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Evidence for an Allee effect in a declining fur seal population

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Allee effects play an important role in the dynamics of many populations and can increase the risk of local extinction. However, some authors have questioned the weight of evidence for Allee effects in wild populations. We therefore exploited a natural experiment provided by two adjacent breeding colonies of contrasting density to investigate the potential for Allee effects in an Antarctic fur seal (*Arctocephalus gazella*) population that is declining in response to climate change-induced reductions in food availability. Biometric time-series data were collected from 25 pups per colony during two consecutive breeding seasons, the first of which was among the worst on record in terms of breeding female numbers, pup birth weights and foraging trip durations. In previous decades when population densities were higher, pup mortality was consistently negatively density dependent, with rates of trauma and starvation scaling positively with density. However, we found the opposite, with higher pup mortality at low density and the majority of deaths attributable to predation. In parallel, body condition was depressed at low density, particularly in the poor-quality season. Our findings shed light on Allee effects in wild populations and highlight a potential emerging role of predators in the ongoing decline of a pinniped species.

1. Background

Many species exhibit a decrease in population fitness or growth as population density declines, a relationship known as the Allee effect [1]. Component mechanisms generating this positive density dependence include *inter alia* mate limitation, cooperative defence, predator satiation, cooperative feeding, dispersal, habitat alteration [2] and combinations thereof [3]. However, component effects need not necessarily result in population declines [4]. Negative density dependence can offset Allee effects through resource competition [2,5] or operate at different stages of the life history [6], thereby negating a demographic Allee effect.

Allee effects are believed to have contributed towards the decline of several once highly abundant species. For example, the passenger pigeon, which historically numbered several billion individuals [7], was driven to extinction by nineteenth-century hunters as population sizes fell below the threshold required for efficient foraging [8,9]. Similarly, the collapse of the northwest Atlantic cod stocks and their failure to recover even after protections were put in place has been attributed to an Allee effect [10], which also appears to be driving the contemporary Gulf of St Lawrence population towards extinction [11].

Despite these and other prominent examples, several authors have questioned the weight of evidence more generally for Allee effects [4,12–14]. Allee effects are particularly difficult to demonstrate in wild populations owing to logistical constraints [1], the difficulty of disentangling Allee effects from declines owing to habitat alteration or destruction [4] and a general reliance on long-term observational data, which can suffer from power limitations

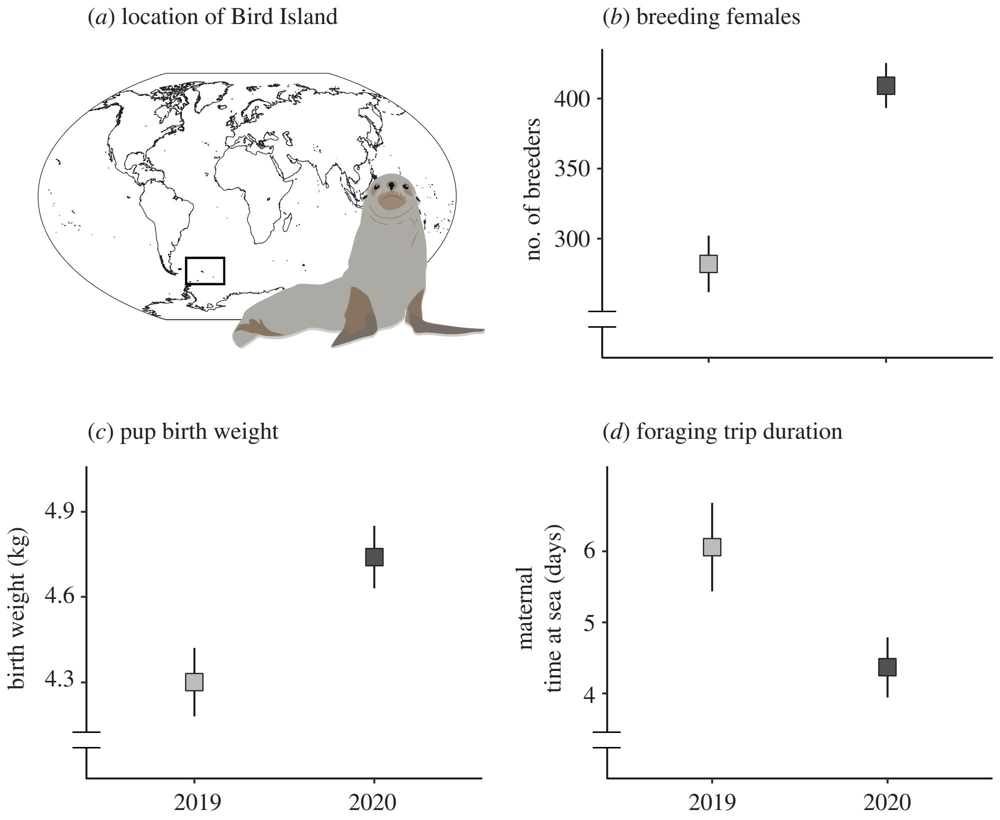

Figure 1. Seasonal differences in female breeding performance. (*a*) The location of Bird Island, South Georgia in the South Atlantic. (*b–d*) The number of breeding females, the birth mass of their pups and the amount of time spent by mothers foraging at sea during the austral summers of 2019 (light grey) and 2020 (dark grey). The square symbols show the means and the vertical lines indicate 95% confidence intervals (CIs).

when population sizes are small [2]. An alternative is to use population-scale experimental manipulations to increase power and reduce ambiguity [2], although this is often impractical or even unethical for some species [1]. Consequently, some authors have advocated the use of ‘natural experiments’, which take advantage of naturally occurring variation in density over space and/or time [2].

Just such a natural experiment is provided by a declining population of Antarctic fur seals (*Arctocephalus gazella*) breeding at Bird Island, South Georgia (figure 1*a*). Females of this species rear their pups in densely packed breeding colonies, where historically the most common causes of offspring mortality were starvation owing to the disruption of mother–pup bonds and traumatic injuries from trampling and bite wounds [15,16]. However, the main land predator of fur seals on Bird Island, the northern giant petrel [17], has been steadily increasing in population size over the past 20 years [18] and its numbers are projected to continuously increase in the future [19]. This coincides with a long-term decline [20] in the availability of the fur seals’ staple diet, Antarctic krill [21], which has led to a substantial reduction in the number of breeding females on Bird Island over the past three decades [22–24]. These ecological changes could potentially alter the relationship between density and offspring mortality as well as the underlying mechanism(s) of density dependence.

To test this hypothesis, we exploited naturally occurring spatial variation in density by comparing offspring fitness measures between two adjacent breeding colonies of high and low density ([25]; figure 2*a*,*b*). As these colonies are only around 200 m apart, females from both localities probably forage in the same area [26]. Consequently, food availability is effectively controlled for and there should be no differences in female nutritive state. Furthermore, a lack of genetic differentiation [27] implies that animals from these colonies form part of the same wider breeding population. We used VHF radio telemetry to follow pups in both colonies from birth until weaning and to track survival as well as changes in body weight and condition over time. We also replicated our study across two consecutive seasons to place density-dependent variation in the context of environmental variation between years. We hypothesized that: (i) especially given increases in the number of land predators, pup survival will correlate positively with population density assuming cooperative defence and predator satiation; and (ii) given that breeding female fur seals are constrained by the distance they can swim and the amount of time they can forage at sea before their pups on land starve, poor environmental conditions in terms of low food availability will lead to a decrease in pup survival.

