



FEATURE ARTICLE

Seabird attacks contribute to calf mortality in a whale population

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ABSTRACT: Reports of seabirds attacking marine mammals have become frequent in the 2000s. Southern right whales *Eubalaena australis* off Península Valdés (PV), Argentina, have suffered the effects of micropredation by kelp gulls *Larus dominicanus* since at least the 1970s. During 2003–2013, this population experienced 9 yr of unprecedented high calf mortality. Using a 25 yr dataset (1995–2019) of focal follows of gull–whale interactions, we studied long-term changes in gull attack intensity (attacks h⁻¹) and frequency, and explored whether they influenced calf mortality. We also asked whether calf mortality was affected by prey density at maternal feeding grounds during gestation. Applying Bayesian models, we found that the intensity and frequency of attacks increased significantly from 1995 to the 2000s, and that in 2004–2019, calves received 2.85 times as many attacks as did mothers. Moreover, attacks significantly contributed to increase the probability of calves dying, such that a year with average overall harassment had 2.26 times the mortality of a hypothetical year with no attacks. In years of high intensity and frequency of attacks, many older calves died near the end of the season, probably reflecting the cumulative effect of gull harassment on calf health. However, calf mortality was not affected by prey density, and extremely high mortality was not related to extremely high frequency or intensity of attacks, indicating that deaths are also influenced by other unidentified factors. These findings imply that chronic micropredation contributed to the unprecedented high calf mortality observed in PV and that other marine mammal populations experiencing seabird attacks could be threatened.

KEY WORDS: Calf deaths · Micropredation · Kelp gulls · Right whales · Stress



A southern right whale calf with gull wounding on its back being harassed by a native kelp gull at Península Valdés, Argentina.

Photo: Nicolás Lewin

1. INTRODUCTION

Trophic interactions between marine mammals and seabirds have been documented extensively. Many are defined as facultative commensalisms in which seabirds benefit from incidental feeding opportunities created by marine mammals without benefiting or harming the mammals (Leung & Poulin 2008). However, commensalism can occasionally transform into parasitism or predation (Aurioles & Llinas 1987, Leung & Poulin 2008, Pavés et al. 2008, Gallagher et al. 2015), given the foraging plasticity of seabirds (Paiva et al. 2010, Chérel et al. 2014, Seguel et al. 2017). Micropredation occurs when an organism attacks and feeds on multiple victims (like a predator) but takes only small amounts of tissue (like a parasite). Micropredators open and/or extend wounds on their victims and increase their energy expenditure

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and stress levels as a consequence of persistent harassment (Rowntree et al. 1998, Poulin 2011, Marón et al. 2015, Fernández Ajó et al. 2020, Azizeh et al. 2021). Prolonged intense micropredation can decrease the growth of prey or host organisms (Jones 2007) and even lead to death, particularly if the victims are young (Aurióles & Llinas 1987, Gallagher et al. 2015, Agrelo et al. 2023). Reports of seabirds attacking marine mammals in coastal and oceanic habitats have become more frequent in recent decades, with many cases involving gulls attacking cetaceans (Groch 2001, Pavés et al. 2008, Gallagher et al. 2015, Seguel et al. 2017, Towers & Gasco 2020, Harkness & Sprogis 2020, Carroll et al. 2022).

Southern right whales (SRWs) *Eubalaena australis* at Península Valdés (PV), Argentina, have been harassed by kelp gulls *Larus dominicanus* since at least the 1970s (Fig. 1A–C) (Thomas 1988, Marón et al. 2015). PV is the largest calving ground for SRWs in the southwest Atlantic Ocean, where mothers give birth to their calves and remain for about 3 mo in winter and/or spring (June–December) (Rowntree et al. 2001). In the decades following the first reported attacks, gulls have undergone behavioural shifts in their interactions with whales at PV. In the 1980s, gulls predominantly attacked mothers and other adults in the northern gulf (Golfo San José; Fig. 1D) (Thomas 1988, Marón et al. 2015). By 1995, attacks were evenly distributed among mothers and calves and were also frequently recorded in the southern gulf (Golfo Nuevo; Fig. 1D) (Rowntree et al. 1998, Marón et al. 2015, Sironi & Rowntree 2019). During the 2000s, calves exhibited 3 times as many gull-inflicted lesions or wounds as their mothers. Today, calves remain the preferred targets of gulls (Marón et al. 2015, Sironi & Rowntree 2019).

