Evidence for an Allee effect in a declining fur seal population

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Abstract

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 amongst 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 also 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.

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 19th century hunters as population sizes fell below the threshold required for efficient foraging [8,9]. Similarly, the collapse and subsequent failure of the northwest Atlantic cod stocks 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 due to logistical constraints [1], the difficulty of disentangling Allee effects from declines due to habitat alteration or destruction [4] and a general reliance on long-term observational data, which can suffer from power limitations 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 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 1a). Females of this species rear their pups in densely packed breeding colonies, where historically the most common causes of offspring mortality were starvation due 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, 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 over the past three decades [22]. 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 ([23]; Figure 2a,b). As these colonies are only around 200-metres apart, females from both localities forage in the same area [24]. Consequently, food availability is effectively controlled for and there should be no differences in female nutritive state. Furthermore, a lack of genetic differentiation [25] 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 the temporal environment. 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 fitness.

Methods

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; Figure 1a). 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 program of the British Antarctic Survey (BAS). Adult females were captured with a noosing pole and held on a restraint board. Pups were captured with a slip noose or by hand and were restrained by hand. After measurement, 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 [26–29].

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 2a), 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 ten 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 two-metre radius of the focal individual, were recorded. The initial capture of fur seal mothers and pups at both colonies was randomized with respect to sex of pup and 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 [30]. During lactation, mothers alternate foraging trips at sea with time spent ashore nursing pups [31] and until pups are approximately 20 days old, females will consistently 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 [32]. Pups in particular range on average 3.3 km (range: 472–12,821 metres) away from their colony of birth [33]. In order 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 [34,35]. 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 Color) applied to the fur, which grew out with the moult. VHF transmitter signals of mothers and pups were monitored during daily visual checks of the island using a hand-held VHF receiver (AOR LTD., AR8200). The transmitters were retrieved from all animals at their last recapture.

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 1978. Radio telemetry as a consistent method for this monitoring program was established in 1992 and approximately $n = 25$ 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. The daily absence or presence of females ashore was noted from 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 females across the entire monitoring period was compared between the two seasons.

At SSB, an elevated scaffold walkway built above the breeding colony [15] 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 [36], 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 and 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.

Pup mortality

The survival of focal pups was tracked from birth until weaning at both colonies. In the absence of direct evidence of a pup having died, mortality was assumed if an individual was

not sighted for ten consecutive days. Following a simplified protocol developed by a veterinarian specializing in pinniped pathology [37], dead pups were examined to determine the most likely cause of death, which was characterized as follows: (a) starvation, characterized by a thin or absent layer of subcutaneous blubber; (b) trauma, where pups exhibited traumatic injuries (e.g. crushed skull or ribs) and associated hematomas; (c) predation, characterized by bite marks on the flippers and around the anus and / or missing organs removed through holes below the flippers or anus; (d) bacterial infection, as indicated by the presence of lesions, pus or swelling in the absence of any obvious signs of trauma or starvation; and (e) unknown, i.e. pups that could not be assigned to any of the above categories. Because mothers exhibit irregular attendance patterns after their pups have died [38], 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 AIC values was implemented to simplify the model.

Pup weight

To determine whether age, sex, maternal weight shortly after birth, season, colony and interactions among these variables explained a significant proportion of the variation in weight among pups, we constructed a linear mixed model (LMM) using the restricted maximum-likelihood (REML) approach in *lmerTest* [39]. Pup ID was included as a random effect in the model to account for repeated measurements of individuals. A 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).

Pup condition

The condition index of all focal individuals was calculated using a scaled mass index according to Peig and Green [40]. This method uses log-transformed scaling between body length and mass in relation to the average body length for the population, thus taking individual differences 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 [40] and resource availability [41]. In pinniped species, body condition has been shown to correlate with pup mortality in

Steller sea lions [42], reproductive success in South African fur seals [43] and harp seals [44] and personality traits in Galápagos sea lions [45,46].

To determine whether age, sex, maternal condition shortly after birth, season, colony and interactions among these variables explained a significant proportion of the variation in condition among pups throughout ontogeny, we constructed a linear mixed model (LMM) using the restricted maximum-likelihood (REML) approach in *lmerTest* [39]. Pup ID was again included as a random effect to account for repeated measurements of individuals. A 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* [47].