2. Methods

(a) Field methods

This study was conducted during the austral summers (December to March) of 2018–2019 (hereafter 2019) and 2019–2020 (hereafter 2020) at Bird Island, South Georgia (54°00′24.8″ S, 38°03′04.1″ W; figures 1*a* and 2*a*). For the capture, restraint and measurement of Antarctic fur seal mothers and their pups, we employed protocols that have been established and refined over 36 consecutive years of the long-term monitoring and survey programme of the British Antarctic Survey (BAS). Adult females were captured with a noosing pole and held on a

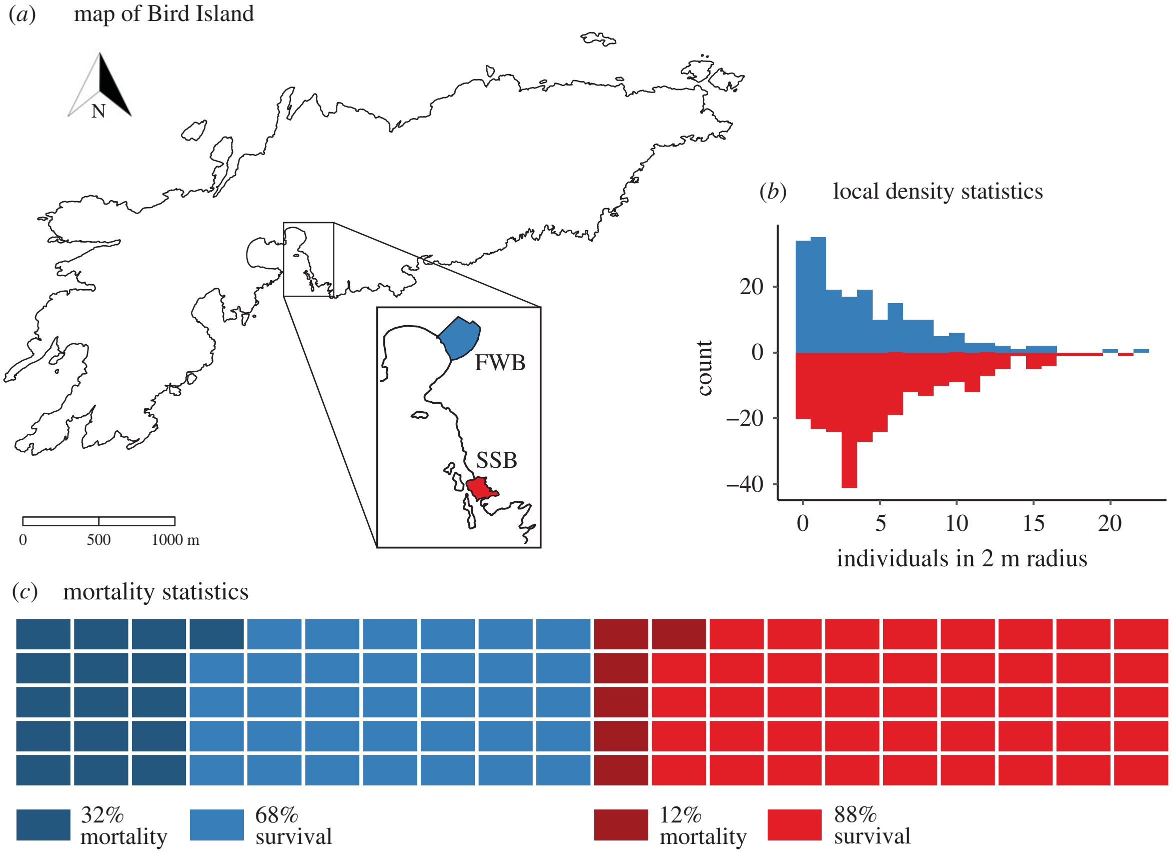

Figure 2. Differences in local density and pup survival between two adjacent breeding colonies on Bird Island, South Georgia. (*a*) The location of the two fur seal breeding colonies from which 50 mother–pup pairs each were captured for the collection of biometric time-series data. Freshwater Beach (FWB) and Special Study Beach (SSB) are approximately 200 m apart. (*b*) The local density distribution of focal pups from both colonies. Local density was defined as the total number of individuals within two adult female body lengths or an approximate 2 m radius of the focal pup at time of sampling. As shown, pups born on FWB were most frequently found throughout the breeding season with only one additional individual in close proximity (range = 0–22 individuals), while pups born on SSB were most frequency found together with three individuals (range = 0–21 individuals). (*c*) provides a visual representation of the number and proportion of focal pups that survived in each colony. Blue = FWB, red = SSB. (Online version in colour.)

restraint board. Pups were captured with a slip noose or by hand and were restrained by hand. After measurements were taken, the seals were released as close to their capture sites as possible, and pups were returned to their mothers when present. Previous research has shown minimal to no chronic effects of repeated physical restraint and handling in several pinniped species [28].

Each season, 25 unique mother–pup pairs were randomly selected from the low-density colony (‘Freshwater Beach’, FWB) and the high-density colony (‘Special Study Beach’, SSB) (figure 2*a*), yielding a total sample size of 200 individuals (2019: $n = 50$ mothers and 50 pups; 2020: $n = 50$ mothers and 50 pups). Each mother and her pup were captured concurrently on two separate occasions: 2–3 days postpartum (December) and again as the pups began to moult shortly before weaning (March). The pups were additionally recaptured and measured every 10 days. At every capture, biometric data (weight, length, span and girth) and local density, quantified as the total number of fur seal individuals present within two adult female body lengths or an approximate 2 m radius of the focal individual, were recorded. The initial capture of fur seal mothers and pups at both colonies was randomized with respect to the sex of the pup and the time during the pupping period. This resulted in a final dataset of 30 male and 20 female pups from FWB and 21 male and 29 female pups from SSB.

At first capture, adult females were fitted with cattle ear tags (Dalton Supplies, Henley on Thames, UK) in the trailing edge of each fore flipper [29]. During lactation, mothers alternate foraging trips at sea with time spent ashore nursing pups [30] and until pups are approximately 20 days old, females repeatedly return to the breeding colony for nursing. As pups mature, however, both mother and pup undertake progressively longer and more distant trips into the densely vegetated regions of tussock grass inland [31], which may afford protection from predators, such as giant petrels [32]. Pups in particular range on average 3.3 km away from their colony of birth [32]. Therefore, to facilitate the tracking and recapture of females, we attached VHF transmitters (Sirtrack core marine glue-on V2G 154C) to the dorsal side of the neck between the shoulder blades with epoxy glue. The pups were similarly fitted with VHF transmitters (Sirtrack core marine glue-on V2G 152A) and were identified using temporary bleach marks (Clairol Nice’n Easy Borne Blonde Permanent Hair Colour) applied to the fur, which grew out with the moult. VHF transmitter signals of mothers and pups were monitored using a hand-held VHF receiver (AOR Ltd., AR8200). The transmitters were retrieved from all animals at their last recapture.