Gull attacks harm the well-being of mother–calf pairs during the vulnerable stage of lactation. Gull attacks cause lesions on the whales' backs (Fig. 1A–C), which may provide entry points for pathogens (Fiorito et al. 2016) and facilitate the development of infections (McAloose et al. 2016). Gull harassment also increases the energy expenditure of mother–calf pairs, tripling the frequency of high-energy-consuming behaviours (e.g. medium and fast travel) and reducing the time dedicated to nursing and resting (Rowntree et al. 1998, Azizeh et al. 2021). This elevated energy consumption occurs at a time when mother–calf pairs depend mostly on maternal stored energy gained in the previous feeding season (Lockyer 2007, Christiansen et al. 2018, Nielsen et al. 2019). Persistent gull harassment also leads to physiological stress in calves, as their adrenal glucocorticoid levels correlate with their degree of wounding (Fernández Ajó et al. 2018, 2020). The energetical and physiological effects of gull micropredation and the gull-inflicted lesions accumulate throughout the calving season (Marón et al. 2015, Fernández Ajó et al. 2018, 2020), slowly degrading mother–calf health.

The SRW population at PV experienced 9 yr with unusually large numbers of dead calves between 2003 and 2013, compared to the previous 3 decades (1971–2002; Rowntree et al. 2013, Sironi et al. 2014, Marón 2015). The number of dead calves was markedly higher than expected relative to the population's growth rate in 2003, 2005 and 2007–2013, and calf mortality in 2012 showed the highest rate ever previously recorded for the species (Rowntree et al. 2013, Marón 2015). Many potential factors of mortality have been considered, including malnourishment, biotoxins, trauma and disease (Thomas et al. 2013, McAloose et al. 2016, Wilson et al. 2016, Fernández

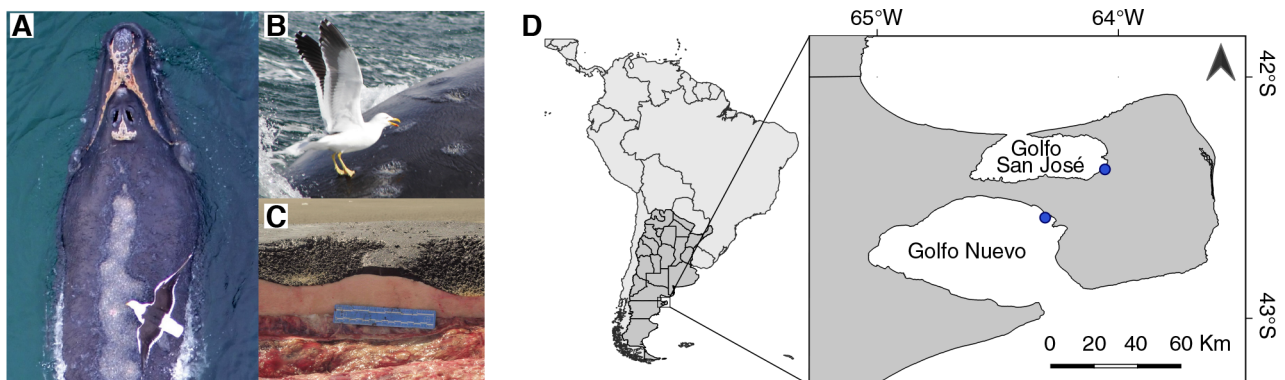


Fig. 1. (A) Southern right whale calf with an extended gull lesion on its back, being attacked by a kelp gull. (B) Kelp gull attacking a calf with several small lesions. (C) Cross-section through skin and blubber of a dead calf showing the depth of 2 gull lesions. The length of the ruler is 15 cm. (D) Peninsula Valdés, Argentina, showing study sites (blue circles). Photo credits: (A) Nicolás Lewin, (B) María Piotta and (C) Mariano Sironi (ICB/SRWHP)