Maternal quality measures

To determine whether 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 (LM) of condition shortly after birth including colony, season and the interaction between colony and season as predictor variables.

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* [48]. All statistical analyses and visualizations were implemented in R version 4.0.2 [49] using the integrated development environment RStudio [50]. Our code and accompanying documentation are provided in the form of an R Markdown file (Supplementary file X).

Animal ethics and permits

Sampling was carried out by the British Antarctic Survey 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

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

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 1b) and mean pup birth weight was around 10% lower (Figure 1c; Welch two sample t-test, $t = -5.279$, $d.f. = 116.560$, $p < 0.001$). In parallel, breeding females on FWB made significantly longer foraging trips in 2019 (Figure 1d and Supplementary Figure S1; Wilcoxon rank sum test, $W = 13080$, $p < 0.001$). These observations suggest that 2019 was a relatively poor quality year in which fewer food resources were available to breeding females [51–55].

Pup mortality

Pup mortality was significantly higher at FWB than SSB (32% versus 12%, respectively, Figure 2c; 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.

Pup weight

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

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 condition shortly after giving birth was not retained as a significant predictor. Pup condition varied significantly across the season (Figure 4a) and tended to be lower in 2019 (Figure 4b) and higher at SSB (Figure 4c). Pups born at FWB had lower condition index values in 2019 than in 2020 (Figure 4d; Tukey's post hoc test, estimate = -0.345, *s.e.* = 0.148, $p = 0.097$), whereas SSB pups showed the opposite tendency (Figure 4d; 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 a 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 4e).

Maternal quality traits

Mothers from the two colonies did not differ significantly in any quality measures at first capture (span, girth, weight, length and condition index; Supplementary Figure S2; Wilcoxon signed rank tests, all $p > 0.05$;). A more detailed linear model to determine whether colony- or season-specific differences in maternal condition were present shortly after giving birth also found no significant effects (Supplementary Table 1; all $p > 0.05$).

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 nearly 35% [22]. Under these low abundance conditions, we found, in contrast to previous studies, a positive effect of increasing density on two fitness components – survival and body condition. Furthermore, pup mortality was mainly due 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.

Study design

The availability of a natural two colony setup 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 [25], they experience comparable environmental conditions, habitat quality does not differ as both beaches comprise homogenous cobblestone substrate, and mothers from the two colonies forage in the same area [24] 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 very few 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 [51–55]. 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 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 [56,57], our dataset captures both immediate and longer-term components of individual fitness.

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 due to trampling and starvation due 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 increasing role of predation correlates with an increasing population size of northern giant petrels [18,19], the main land predator of fur seals [17], over the same period for which fur seal densities have been in decline [22].

These findings are consistent with previous studies of predator-driven Allee effects [3,58], 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 due to territorial defence by males [59], and harbour seals, where larger groups exhibit greater vigilance [60]. 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 much 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 282 in 2019 and 409 in 2020. Thus, even our high-density colony (SSB) is currently experiencing local density conditions far below the historical average, while the 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 negatively impact offspring body condition especially 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 on pinniped species, where foetal mortality during late pregnancy [61] and pup condition at birth [62] 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 suggest 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.

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 due 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 [63].

Conclusions

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 [58]. 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.

Competing interests

We have no competing interests.

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Tables

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 (CI) are presented. Significant *p*-values are in bold. 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.

Coeffcient	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 weight after birth	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			

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 are presented. Significant *p*-values are in bold. 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.