(b) Seasonal variation

As part of the BAS contribution to the Ecosystem Monitoring Programme of the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR), the attendance behaviour of breeding females has been monitored since 1982. Radio telemetry as a consistent method for this monitoring programme was established in 1992 and approximately 25 adult females per season on FWB have since been tracked. We contributed towards this ongoing effort by collecting attendance data for our focal mothers on FWB using a fixed-position radio antenna

(Televilt RX900) combined with visual checks of the island using a hand-held VHF receiver (AOR Ltd., AR8200). Given the location of the radio antenna and the terrain of Bird Island, only individuals in the immediate vicinity of FWB could be reliably detected and time constraints prevented visual checks of the island for every focal female. The daily presence or absence of females ashore was therefore recorded for focal FWB females from the time of the first capture until the final measurement, when their pups either weaned or died. To determine if the attendance behaviour of breeding females differed between the two seasons, we performed a Wilcoxon rank-sum test, where the mean foraging trip duration (i.e. time absent from land) for all focal FWB females across the entire monitoring period was compared between the two seasons.

At SSB, an elevated scaffold walkway built above the breeding colony provides access to all parts of the beach and allows the animals to be observed and sampled with minimal disturbance. Twice a day, the colony was scanned for newborn pups, which were sexed, weighed and given a temporary bleach mark. Because almost all females give birth to a single pup each year [33], we used pup counts as a proxy of the total number of breeding females in the colony; associated 95% confidence intervals were determined based on the observed number of females that bred and those that did not breed. Following Forcada & Hoffman [22], annual mean pup birth weights were calculated only for female pups to avoid sex biases. To determine if the mean birth weight of pups differed between the two seasons, we performed a Welch two-sample *t*-test. Note: we chose to focus solely on SSB pups for this analysis for two reasons. First, all of the pups born on SSB were measured in both years, providing a much larger sample size than our focal dataset of pups from both colonies. Second, comprehensive data from SSB can be more readily compared against the historical time-series [22].

(c) Pup mortality

The survival of focal pups was tracked from birth until weaning in both colonies. Following a simplified protocol developed by a veterinarian specializing in pinniped pathology [34], dead pups were examined to determine the most likely cause of death, which was characterized as follows: (i) starvation, characterized by a thin or absent layer of subcutaneous blubber; (ii) trauma, where pups exhibited traumatic injuries (e.g. crushed skull or ribs) and associated haematomas; (iii) predation, characterized by bite marks on the flippers and around the anus and/or missing organs removed through holes below the flippers or anus; (iv) bacterial infection, as indicated by the presence of lesions, pus or swelling in the absence of any obvious signs of trauma or starvation; and (v) unknown, i.e. pups that could not be assigned to any of the above categories. In the absence of direct evidence of a pup having died, mortality was assumed if an individual was not sighted for 10 consecutive days. Because mothers exhibit irregular attendance patterns after their pups have died [35], we recaptured the mothers of dead pups to remove their VHF transmitters and to collect a final set of biometric observations. To determine whether maternal condition, sex, birth weight and breeding colony explained a significant proportion of the variance in pup mortality, we used a generalized linear model (GLM) with a binomial distribution. A backward elimination procedure based on Akaike information criterion (AIC) values was implemented to simplify the model. No interactions were tested in this model as their inclusion led to a perfect or quasi-perfect separation, which results in inflated coefficient estimates.

(d) Pup weight

To determine whether age, sex, maternal postpartum weight, season, colony and interactions among these variables explained a significant proportion of the variation in pup weight, we constructed a linear mixed model (LMM) using the restricted maximum-likelihood (REML) approach in *lmerTest* [36]. Pup identity (ID) was included as a random effect in the model to account for repeated measurements of individuals. Backward elimination based on AIC values was implemented to simplify the model and the statistical significance of fixed predictors was assessed using type III ANOVA (Satterthwaite's approximation of denominator degrees of freedom).

(e) Pup condition

The condition index of all focal individuals was calculated using a scaled mass index according to Peig & Green [37]. This method uses log-transformed scaling between body length and mass in relation to the average body length for the population, thus taking individual variation in relative size into consideration. The condition index serves as a reliable indicator of overall fitness in terms of the relative size of energy reserves [37] and resource availability [38]. In pinniped species, body condition has been shown to correlate with pup mortality in Steller sea lions [39], with reproductive success in South African fur seals [40] and harp seals [41] and with personality traits in Galápagos sea lions [42].

To determine whether age, sex, maternal postpartum condition, season, colony and interactions among these variables explained a significant proportion of the variation in pup condition throughout ontogeny, we constructed a LMM using the REML approach in *lmerTest* [36]. Pup ID was again included as a random effect to account for repeated measurements of individuals. Backward elimination based on AIC values was implemented to simplify the model and the statistical significance of fixed predictors was assessed using type III ANOVA. Significant interactions between variables were further investigated using *post hoc* least-squares means corrected for multiple testing (Tukey method) in *emmeans* [43].

(f) Maternal quality

To determine whether postpartum maternal quality measures (span, girth, weight, length and condition index) differed significantly between colonies, we performed Wilcoxon signed-rank tests. To further test for a difference in maternal condition between seasons, we constructed a linear model of the postpartum condition including colony, season and interaction between colony and season as predictor variables.

(g) Statistics

For our statistical models, we checked if the data were normally distributed using Shapiro–Wilk's tests. The residuals of the models were visually inspected for linearity and equality of error variances (using plots of residuals versus fits) and normality (using Q-Q plots). Homogeneity of variance was further checked using Levene's test in *car* [44]. All statistical analyses and visualizations were implemented in R v. 4.0.2 [45] using the integrated development environment RStudio. Our code and accompanying documentation are provided in the form of an R Markdown file (electronic supplementary material). The data used for this study are available via Dryad, https://doi.org/10.5061/dryad.zcrjdfnb0 [46].

3. Results

To investigate density-dependent effects on offspring survival and growth, we gathered biometric time-series data from a total of 100 Antarctic fur seal mothers and their offspring. These focal animals comprised 50 mother–pup pairs

Table 1. Parameter estimates from the REML best fit linear mixed model of pup weight. Pup ID was included as a random effect to account for repeated measures. Estimates together with their standard errors and 95% confidence intervals (CIs) are presented. Significant *p*-values are italicized. The mean squared error (σ^2), intraclass correlation coefficient (ICC; the consistency within an individual across multiple measurements) and sample size (*n*) are given for the random effect.)

coefficient	estimate	standard error	95% CI	*p*-value
intercept	2.243	0.836	0.603–3.882	*0.008*
age	0.080	0.002	0.076–0.084	*<0.001*
maternal postpartum weight	0.079	0.024	0.032–0.125	*0.001*
sex	0.857	0.211	0.444–1.270	*<0.001*
random effect				
σ^2	0.86			
ICC	0.54			
n	100			

from a low-density colony (FWB) and 50 mother–pup pairs from a high-density colony (SSB) (figure 2*a*,*b*). Data collection was spread over two consecutive breeding seasons ($n = 25$ pairs per colony per season).