Ajó et al. 2020, Marón et al. 2021); alone, none of them explain this unusual mortality. However, 2 factors remain to be evaluated: prey density in feeding grounds and gull attacks. Prey density is known to affect female reproductive success, as SRWs off PV and Brazil have fewer calves when the abundance of Antarctic krill *Euphausia superba* decreases in their feeding grounds such as Islas Georgias del Sur/South Georgia (Leaper et al. 2006, Seyboth et al. 2016). Even though signs of malnutrition were not evident in stranded calves at PV (Fernández Ajó et al. 2020, Marón et al. 2020, 2021), prey density should be considered as a relevant variable potentially affecting female reproduction and calf mortality at PV. Kelp gull micropredation is another variable that should be assessed, as it is consistently found to affect the whales' behaviour, physiology and overall well-being throughout the study period (Rowntree et al. 1998, Thomas et al. 2013, Marón et al. 2015, Fiorito et al. 2016, Fernández Ajó et al. 2020, Azizeh et al. 2021). Although previous studies have suggested that gull attacks might explain the unprecedented high calf mortality recorded, the difficulty involved with testing this hypothesis has also been emphasised (IWC 2013, 2016).

Here, we present an analysis of long-term temporal and spatial changes in kelp gull attacks on mothers and calves and explore potential causes of the unusually high calf mortality at PV. Using multi-decade data sets on SRW necropsies, gull–whale interactions and prey density in feeding grounds, we inquire whether (1) the intensity (attacks h^{-1}) and frequency of attacks changed for mothers and calves, gulfs and years in 1995–2019; (2) gull harassment and prey density may have increased calf mortality; and (3) the attacks may have specifically contributed to late-season calf deaths by degrading calf health through the calving season.

2. MATERIALS AND METHODS

2.1. Data set

2.1.1. Gull-attack observations

We used the 25 yr Gull Attack Monitoring Program data set gathered at PV by the Instituto de Conservación de Ballenas (ICB). Data were collected in Golfo San José (Campamento 39; 42° 34' 38.4" S, 64° 18' 25.2" W) in 1995–2019, and in Golfo Nuevo (Punta Pirámides-La Adela; 42° 22' 52.9" S, 64° 03' 19.0" W) in 1995 and 2005–2019 (Fig. 1D).

Observations were made in September, a month with high abundance of whales and high frequency of kelp gull attacks (Payne 1986, Sironi et al. 2009, Fazio et al. 2012, Crespo et al. 2019). As described by Rowntree et al. (1998), we made our observations from cliffs, using 20× wide-angle spotting scopes to visually follow mother–calf pairs and record whether they were attacked by gulls. Focal pairs were selected by their proximity to the observation site and were abandoned when they were too far away to detect whether gulls were attacking them. We identified focal individuals by their callosity patterns (Payne & Dorsey 1983), pigmentation patterns (Eroh et al. 2017) and/or by the overall severity of gull-inflicted lesions (less, moderate or extremely injured) on their backs. This short-term identification protocol allowed us to distinguish whales from their immediate neighbours of the day but not between different days or years. We defined a 'gull attack' as any event in which the bill of a kelp gull reached the body of a whale (Thomas 1988, Rowntree et al. 1998, Sironi et al. 2009). During each focal follow, we recorded the occurrence and the number of attacks on mother–calf pairs during 5 min intervals (Table S1 in the Supplement at www.int-res.com/articles/suppl/m746p001_suppl.pdf).

2.1.2. Gull attack indexes

Three gull attack indexes were defined to characterise the intensity and frequency of kelp gull attacks on mother–calf pairs: gull attack pressure on calves (GAPC), gull attack pressure on mothers (GAPM) and gull attack frequency (GAF). GAPC and GAPM are the daily average number of attacks per hour on calves and mothers, respectively, and represent the intensity of attacks. We calculated GAPC and GAPM as the quotient of the total number of attacks in one day over the number of observation hours on that day. GAF is the daily proportion of observation intervals with at least one attack on either the mother or the calf, considered together, and represents the frequency with which attacks occurred at any intensity (also the proportion of daylight time during which a mother–calf pair experienced an attack). GAF on the pair was calculated as the fraction of 5 min intervals with at least one attack on either mother or calf using the attack-occurrence data. Annual means of the gull attack indexes were calculated as the averages of their daily values for September. Data from 1996 to 2003 in Golfo San José and from 1996 to 2004 in Golfo Nuevo were excluded because sample sizes were too small to adequately support the analyses.