Coeffcient	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			

(A) Location of Bird Island
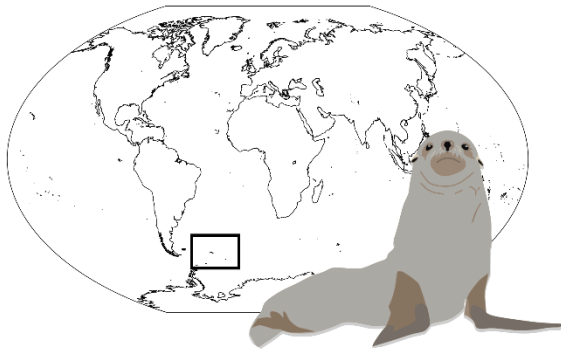
(B) Breeding females
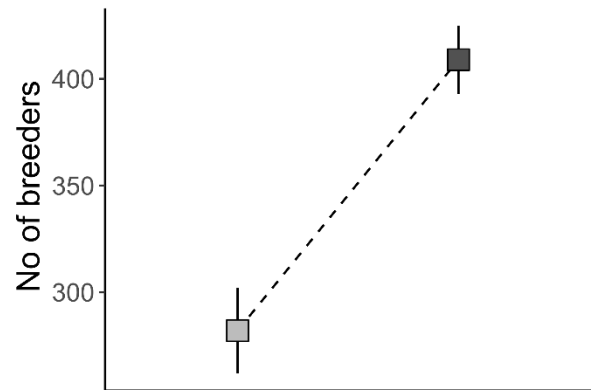
(C) Pup birth weight
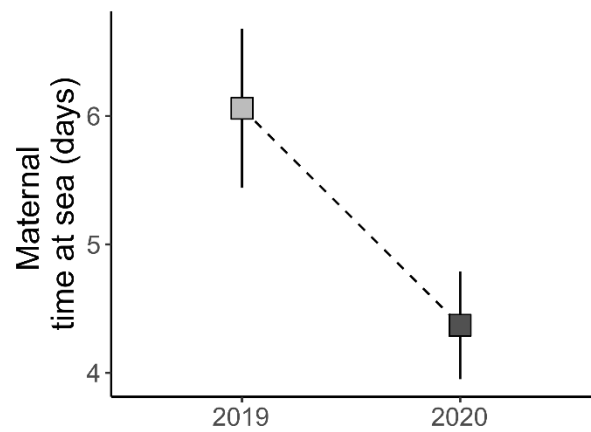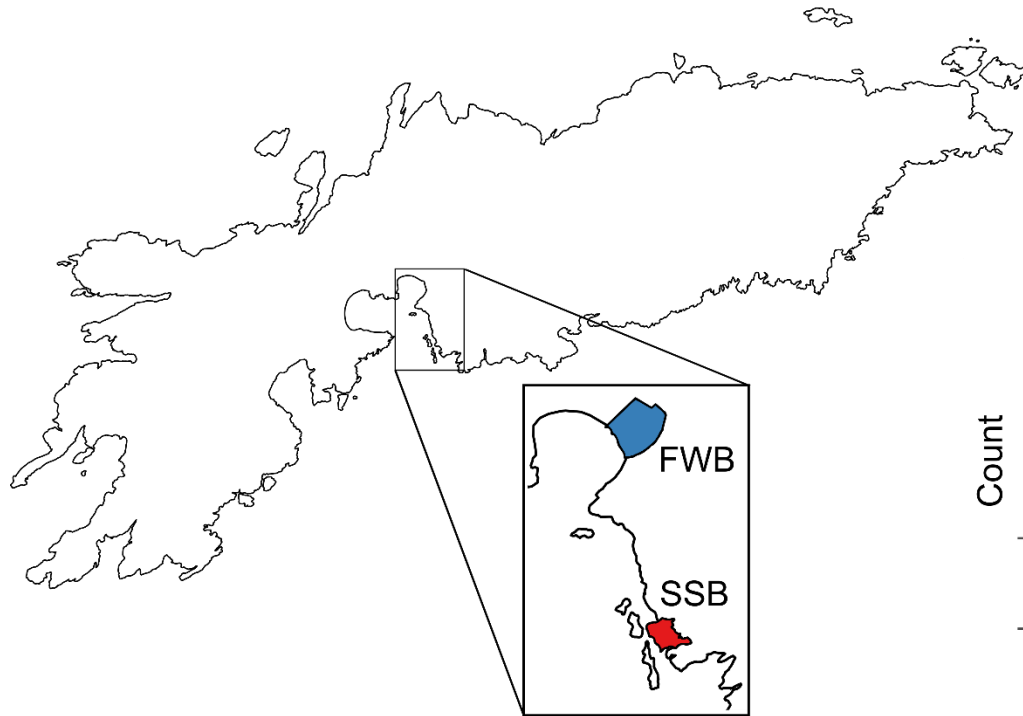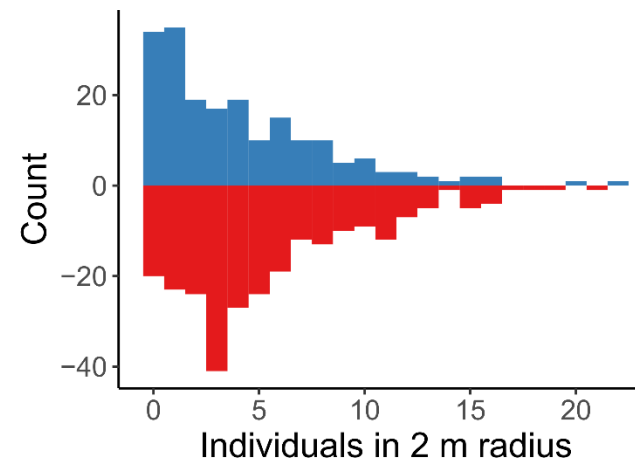
(D) Foraging trip duration