(a) Interannual variation

Comparison of census, biometric and female attendance data from 2019 and 2020 revealed appreciable interannual variation. The number of breeding females at SSB was around 45% lower in 2019 (figure 1*b*) and mean pup birth weight was around 10% lower (figure 1*c*; Welch two-sample *t*-test, $t = -5.279$, $p < 0.001$). In parallel, breeding females on FWB made significantly longer foraging trips in 2019 (figure 1*d*; electronic supplementary material, figure S1; Wilcoxon rank-sum test, $W = 13\,080$, $p < 0.001$). These observations suggest that 2019 was a relatively poor-quality year in which fewer food resources were available to breeding females at both study sites [24,47–49].

(b) Pup mortality

Pup mortality was significantly higher at FWB than SSB (32% versus 12%, respectively, figure 2*c*; GLM, estimate = -1.186, s.e. = 0.545, $z = -2.177$, $p = 0.030$) and showed a negative association with birth weight (GLM, estimate = -0.714, s.e. = 0.321, $z = -2.223$, $p = 0.026$). Neither maternal condition shortly after giving birth nor sex were retained as significant predictors in the model. Necropsies of 16 pups indicated that the most likely causes of death were predation ($n = 9$), starvation ($n = 5$) and infection ($n = 1$), while the cause of death of one pup could not be determined.

(c) Pup weight

The best supported model of pup weight contained age ($p < 0.001$), sex ($p < 0.001$) and maternal postpartum weight ($p = 0.001$) as fixed effects (table 1). Neither season nor colony of birth were retained as significant predictors. Overall, pup weight increased significantly with age (figure 3*a*) and was higher for males than females (figure 3*b*). A positive, linear relationship was observed between pup weight and maternal postpartum weight (figure 3*c*), indicating that heavier mothers tended to produce heavier pups.

(d) Pup condition index

The best-supported model of pup condition throughout ontogeny contained age ($p < 0.001$), season ($p = 0.020$), colony ($p = 0.001$), the interaction between season and colony ($p = 0.029$) and the interaction between colony and age ($p = 0.039$) as fixed effects (table 2). Maternal postpartum condition was not retained as a significant predictor. Pup condition varied significantly by age (figure 4*a*) and tended to be lower in 2019 (figure 4*b*) and higher at SSB (figure 4*c*). Pups born at FWB had lower condition index values in 2019 than in 2020 (figure 4*d*; Tukey's *post hoc* test, estimate = -0.345, s.e. = 0.148, $p = 0.097$), whereas SSB pups showed the opposite tendency (figure 4*d*; Tukey's *post hoc* test, estimate = 0.099, s.e. = 0.136, $p = 0.887$). This pattern of colony- and season-dependent variation in body condition was already present within the first 2–3 days of life, with pups born at FWB having lower condition shortly after birth in 2019 compared with 2020 (Tukey's *post hoc* test, estimate = -0.346, s.e. = 0.148, $p = 0.097$), while SSB pups did not (Tukey's *post hoc* test, estimate = 0.099, s.e. = 0.136, $p = 0.887$). By implication, FWB pups were more adversely affected by unfavourable environmental conditions in the 2019 season, although they also exhibited greater improvement in condition as the season progressed relative to SSB pups, whose condition remained relatively stable over time (figure 4*e*).

(e) Maternal quality traits

Mothers from the two colonies did not differ significantly in any postpartum quality measures (span, girth, weight, length and condition index; electronic supplementary material, figure S2; Wilcoxon signed-rank tests, all $p > 0.05$). A more comprehensive linear model to test for a difference in maternal postpartum condition between seasons and a possible interaction between season and colony also revealed no significant effects (electronic supplementary material, table S1; all $p > 0.05$).

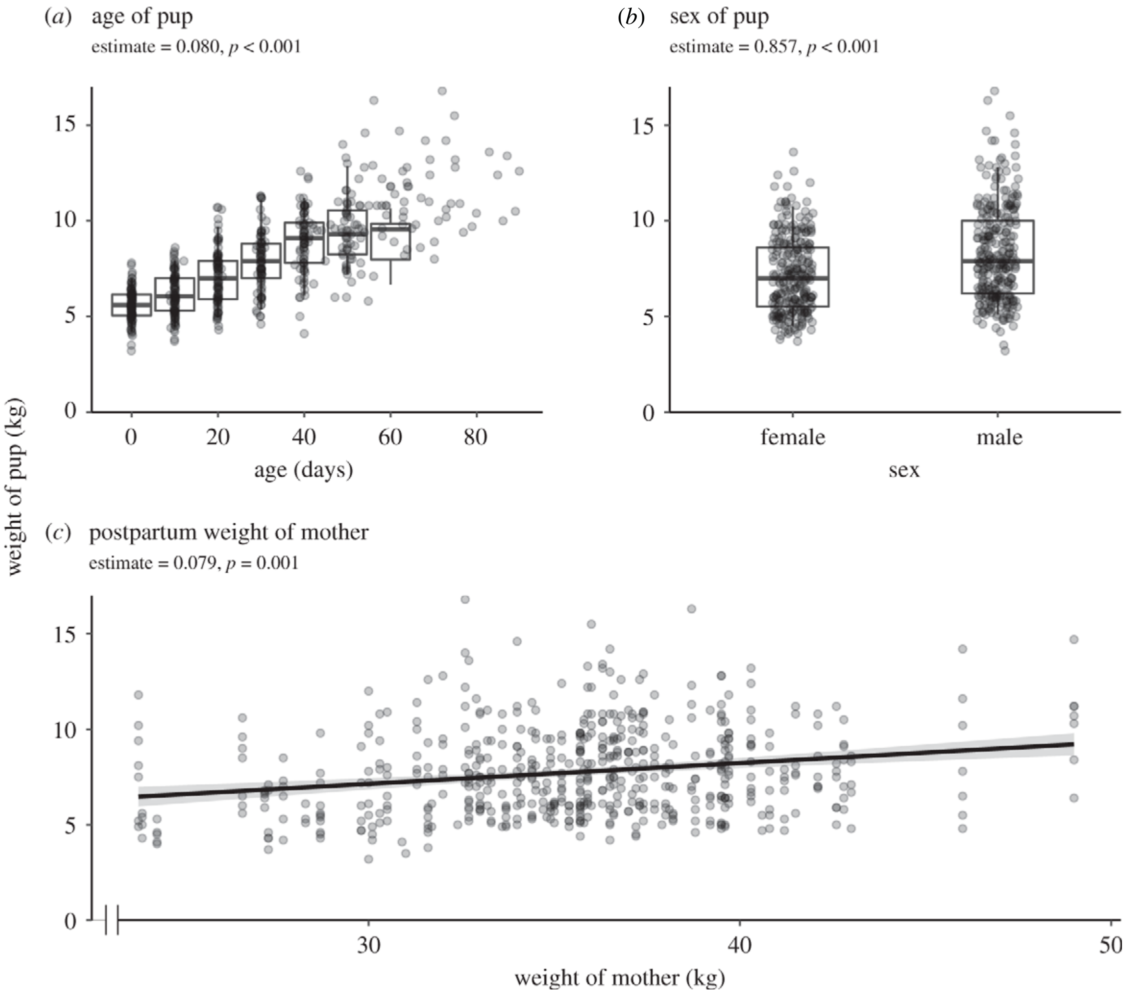

Figure 3. Results of a linear mixed model of pup weight. Significant main effects of pup age, pup sex and maternal postpartum weight are shown in (*a*–*c*), respectively. Parameter estimates and *p*-values are shown; further details of the model output can be found in table 1. Boxes in (*a*) and (*b*) show the means ± 75% quantiles, with the vertical lines indicating 95% confidence intervals (CIs).