2.1.3. Dead calf data

Necropsies of SRW calves were conducted annually by the Southern Right Whale Health Monitoring Program (SRWHMP). From June to December, the SRWHMP field team located dead calves following reports of sightings from the community and by land-based and aerial surveys along the PV coastline (495 km). Along with the apparent date of death and location of each calf, the SRWHMP provided calf length (straight length from snout to fluke notch, in m) and the condition of its umbilicus (open or healed, when available) for all dead calves reported in 2003–2019. We studied calf age considering their length and the condition of the umbilicus (proxies of calf age; McAloose et al. 2016, Christiansen et al. 2022). Although the present study does not work with calves' age classes, hereafter we will refer to calves with an open umbilicus and <5 m in length as newborns or neonates (<2 wk old) and calves with a healed umbilicus and >5 m in length as older calves (2 wk–3 mo; McAloose et al. 2016, Christiansen et al. 2022).

2.1.4. Annual calf counts

A photo-identification survey was conducted by the ICB and Ocean Alliance every year near the time of peak whale abundance in early September (Payne 1986, Crespo et al. 2019). Mother–calf pairs along the coast were counted during each survey. Since many mothers and calves stay for around 3 mo in the gulf where the calf is born (Rowntree et al. 2001), we approximated the number of calves born each season in each gulf as the sum of the number of living calves counted during surveys and the number of calves that died before the surveys were conducted.

2.1.5. Prey density: sea surface temperature as a proxy for krill density

Islas Georgias del Sur/South Georgia is one of the feeding grounds for SRWs in the South Atlantic (Best et al. 1993, Zerbini et al. 2016, Valenzuela et al. 2018, Derville et al. 2023), where euphausiids are their primary prey (Tormosov et al. 1998, Valenzuela et al. 2018). The density of krill on its coast is negatively correlated with sea surface temperature (SST) anomalies (Trathan et al. 2003, Fielding et al. 2014). Consequently, the SST anomalies can serve as a proxy for krill densities and thereby indicate the likely effects of prey availability for pregnant females on calf mor-

tality. We derived SST anomalies at Islas Georgias del Sur/South Georgia from the database of Reynolds et al. (2008) using Google Earth Engine (Gorelick et al. 2017) and computed the average anomaly between August and October in each year (see Text S1 in the Supplement). We chose the SST anomalies in this monthly range because they are correlated with krill density on this feeding ground during summer (i.e. winter temperature relates to the foraging condition in summer; Fielding et al. 2014), when pregnant females would have fed prior to the calf mortality detected on the PV calving ground.

To our knowledge, there are no consistent and long-term data on the abundance of calanoid copepods or euphausiids during 1995–2019 in other feeding grounds in the South Atlantic. Consequently, we did not include information on prey densities in other feeding grounds in our models.

2.2. Statistical analysis

2.2.1. Describing gull attack pressure and frequency

To describe differences in GAPC, GAPM and GAF between gulfs and years, we fitted a joint generalised linear mixed model using a Bayesian approach. For gull attack pressures, we assumed a negative binomial distribution of the daily number of attacks to account for overdispersion, and modelled its mean using a log-link function. Gulf, mother vs. calf and their interaction were considered as fixed factors, and the interactions year \times gulf and year \times gulf \times mother vs. calf were included as random effects. For GAF, we assumed a binomial distribution of the daily number of intervals with attacks and modelled the attack probability with a logit-link function. As GAF data did not distinguish among mothers or calves, the only fixed factor included was gulf. We fitted the model using Stan (Stan Development Team 2020a) through its R interface, rstan (Stan Development Team 2020b), and defined weakly informative priors based on simulations. We ran 10 chains for 2000 iterations, leaving 1000 for warm-up. The minimum effective sample size was 1260 and maximum \hat{R} was 1.0087, indicating convergence (Fig. S1) (Vehtari et al. 2021). Based on posterior predictive checks, the models showed a good fit to the data (Fig. S2). We calculated the estimated values of GAPC, GAPM and GAF for each year and gulf. Furthermore, to compare the attack indexes between mothers and calves, gulfs and periods, we reported the quotient between the estimated means of the categories of interest, using the higher mean

category in the numerator. These predictions were computed averaging over all years.