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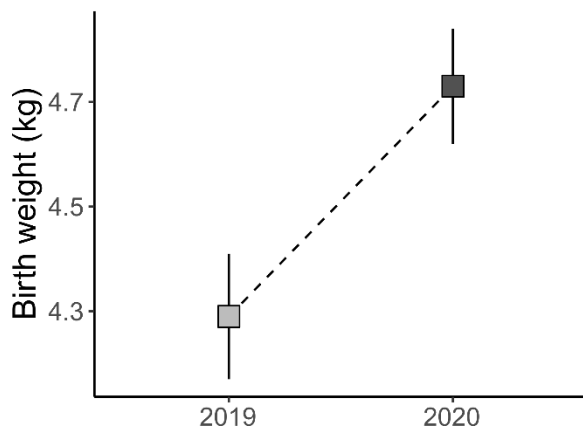
Figure 1: Seasonal differences in female breeding performance. Panel A shows the location of Bird Island, South Georgia, in the South Atlantic. Panels B–D show the number of breeding females, the birth mass of their pups and the amount of time spent by mothers foraging at sea during the austral summers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

(A) Map of Bird Island

FWB

SSB

(B) Local density statistics

Count

20

0

−20

−40

0   5   10   15   20

Individuals in 2 m radius

(C) Mortality statistics

32%