Table 2. Parameter estimates from the REML best fit linear mixed model of pup condition index. Pup ID was included as a random effect to account for repeated measures. Estimates together with their standard errors and 95% confidence intervals (CIs) are presented. Significant *p*-values are italicized. The mean squared error (σ^2), intraclass correlation coefficient (ICC; the consistency within an individual across multiple measurements) and sample size (*n*) are given for the random effect.)

coefficient	estimate	standard error	95% CI	*p*-value
intercept	6.975	0.118	6.745–7.206	*<0.001*
age	0.010	0.003	0.005–0.016	*<0.001*
season	0.345	0.148	0.055–0.636	*0.020*
colony	0.535	0.163	0.216–0.855	*0.001*
season : colony	−0.444	0.201	−0.838–−0.050	*0.027*
age : colony	−0.008	0.004	−0.015–0.000	*0.039*
random effect				
σ^2	0.71			
ICC	0.13			
n	100			

4. Discussion

We used a unique natural experiment to test for Allee effects in an Antarctic fur seal population in the South Atlantic. Long-term monitoring of this population has revealed a steady decline in the number of breeding individuals since the 1980s, with the past decade witnessing a decline in female numbers of about 30% [22]. In contrast to previous studies, under these low abundance conditions we found a positive effect of increasing density on two

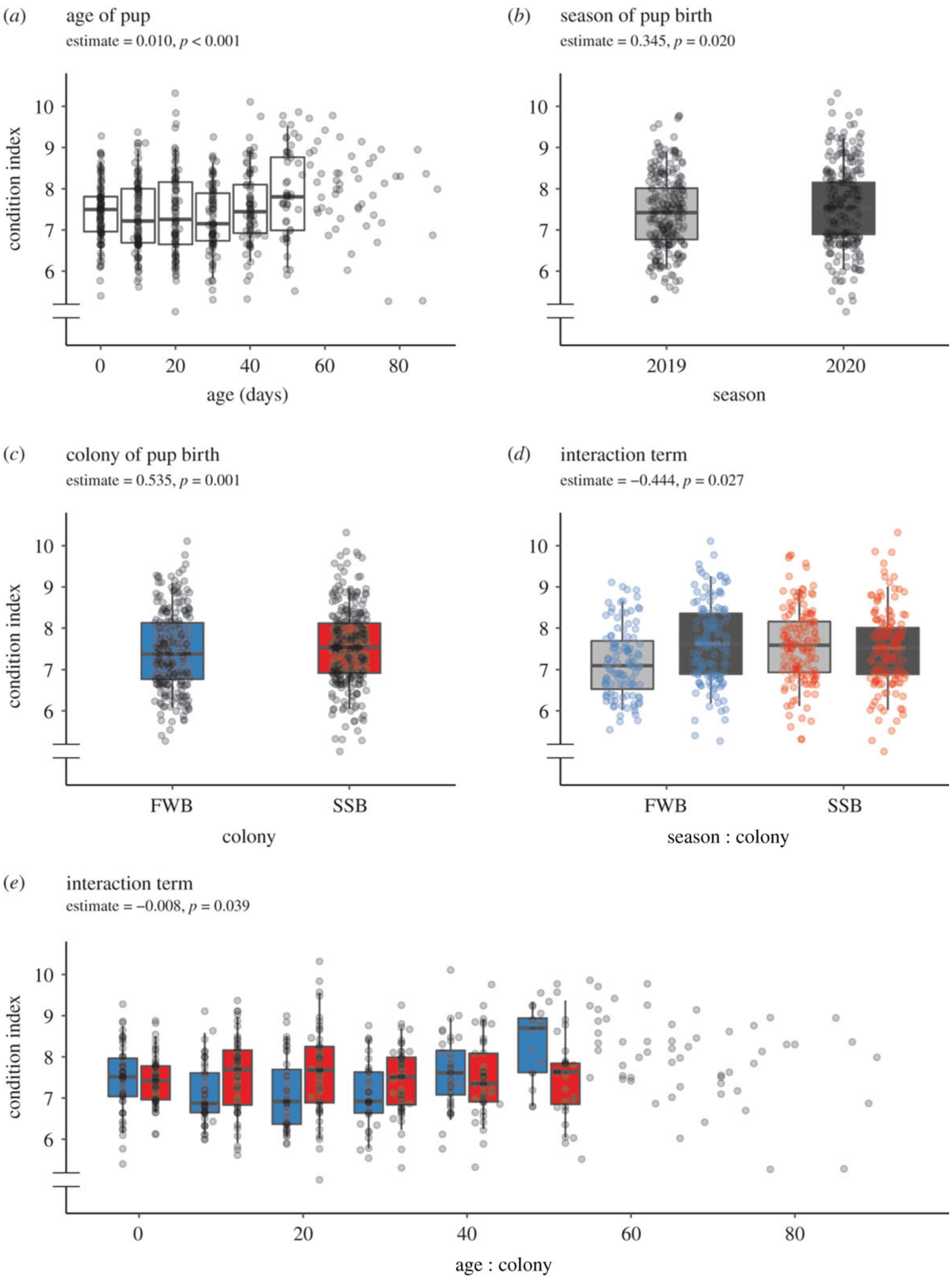

Figure 4. Results of a linear mixed model of pup condition index. Significant main effects of pup age, season of birth and breeding colony are shown in (*a*–*c*) respectively, while (*d*) and (*e*) depict the interactions between season and colony, and age and colony. Parameter estimates and *p*-values are provided; further details of the model output can be found in table 2. Boxes show the means ± 75% quantiles, with the vertical lines indicating 95% confidence intervals (CIs). Blue = FWB, red = SSB, light grey = 2019, dark grey = 2020. (Online version in colour.)

fitness components—survival and body condition. Furthermore, pup mortality was mainly owing to predation, a cause of death that was relatively unimportant in earlier studies, while variation in offspring condition was primarily influenced by seasonal and density effects. Our findings suggest that component Allee effects on offspring survival and condition may contribute increasingly towards the population dynamics of this species as local densities continue to decline.

(a) Study design

The availability of a natural two colony set-up provided us with a unique opportunity to investigate density-dependent effects on fur seal pups while controlling for a number of potentially confounding factors. Specifically, the close proximity of the two colonies means that they are genetically undifferentiated [27], they experience comparable environmental conditions, habitat quality does not differ as both beaches comprise homogeneous cobblestone substrate, and mothers from the two colonies probably forage in the same area [26] so do not differ appreciably in quality traits such as body size or condition.