2.2.2. Modelling probability of calves dying

To evaluate whether gull attacks increased the probability that a calf would die (i.e. calf mortality) before leaving PV, we fitted 3 Bayesian generalised linear models to the data on yearly calf mortality and gull attack indexes. We modelled the number of dead calves by year and gulf following a beta-binomial distribution to account for overdispersion. Using a logit-link function, the probability of calves dying was modelled as a linear function of any of the 3 annual gull attack indexes, the gulf and their interaction. We also included the SST anomalies in Islas Georgias del Sur/South Georgia as a covariate and allowed the dispersion parameter to vary between gulfs. The models were fitted using JAGS through its R interface, jagsUI (Plummer 2003). Weakly informative priors were specified for all parameters based on prior predictive checks (see Text S1). Two chains of 20 000 iterations were run for each model, leaving 5000 for the warm-up, yielding a total of 30 000 posterior samples for inference. The mean effective sample sizes were 21 620 for the GAPC model, 21 669 for GAPM and 20 659 for GAF, with a minimum of 2005 in the GAF model. All \hat{R} values were equal to 1.00, indicating convergence (Tables S2–S4; Vehtari et al. 2021). Posterior predictive checks showed that the models fit the data well (Fig. S3). We reported the estimated calf mortality in both gulfs at different values of the covariates of interest, and the magnitude of change of calf mortality between those values.

2.2.3. Relationship between temporal distribution of calf deaths and gull attacks

Gull attacks are hypothesised to have cumulative effects on calf health, causing degradation over the calving season. If these cumulative effects do not contribute to calf mortality, then the time course of observed calf deaths would be expected to follow the time course of births (perinatal calf death), peaking around the time of maximum calf abundance at PV (August–September). Consequently, most of the calves that die should be newborns or neonates, and their dates of death should not vary in a systematic way with the frequency or intensity of attacks. However, if gull attacks do contribute to mortality, then the peak of calf deaths would be expected to occur

later in the season, after many calves have accumulated significant numbers of lesions and suffered the effects of the resulting stress (Marón et al. 2015, Fernández Ajó et al. 2018, 2020). In this scenario, most dead calves would tend to be older, and their average dates of death would be expected to vary yearly with the average frequencies and intensities of gull attacks.

Two Pearson correlations were computed to assess whether calf age at death varied over the calving season. The monthly average length of dead calves and the relative frequency of open and healed umbilici were used as proxies of calf age (McAloose et al. 2016, Christiansen et al. 2022) and were associated with the month of calf death. In both cases, the sample size was equal to 6, as data from all years and calves were aggregated by month. We reported Pearson correlation coefficients (r) and their p -values.

Moreover, to test whether calf death throughout the season could be explained by gull attack indexes, we modelled the month when calves died as a function of the gulf and each of the 3 gull attack indexes. We included the interaction term between the gulf and the corresponding gull attack index as covariates and also a random effect for the year. The month of death was assumed to follow an ordered categorical distribution, coded with integers between 6 and 12 from June to December. Using the 3 gull attack indexes as predictors separately, we fitted 3 cumulative logistic models (Bürkner & Vuorre 2019) using ‘brms’ (Stan Development Team 2020a, Bürkner 2017). Weakly regularising priors were set for the intercept parameters and for the among-years standard deviation (Student’s t ; $\mu = 0$, $\sigma = 2.5$, $df = 3$), which was zero-truncated for standard deviation parameters, and flat improper priors on the remaining regression coefficients. The minimum sample size of the 3 models was 2669 and the maximum \hat{R} value was lower than 1.01. Based on these diagnostics, all models showed a good fit to the data (Fig. S4).

2.2.4. Model estimates and posterior probabilities

We summarised the estimates of all models by their posterior distribution means and their 95% equal-tailed credible intervals. From the posterior distributions, we computed the posterior probabilities (Pr) of some relevant statements. For example, the probability of the quotient (q) between 2 predicted means being larger than one ($\text{Pr}[q > 1]$) (Section 2.2.1), or the probability of a slope parameter (β) being larger or smaller than zero ($\text{Pr}[\beta > 0]$ and $\text{Pr}[\beta < 0]$).