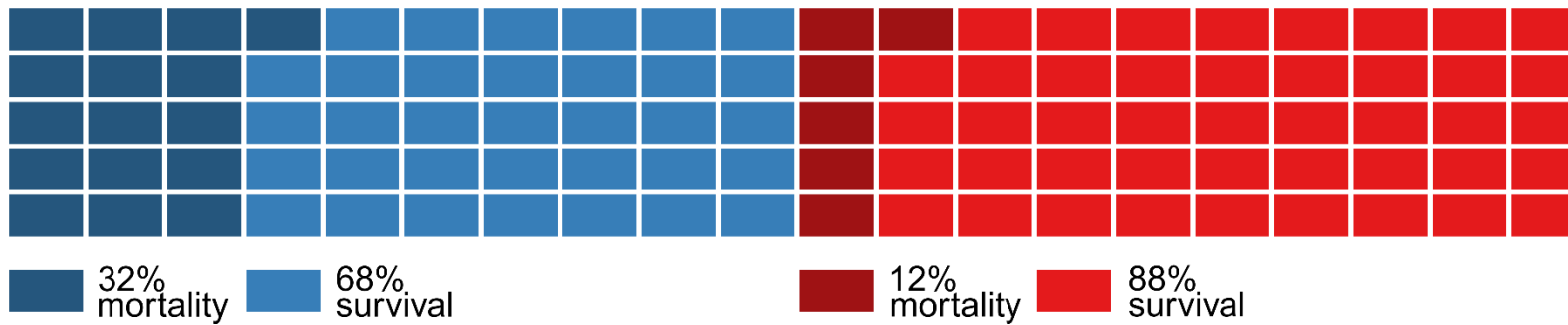mortality

68%
survival

12%
mortality

88%
survival

Figure 2: Differences in local density and pup survival between two adjacent breeding colonies on Bird Island, South Georgia. Panel A shows 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-metres apart. Panel B shows 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 two-metre 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). Panel C provides a visual representation of the number and proportion of focal pups that survived in each colony. Blue = FWB, red = SSB.
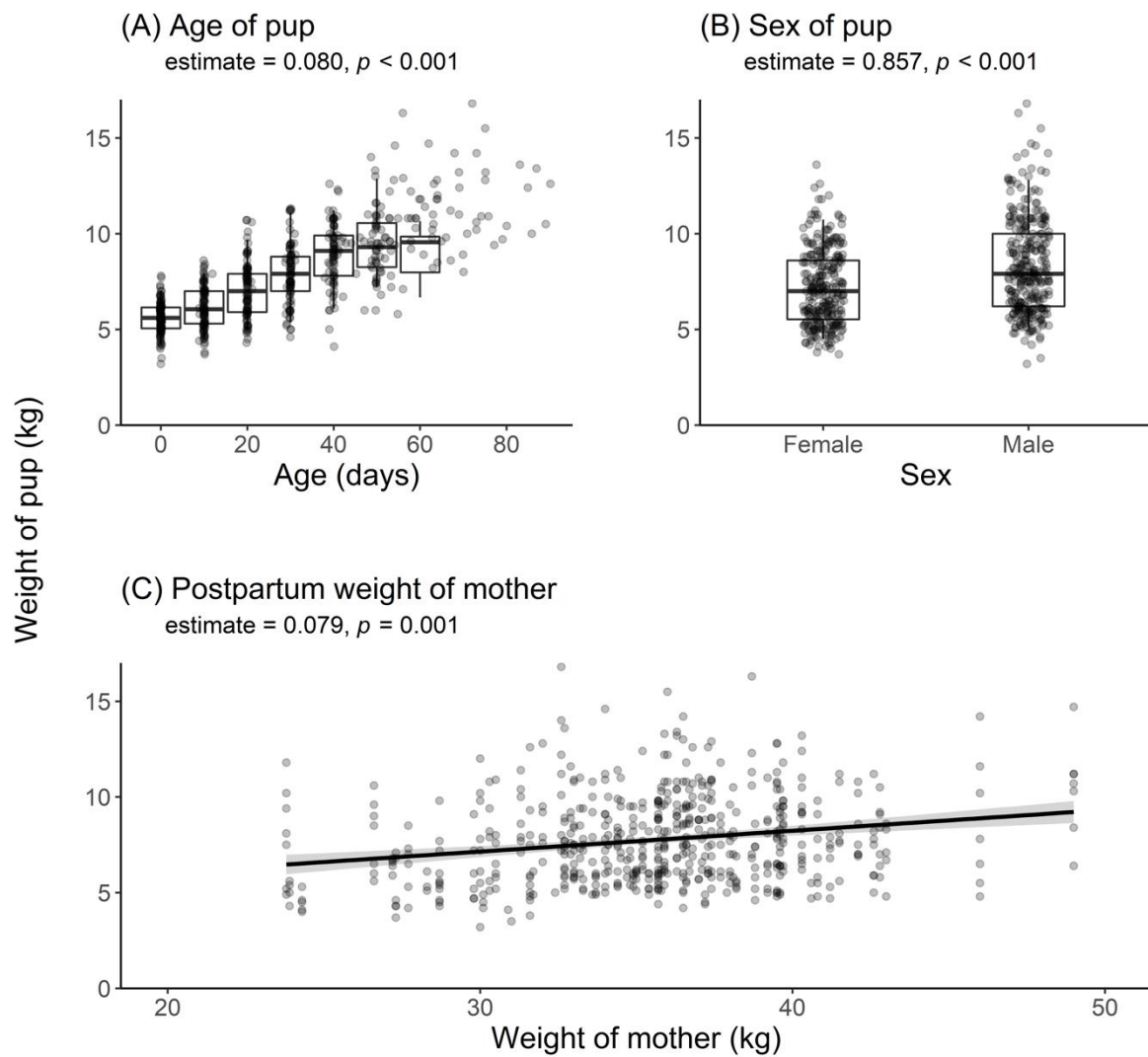