Although logistical constraints only allowed us to compare animals from two colonies, our study was replicated over two consecutive seasons. By chance, one of these years was among the worst ever recorded [22], with fewer females being able to amass sufficient resources to breed, pup birth masses being depressed and female foraging trips being substantially longer, indicating that they had to spend more time at sea in search of prey [24,47–49]. Thus, our study incorporated substantial environmental variation, allowing us to test for main effects of both season and colony, as well as their interactions, on fitness variation.

Another strength of the current study was our ability to integrate fitness data gathered using consistent protocols from birth to shortly before weaning. This was only possible through the use of radio telemetry, which allowed us to track the pups as they became increasingly mobile and ventured away from the breeding beaches and inland into the tussock grass. This was important because it allowed us to monitor both survival and changes in weight and body condition throughout ontogeny. As body weight and condition at weaning are important predictors of survival to adulthood in pinnipeds [50,51], our dataset captures both immediate and longer term components of individual fitness.

(b) Variation in offspring survival and body condition

Two previous studies of offspring mortality in Antarctic fur seals, one based on several years of data from SSB [16] and the other comparing SSB with a low-density colony on the South Georgia mainland [15], found clear evidence for negative density dependence. In both temporal and spatial contexts, rates of pup mortality were reported to scale positively with population density, with the main causes of death being traumatic injuries owing to trampling, and starvation owing to the disruption of mother–pup bonds. However, our data revealed a very different pattern, with almost three times as many pups dying at low density and the major cause of mortality being predation. Furthermore, the rate of predation was higher under low-density conditions, with half of the pups that could be assigned a cause of death on FWB being predated ($n = 8$) as opposed to just one out of six pups at SSB. This greater role of predation correlates with an increasing population size of northern giant petrels [18,19], the main land predator of Antarctic fur seals [17], over the same period during which fur seal densities have been in decline [22].

These findings are consistent with the results of previous studies of predator-driven Allee effects [3,52], which are commonly attributed either to differences in the ability of a group of animals to defend their offspring from predators, or to predator satiation, where predators are only able to harvest a small proportion of prey at high density [3]. While it is difficult to distinguish between these two possibilities in Antarctic fur seals, anecdotally we have observed fewer northern giant petrels at SSB as well as females from both colonies defending their offspring from predators. This is in line with observations in other pinnipeds, including South American fur seals, where predators are less likely to infiltrate high-density colonies owing to territorial defence by males [53], and harbour seals, where larger groups exhibit greater vigilance [54]. Thus, improved opportunities for predators to infiltrate low-density breeding aggregations appear to reduce offspring survival in Antarctic fur seals. Previous studies may have failed to detect such an effect because they were conducted over a decade ago when population densities were far higher. For example, annual pup counts (a proxy for breeding female numbers) at SSB averaged 680 (s.d. ± 112) between 1989 and 2003 [16] as compared to $n = 282$ in 2019 and $n = 409$ in 2020. Thus, even our high-density colony (SSB) is currently experiencing local density conditions far below the historical average, while the relative density of animals at FWB is even lower.

In parallel to density-dependent differences in pup mortality, we also found that offspring body condition was influenced by season, colony and an interaction between season and colony. This suggests that poor-quality environmental conditions have the greatest negative impact on offspring body condition at low density. While maternal condition did not explain a significant proportion of the variation in offspring condition, implying the lack of a direct maternal effect, the same overall pattern of seasonal and density-dependent variation in pup condition was already apparent shortly after birth. One possible explanation for this could be that differences in maternal investment during the latter stages of gestation depend on season quality. This is in line with previous studies of pinniped species, where fetal mortality during late pregnancy [55] and pup condition at birth [56] can be linked with environmental factors such as food availability. However, this fails to explain the fact that strong density dependence was only observed in the poor-quality season. We therefore speculate that offspring condition may have been affected by the density of conspecifics ashore during the first 2–3 days of life. Such an effect could potentially be mediated by a negative effect of predator-induced stress hormones on growth or increased energy expenditure on movement, possibilities that should be investigated in future studies.

(c) Implications

Antarctic fur seals at Bird Island, South Georgia have been steadily declining over the past three decades [22]. Consequently, falling densities could potentially shift the balance in favour of predators and accelerate the rate of decline, assuming that component Allee effects in early life are not offset by negative density dependence in other fitness components such as lifetime reproductive success [2]. Furthermore, multiple component Allee effects, including reduced foraging efficiency owing to diminishing prey abundance [20] and increased exposure to predators at low density, may combine to produce a stronger overall Allee effect [3]. These so-called 'dormant' components may explain why previous studies have found little support for demographic Allee effects in pinniped populations [57].

This study also shows how the lower density of pups combined with reduced body condition, particularly in the first year of the study, provided increased opportunities for predators and scavengers such as giant petrels. A few thousand of these seabirds breed on the island during the pupping season, and the high energetic demands of their chicks are largely met with seal carrion and live pups [17,58]. Therefore, the higher observed predation, especially of weak pups, is an excellent indicator of not only the causes of fluctuations in fur seal numbers, but also of the potential repercussion on their predators, with consequences for predator–prey interactions. The extent of the interaction between pup production, body condition and differential predation by seabirds on an interannual basis could therefore provide invaluable information for ecosystem studies based on predator performance feedback.

5. Conclusion

We describe component Allee effects for offspring survival and body condition in a declining fur seal population. Our findings are consistent with the notion that Allee effects may impact even once numerically abundant species [8] and can occur regardless of a species' life history so long as predation is a major source of mortality [52]. Finally, Allee effects have been extensively discussed in the context of heavily exploited populations, but are rarely mentioned in the context of climate change. Our study suggests that Allee effects might play an important role in shaping demographic responses to ongoing environmental change.

Ethics. Sampling was carried out by BAS under permits from the Government of South Georgia and the South Sandwich Islands (Wildlife and Protected Areas Ordinance (2011), RAP permit numbers 2018/024 and 2019/032). The samples were imported into the UK under permits from the Department for Environment, Food and Rural Affairs (Animal Health Act, import license number ITIMP18.1397) and from the Convention on International Trade in Endangered Species of Wild Fauna and Flora (import nos 578938/01-15 and 590196/01-18). All procedures used were approved by the BAS Animal Welfare and Ethics Review Body (AWERB applications 2018/1050 and 2019/1058).

Data accessibility. Raw data, R code and documentation are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.zcrjdfnb0 [46]. R code and documentation are also available as part of the electronic supplementary material.

Authors' contributions. J.I.H. and J.F. conceived the study and contributed funding and materials. R.N., C.S., C.F.-C. and C.T. collected the data and R.N. analysed the data. R.N. and J.I.H. drafted the manuscript and all of the authors commented on and approved the final manuscript.

Competing interests. We declare we have no competing interests.