0], respectively) (Sections 2.2.2 and 2.2.3). These probabilities are 1 if there is complete certainty about the statement being true, or 0 if there is complete certainty about the statement being false. Hence, $\Pr(q > 1) = 1$ indicates that the numerator in the quotient is larger than the denominator with complete certainty; similarly $\Pr(\beta > 0) = 1$ indicates that β is positive with complete certainty; i.e. that the covariate has a positive effect on the response variable. Accordingly, $\Pr(\beta > 0) = 0$ indicates that β is negative with complete certainty (which is equivalent to $\Pr[\beta < 0] = 1$), and $\Pr = 0.5$ indicates complete uncertainty about the veracity of the statement.

All statistical analyses were performed using R software version 4.2.0.1 (R Core Team 2021). For details on the models see Text S1.

3. RESULTS

3.1. Spatial and temporal variation in gull attacks

A total of 17060 intervals of 5 min observations were conducted in Golfo Nuevo during 1995 and 2005–2019, and 11814 intervals in Golfo San José during 1995 and 2004–2019 (Table S1). In total, 2767 mother–calf pairs were observed in both gulfs. The years with the least sampling effort were 2006 in Golfo Nuevo (532 intervals) and 2005 in Golfo San José (316 intervals; Table S1).

Averaging all years and both gulfs, the estimated GAPC (posterior mean [95% CI]) was 4.77 [3.74, 6.29], the estimated GAPM was 1.70 [1.32, 2.34] and the estimated GAF was 0.22 [0.19, 0.24]. Comparing GAPC versus GAPM, the estimated mean of GAPC was 2.85 [2.17, 3.71] times as high as the estimated mean of GAPM ($\Pr[q > 1] = 1$). Considering the gulfs separately, GAPC was 2.94 [2.08, 3.8] and 2.75 [1.72, 4.3] times higher than GAPM in Golfo Nuevo and Golfo San José, respectively ($\Pr[q > 1] = 1$ for both gulfs) (Table 1). Comparing both gulfs, GAPC and GAPM were higher in Golfo Nuevo than in Golfo San José by a factor of 1.55 [0.9, 2.46] ($\Pr[q > 1] = 0.94$) and 1.44 [0.79, 2.38] ($\Pr[q > 1] = 0.89$), respectively (Table 1). Similarly, GAF was higher in Golfo Nuevo than in Golfo San José by a factor of 1.22 [0.99, 1.5] ($\Pr[q > 1] = 0.97$) (Table 1).

The inter-annual trends of GAPC, GAPM and GAF were similar for both gulfs (Fig. 2A–C). In general, all 3 indexes tended to increase from 1995

to 2011–2013 ($\Pr[2011–2013 > 1995]_{\text{GAPC}} = 1$, $\Pr[2011–2013 > 1995]_{\text{GAPM}} = 0.97$, $\Pr[2011–2013 > 1995]_{\text{GAF}} = 1$). Furthermore, 3 periods could be discerned between 2004 and 2019: a first period with increasing or high and stable values extending from 2004 to 2010 in Golfo San José and from 2005 to 2010 in Golfo Nuevo; a short second period between 2011 and 2013 during which the trends fluctuate and some indexes peaked; and a third period of low and stable or decreasing values from 2014 to 2019 at both sites (Fig. 2A–C). In Golfo Nuevo, GAPC and GAF remained higher than in 1995 from 2004 onwards ($\Pr[2004 \text{ onwards} > 1995] = 0.99$ for both GAPC and GAF), whereas GAPM values from 2014 to 2019 tended to be lower than in 1995 and in 2004–2010 ($\Pr[2014–2019 < 1995] = 0.79$ and $\Pr[2014–2019 < 2004–2010] = 1$).

GAPC varied more among years than did GAPM, and both GAPC and GAPM were more variable in Golfo Nuevo than in Golfo San José (Fig. 2A,B, Table 1). Like GAPC and GAPM, GAF showed more annual variation in Golfo Nuevo than in Golfo San José (Table 1). The variation among sampling days (i.e. unexplained variation) was considerable for the 3 gull attack indexes (Fig. S2). This is reflected in the low Bayesian R^2 values (Gelman et al. 2019) for the gull attack models (GAPC = 0.18 [0.14, 0.24]; GAPM = 0.15 [0.1, 0.22]; GAF = 0.19 [0.11, 0.27]).