Figure 3: Results of a linear mixed model of pup weight. Significant main effects of pup age, pup sex and mother's weight when the pup was born are shown in panels A–C, respectively. Parameter estimates and p-values are provided; further details of the model output can be found in Table 1. Boxes in panels A and B show the means $\pm$ 75% quantiles, with the vertical lines indicating 95% CIs.
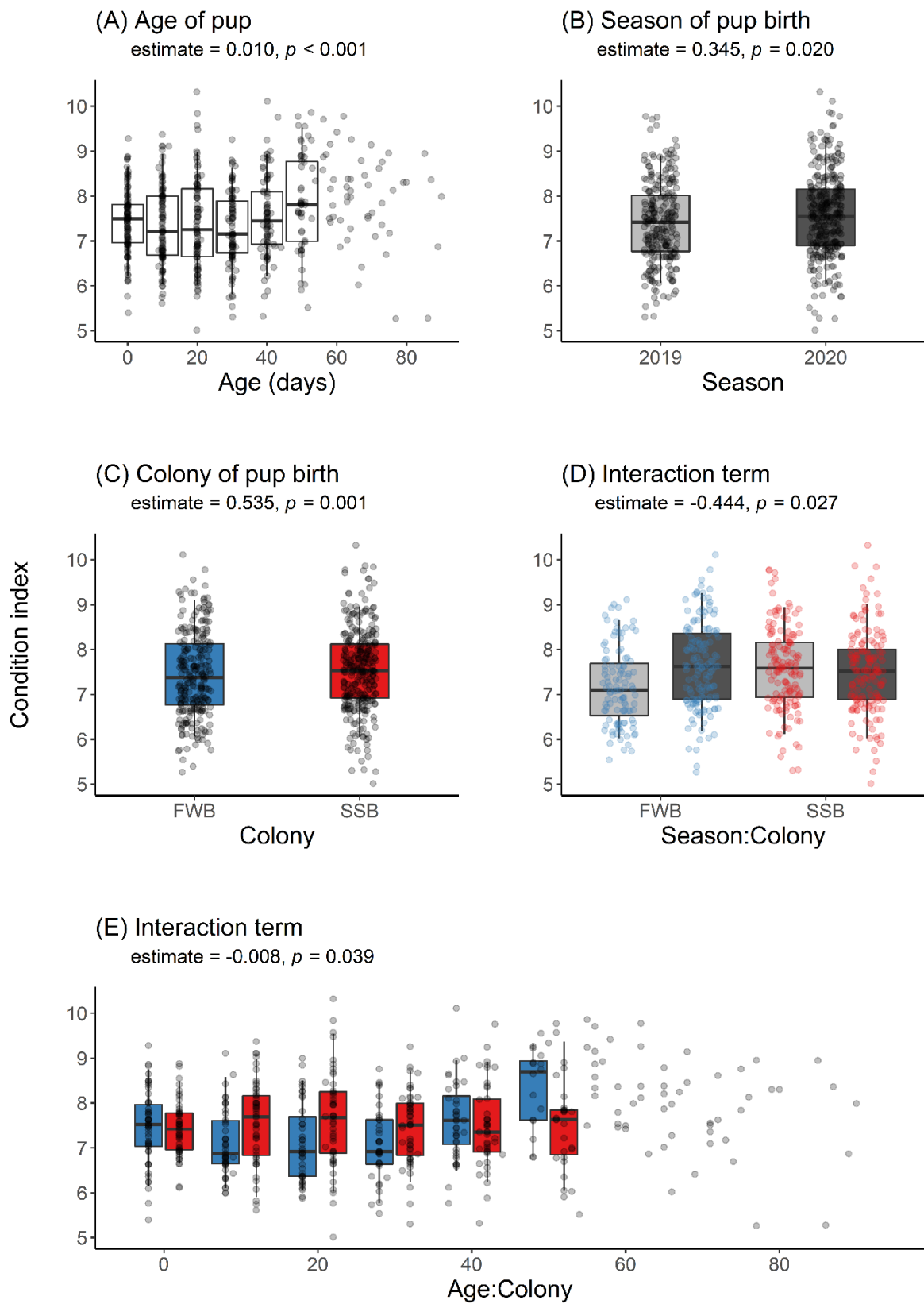
Figure 4: Results of a linear mixed model of pup condition index. Significant main effects of pup age, season of birth and breeding colony are shown in panels A–C respectively, while