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References

1. Courchamp F, Clutton-Brock T, Grenfell B. 1999 Inverse density dependence and the Allee effect. *Trends Ecol. Evol.* **14**, 405–410. (doi:10.1016/S0169-5347(99)01683-3)
2. Kramer AM, Dennis B, Liebhold AM, Drake JM. 2009 The evidence for Allee effects. *Popul. Ecol.* **51**, 341–354. (doi:10.1007/s10144-009-0152-6)
3. Berec L, Angulo E, Courchamp F. 2007 Multiple Allee effects and population management. *Trends Ecol. Evol.* **22**, 185–191. (doi:10.1016/j.tree.2006.12.002)
4. Hutchings JA. 2015 Thresholds for impaired species recovery. *Proc. R. Soc. B* **282**, 20150654. (doi:10.1098/rspb.2015.0654)
5. Fronhofer EA, Kropf T, Altermatt F. 2015 Density-dependent movement and the consequences of the Allee effect in the model organism *Tetrahymena*. *J. Anim. Ecol.* **84**, 712–722. (doi:10.1111/1365-2656.12315)
6. Zhu Y, Queenborough SA, Condit R, Hubbell SP, Ma KP, Comita LS. 2018 Density-dependent survival varies with species life-history strategy in a tropical forest. *Ecol. Lett.* **21**, 506–515. (doi:10.1111/ele.12915)
7. Hung CM, Shaner PJL, Zink RM, Liu WC, Chu TC, Huang WS, Li SH. 2014 Drastic population fluctuations explain the rapid extinction of the passenger pigeon. *Proc. Natl Acad. Sci. USA* **111**, 10 636–10 641. (doi:10.1073/pnas.1401526111)
8. Halliday TR. 1980 The extinction of the passenger pigeon *Ectopistes migratorius* and its relevance to contemporary conservation. *Biol. Conserv.* **17**, 157–162. (doi:10.1016/0006-3207(80)90046-4)
9. Stephens PA, Sutherland WJ. 1999 Consequences of the Allee effect for behaviour, ecology and conservation. *Trends Ecol. Evol.* **14**, 401–405. (doi:10.1016/S0169-5347(99)01684-5)
10. Swain DP, Benoît HP. 2015 Extreme increases in natural mortality prevent recovery of collapsed fish populations in a Northwest Atlantic ecosystem. *Mar. Ecol. Prog. Ser.* **519**, 165–182. (doi:10.3354/meps11012)
11. Neuenhoff RD, Swain DP, Cox SP, McAllister MK, Trites AW, Walters CJ, Hammill MO. 2019 Continued decline of a collapsed population of Atlantic cod (*Gadus morhua*) due to predation driven Allee effects. *Can. J. Fish. Aquat. Sci.* **76**, 168–184. (doi:10.1139/cjfas-2017-0190)
12. Hutchings JA, Reynolds JD. 2004 Marine fish population collapses: consequences for recovery and extinction risk. *Bioscience* **54**, 297–309. (doi:10.1641/0006-3568(2004)054[0297:MFPCCF]2.0.CO;2)
13. Courchamp F, Berec L, Gascoigne J. 2008 *Allee effects in ecology and conservation*. Oxford, UK: Oxford University Press.
14. Liermann M, Hilborn R. 1997 Depensation in fish stocks: a hierarchic Bayesian meta-analysis. *Can. J. Fish. Aquat. Sci.* **54**, 1976–1984. (doi:10.1139/f97-105)
15. Doidge DW, Croxall JP, Baker JR. 1984 Density-dependent pup mortality in the Antarctic fur seal *Arctocephalus gazella* at South Georgia. *J. Zool. Lond.* **202**, 449–460. (doi:10.1111/j.1469-7998.1984.tb05095.x)
16. Reid K, Forcada J. 2005 Causes of offspring mortality in the Antarctic fur seal, *Arctocephalus gazella*: the interaction of density dependence and ecosystem variability. *Can. J. Zool.* **83**, 604–609. (doi:10.1139/z05-045)
17. Hunter S. 1983 The food and feeding ecology of the giant petrels *Macronectes halli* and *M. giganteus* at South Georgia. *J. Zool.* **200**, 521–538. (doi:10.1111/j.1469-7998.1983.tb02813.x)
18. Poncet S, Wolfaardt AC, Barbraud C, Reyes-Arriagada R, Black A, Powell RB, Phillips RA. 2020 The distribution, abundance, status and global importance of giant petrels (*Macronectes giganteus* and *M. halli*) breeding at South Georgia. *Polar Biol.* **43**, 17–34. (doi:10.1007/s00300-019-02608-y)
19. Gianuca D *et al.* 2019 Sex-specific effects of fisheries and climate on the demography of sexually dimorphic seabirds. *J. Anim. Ecol.* **88**, 1366–1378. (doi:10.1111/1365-2656.13009)
20. Atkinson A *et al.* 2019 Krill (*Euphausia superba*) distribution contracts southward during rapid regional warming. *Nat. Clim. Chang.* **9**, 142–147. (doi:10.1038/s41558-018-0370-z)
21. Reid K, Arnould JPY. 1996 The diet of Antarctic fur seals *Arctocephalus gazella* during the breeding season at South Georgia. *Polar Biol.* **16**, 105–114. (doi:10.1007/BF02390431)
22. Forcada J, Hoffman JI. 2014 Climate change selects for heterozygosity in a declining fur seal population. *Nature* **511**, 462–465. (doi:10.1038/nature13542)
23. Reid K, Croxall JP. 2001 Environmental response of upper trophic-level predators reveals a system

change in an Antarctic marine ecosystem. *Proc. R. Soc. Lond. B* **268**, 377–384. (doi:10.1098/rspb.2000.1371)