3.2. Gull attacks and the probability of calves dying

Between 2003 and 2019, at least 790 SRW calves died, out of at least 3801 that were born in Golfo Nuevo and Golfo San José. We found that their probability of dying increased with GAPC, GAPM and GAF in both gulfs, with the most significant effect observed in Golfo Nuevo (Fig. 3). Notably, no effect of SST anomalies around Islas Georgias del Sur/South Georgia was found on calf mortality (Fig. S5).

Table 1. Estimated means of gull attack pressure on calves (GAPC) and mothers (GAPM), gull attack frequency (GAF) and inter-annual variability (standard deviation) across years by gulf and mother vs. calf. Point estimates are posterior means; 95% equal-tailed credible intervals are shown in brackets

Variable	Gulf	Mean	Inter-annual variation
GAPC	Nuevo	5.71 [4.32, 8.13]	2.11 [1.42, 2.98]
	San José	3.83 [2.64, 5.84]	1.59 [1.18, 2.09]
GAPM	Nuevo	1.9 [1.40, 2.97]	0.86 [0.60, 1.22]
	San José	1.43 [1.01, 2.20]	0.63 [0.39, 1.04]
GAF	Nuevo	0.24 [0.20, 0.27]	0.06 [0.04, 0.08]
	San José	0.20 [0.17, 0.22]	0.04 [0.02, 0.06]