panels 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 $\pm$ 75% quantiles, with the vertical lines indicating 95% CIs. Blue = FWB, red = SSB, light grey = 2019, dark grey = 2020.

Table S1. Results of a linear model of maternal condition index shortly after giving birth. No significant effects were detected.

	Estimate	**Standard error**	*t*-**value**	*p*-**value**
Intercept	34.52	0.787	43.85	**< 2 e-16**
Season	0.88	1.124	0.78	0.438
Colony	1.69	1.124	1.50	0.137
Season: Colony	-2.50	1.598	-1.57	0.121

(A) 2019
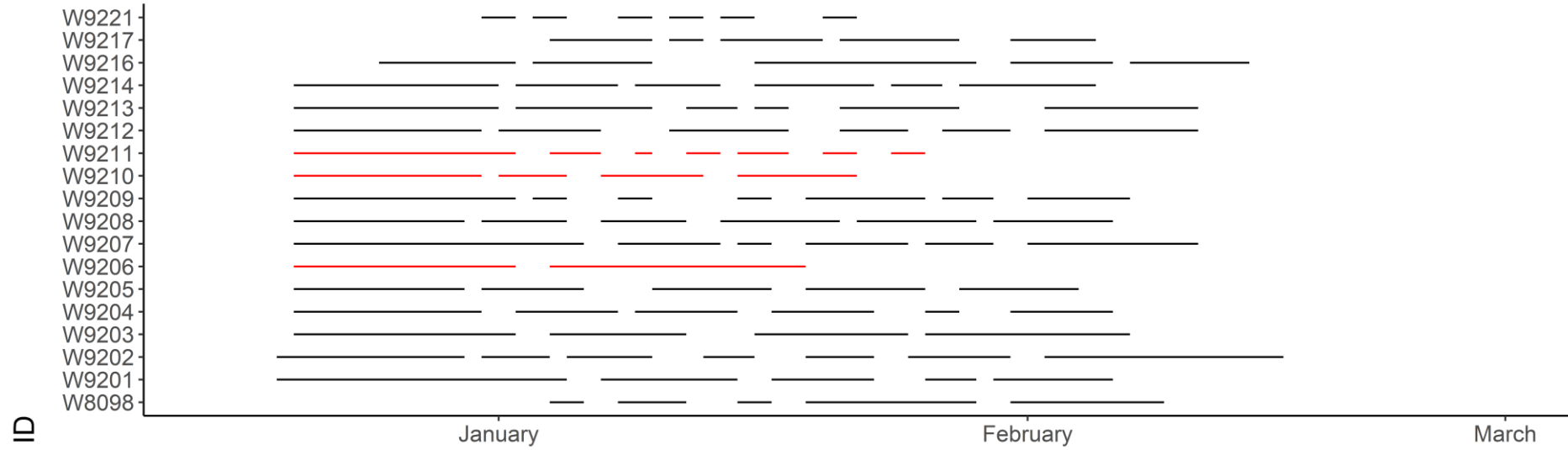
(B) 2020