24. Croxall JP, McCann TS, Prince PA, Rothery P. 1988 Reproductive performance of seabirds and seals at South Georgia and Signy Island, South Orkney Islands, 1976–1987: implications for Southern Ocean monitoring studies. In *Antarctic ocean and resources variability* (ed. D Sahrhage), pp. 261–285. Berlin, Germany: Springer.
25. Meise K, Von Engelhardt N, Forcada J, Hoffman JI. 2016 Offspring hormones reflect the maternal prenatal social environment: potential for foetal programming? *PLoS ONE* **11**, e0145352. (doi:10.1371/journal.pone.0145352)
26. Hunt GL, Heinemann D, Everson I. 1992 Distributions and predator-prey interactions of macaroni penguins, Antarctic fur seals, and Antarctic krill near Bird Island, South Georgia. *Mar. Ecol. Prog. Ser.* **86**, 15–30. (doi:10.3354/meps086015)
27. Stoffel MA, Caspers BA, Forcada J, Giannakara A, Baier M, Eberhart-Phillips L, Müller C, Hoffman JI. 2015 Chemical fingerprints encode mother–offspring similarity, colony membership, relatedness, and genetic quality in fur seals. *Proc. Natl Acad. Sci. USA* **112**, E5005–E5012. (doi:10.1073/pnas.1506076112)
28. McMahon C, van den Hoff J, Burton H. 2005 Handling intensity and the short- and long-term survival of elephant seals: addressing and quantifying research effects on wild animals. *Ambio* **34**, 426–429. (doi:10.1579/0044-7447-34.6.426)
29. Gentry RL, Holt JR. 1982 Equipment and techniques for handling northern fur seals. NOAA Tech. Rep. NMFS SSRF-758, Seattle, Washington, USA.
30. Forcada J, Staniland IJ. 2018 Antarctic fur seal. In *Encyclopedia of marine mammals* (eds B Würsig, JGM Thewissen, KM Kovacs), pp. 25–27. New York, NY: Academic Press.
31. Doidge DW, Mccann TS, Croxall JP. 1985 Attendance behavior of Antarctic fur seals. In *Fur seals: maternal strategies on land and at sea* (eds RL Gentry, GL Kooyman), pp. 102–114. Princeton, NJ: Princeton University Press.
32. Jones KA, Wood H, Jonathan P, Ratcliffe N, Votier SC, Staniland IJ. 2020 Risk exposure trade-offs in the ontogeny of sexual segregation in Antarctic fur seal pups. *Behav. Ecol.* **31**, 719–730. (doi:10.1093/beheco/araa018)
33. Hoffman JI, Forcada J, Trathan PN, Amos W. 2007 Female fur seals show active choice for males that are heterozygous and unrelated. *Nature* **445**, 912–914. (doi:10.1038/nature05558)
34. Baker JR, Doidge DW. 1984 Pathology of the Antarctic fur seal (*Arctocephalus gazella*) in South Georgia. *Br. Vet. J.* **140**, 210–219. (doi:10.1016/0007-1935(84)90084-8)
35. Boyd IL, Lunn NJ, Barton T. 1991 Time budgets and foraging characteristics of lactating Antarctic fur seals. *J. Anim. Ecol.* **60**, 577–592. (doi:10.2307/5299)
36. Kuznetsova A, Brockhoff PB, Christensen RHB. 2017 lmerTest package: tests in linear mixed effects models. *J. Stat. Softw.* **82**, 1–26. (doi:10.18637/jss.v082.i13)
37. Peig J, Green AJ. 2009 New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* **118**, 1883–1891. (doi:10.1111/j.1600-0706.2009.17643.x)
38. Stevenson RD, Woods WA. 2006 Condition indices for conservation: new uses for evolving tools. *Integr. Comp. Biol.* **46**, 1169–1190. (doi:10.1093/icb/icl052)
39. Trites AW, Jonker RAH. 2000 Morphometric measurements and body conditions of healthy and starveling Steller sea lion pups (*Eumetopias jubatus*). *Aquat. Mamm.* **26.2**, 151–157.
40. Guinet C, Roux JP, Bonnet M, Mison V. 1998 Effect of body size, body mass, and body condition on reproduction of female South African fur seals (*Arctocephalus pusillus*) in Namibia. *Can. J. Zool.* **76**, 1418–1424. (doi:10.1139/z98-082)
41. Hammill MO, Sauvé C. 2017 Growth and condition in harp seals: evidence of density-dependent and density-independent influences. *ICES J. Mar. Sci.* **74**, 1395–1407. (doi:10.1093/icesjms/fsw237)
42. DeRango EJ, Schwarz JFL, Piedrahita P, Páez-Rosas D, Trillmich F, Krüger O. 2019 Intraspecific variation in boldness and exploration shapes behavioral responses to stress in Galápagos sea lion pups. *Behav. Ecol. Sociobiol.* **73**, 166. (doi:10.1007/s00265-019-2775-8)
43. Lenth R. 2020 emmeans: estimated marginal means, aka least-squares means. R package version 1.5.0. See https://cran.r-project.org/package=emmeans.
44. Fox J, Weisberg S. 2019 *An {R} companion to applied regression*, 3rd edn. Thousand Oaks, CA: Sage. See https://socialsciences.mcmaster.ca/jfox/Books/Companion/.
45. R Core Team. 2019 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See https://www.R-project.org/.
46. Nagel R, Stainfield C, Fox-Clarke C, Toscani C, Forcada J, Hoffman JI. 2021 Evidence for an Allee effect in a declining fur seal population. Dryad Digital Repository. (https://doi.org/10.5061/dryad.zcrjdfnb0)
47. Lunn NJ, Boyd IL, Barton T, Croxall JP. 1993 Factors affecting the growth rate and mass at weaning of Antarctic fur seals at Bird Island, South Georgia. *J. Mamm.* **74**, 908–919. (doi:10.2307/1382429)
48. Boyd IL, Arnould JPY, Barton T, Croxall JP. 1994 Foraging behaviour of Antarctic fur seals during periods of contrasting prey abundance. *J. Anim. Ecol.* **63**, 703–713. (doi:10.2307/5235)
49. Bengtson JL. 1988 Long-term trends in the foraging patterns of female Antarctic fur seals at South Georgia. In *Antarctic ocean and resources variability* (ed. D Sahrhage), pp. 286–291. Berlin, Germany: Springer.
50. Beauplet G, Barbraud C, Chambellant M, Guinet C. 2005 Interannual variation in the post-weaning and juvenile survival of subantarctic fur seals: influence of pup sex, growth rate and oceanographic conditions. *J. Anim. Ecol.* **74**, 1160–1172. (doi:10.1111/j.1365-2656.2005.01016.x)
51. Gastebois C, Viviant M, Guinet C. 2011 Ontogeny of aquatic behaviours in Antarctic fur seal (*Arctocephalus gazella*) pups in relation to growth performances at Kerguelen Islands. *Polar Biol.* **34**, 1097–1103. (doi:10.1007/s00300-011-0965-6)
52. Gascoigne JC, Lipcius RN. 2004 Allee effects driven by predation. *J. Appl. Ecol.* **41**, 801–810. (doi:10.1111/j.0021-8901.2004.00944.x)
53. Harcourt R. 1992 Factors affecting early mortality in the South American fur seal (*Arctocephalus australis*) in Peru: density-related effects and predation. *J. Zool.* **226**, 259–270. (doi:10.1111/j.1469-7998.1992.tb03838.x)
54. da Silva J, Terhune JM. 1988 Harbour seal grouping as an anti-predator strategy. *Anim. Behav.* **36**, 1309–1316. (doi:10.1016/S0003-3472(88)80199-4)
55. McKenzie J, Parry LJ, Page B, Goldsworthy SD. 2005 Estimation of pregnancy rates and reproductive failure in New Zealand fur seals (*Arctocephalus forsteri*). *J. Mamm.* **86**, 1237–1246. (doi:10.1644/05-MAMM-A-085R.1)
56. Banuet-Martínez M, Espinosa-de Aquino W, Elorriaga-Verplancken FR, Flores-Morán A, García OP, Camacho M, Acevedo-Whitehouse K. 2017 Climatic anomaly affects the immune competence of California sea lions. *PLoS ONE* **12**, e0179359. (doi:10.1371/journal.pone.0179359)
57. Gerber LR, Hilborn R. 2001 Catastrophic events and recovery from low densities in populations of otariids: implications for risk of extinction. *Mamm. Rev.* **31**, 131–150. (doi:10.1046/j.1365-2907.2001.00081.x)
58. Hunter S. 1984 Breeding biology and population dynamics of giant petrels *Macronectes* at South Georgia (Aves: Procellariiformes). *J. Zool.* **203**, 441–460. (doi:10.1111/j.1469-7998.1984.tb02343.x)