 2011), the future of the Slettnes colony seems bleak. The alternative strategy used by Arctic Skua pairs, to breed in single pairs at isolated sites (Gotmark and Andersson 1980), may be more successful in a situation with increased predation pressure.

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Appendix A

The expected lifetime reproductive output of a female individual, R_0 follows from summing the expected reproductive contribution at each reproductive age:

$$R_0 = S_j \cdot f_a + S_j \cdot \varphi_a \cdot f_a + S_j \cdot \varphi_a^2 \cdot f_a + \ldots + S_j \cdot \varphi_a^{m-1} \cdot f_a \quad (A1)$$

where φ_a is the annual survival probability of an individual that will breed the upcoming summer (age 3 years or older), m is the number of reproductively active years and S_j is the survival probability from hatching up to the age at first breeding. We assume that the annual survival probability during the immature years increases linearly from the annual first-year survival probability φ_j, to the annual adult survival probability φ_a. The cumulative survival probability during the immature years is then given by:

$$S_j = \prod_{i=0}^{3} \left(\varphi_j + i \frac{(\varphi_a - \varphi_j)}{3} \right) \quad (A2)$$

Equation (A1) can be simplified to:

$$R_0 = S_j \cdot f_a \cdot \left(1 + \sum_{i=1}^{m-1} \varphi_a^i \right) \quad (A3)$$

$$R_0 = S_j \cdot f_a \cdot \left(\frac{1 - \varphi_a^m}{1 - \varphi_a} \right) \quad (A4)$$

A stable population requires that $R_0 = 1$, which leads to the required fecundity of:

$$f_a = S_j^{-1} \cdot \left(\frac{1 - \varphi_a}{1 - \varphi_a^m} \right) \quad (A5)$$