Figure S1: Records of the presence (lines) and absence (gaps) of focal mothers breeding at FWB during the 2019 (panel A) and 2020 (panel B) breeding seasons. Foraging patterns of those mothers whose pups died are marked in red.
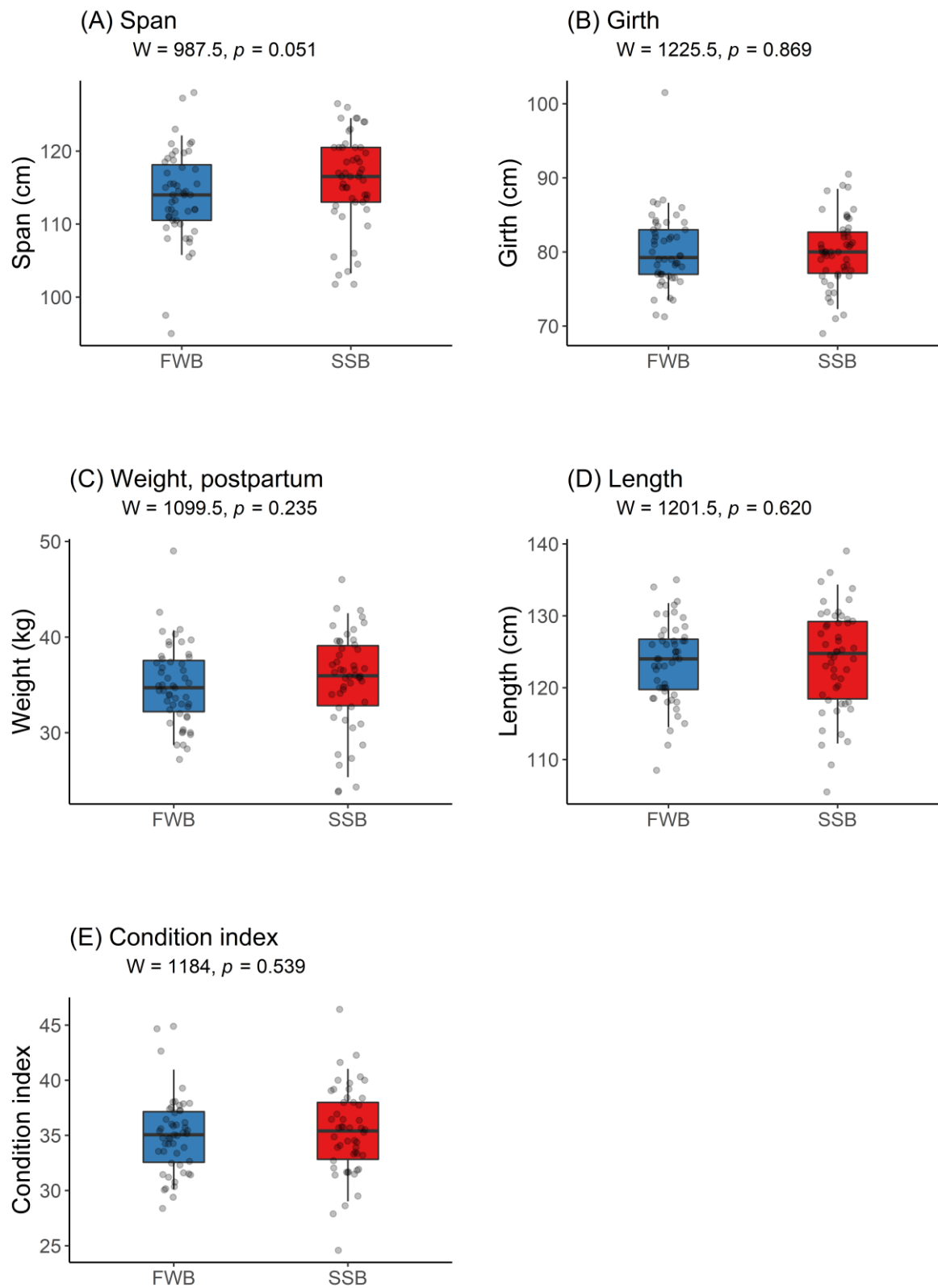
Figure S2: Results of independent Wilcoxon rank sum tests with continuity correction on five quality traits of focal mothers: span (panel A), girth (panel B), weight shortly after giving birth

(panel C), length (panel D) and condition index (panel E). No significant differences between animals from the two colonies were detected. The Wilcoxon's rank-sum statistic (W) and *p*-values are provided. Boxes show the means ± 75% quantiles, with the vertical lines indicating 95% CIs. Blue = FWB, red = SSB.