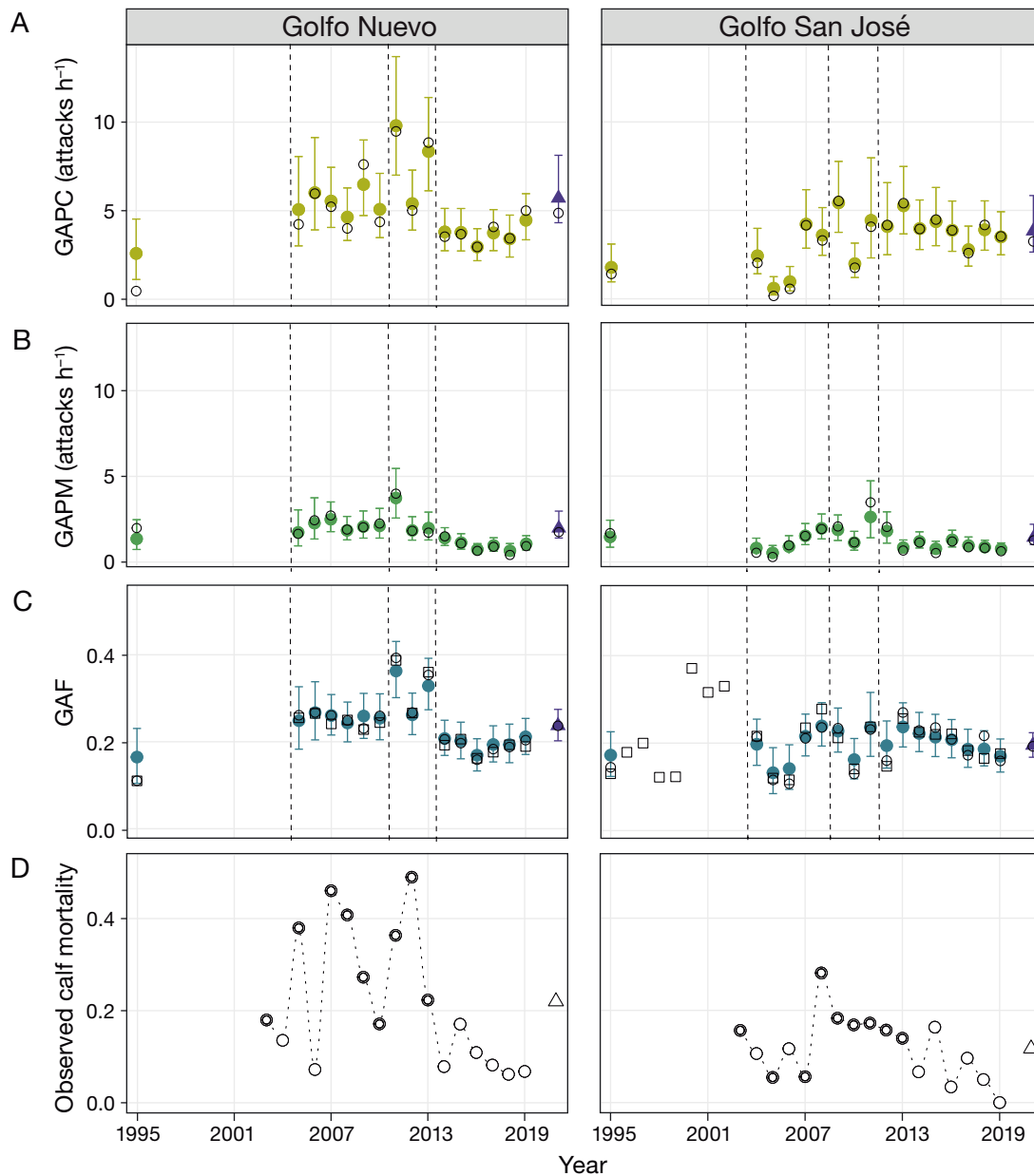


Fig. 2. Gull attack dynamics and calf mortality trends in 1995–2019. (A) Gull attack pressure on calves (GAPC), (B) gull attack pressure on mothers (GAPM) and (C) gull attack frequency (GAF) estimated and observed values in Golfo Nuevo and Golfo San José for 1995 and 2004–2019. Solid circles: posterior distribution means by year and gulf; solid triangles: means by gulf averaging years; bars: 95% credible intervals. Empty circles: observed means; empty squares: GAF observed values for 1996–2003. Dashed vertical lines separate the 3 main periods of change in gull attacks indexes. (D) Observed calf mortality calculated as the number of dead calves divided by the number of calves born each year. Circles: observed mortality in each gulf; triangles: overall mean; thick circles: years of high calf mortality (2003, 2005, 2007–2013); thin circles: years of low calf mortality

In Golfo Nuevo, the probability of calves dying exhibited increases of 0.16 [−0.1, 0.42], 0.32 [0.03, 0.59] and 0.3 [0.03, 0.57] units, when GAPC, GAPM and GAF increased from their minimum to their maximum annual values observed in the gulf (Fig. 3; $\text{Pr}[\beta > 0]_{\text{GAPC}} = 0.89$, $\text{Pr}[\beta > 0]_{\text{GAPM}} = 0.98$, $\text{Pr}[\beta > 0]_{\text{GAF}} = 0.99$). Specifi-

cally, calf mortality rose from 0.19 [0.1, 0.3] when annual GAPC was 2.95 attacks h^{-1} , to 0.35 [0.16, 0.57] when annual GAPC was 9.48 attacks h^{-1} . Regarding GAPM and GAF, calf mortality increased from 0.14 [0.07, 0.24] to 0.46 [0.23, 0.69] as annual GAPM escalated from 0.42 to 3.99 attacks h^{-1} , and from 0.15

[0.08, 0.25] to 0.45 [0.23, 0.67] when annual GAF increased from 0.16 to 0.39. In Golfo San José, the probability of calves dying increased by 0.05 [−0.09, 0.20], 0.17 [−0.01, 0.37] and 0.1 [−0.04, 0.26] units when GAPC, GAPM and GAF rose from their minimum to their maximum observed values (Fig. 3; $\Pr[\beta > 0]_{\text{GAPC}} = 0.78$, $\Pr[\beta > 0]_{\text{GAPM}} = 0.97$, $\Pr[\beta > 0]_{\text{GAF}} = 0.92$). The GAPC model estimated an increase in calf mortality from 0.10 [0.03, 0.2] to 0.15 [0.8, 0.25] as the annual attack pressure climbed from 0.16 to 5.53 attacks h^{-1} . In the case of the GAPM and GAF models, calf mortality increased from 0.08 [0.05, 0.14] to 0.25 [0.11, 0.44] as annual GAPM increased from 0.34 to 3.47 attacks h^{-1} , and from 0.08 [0.03, 0.16] to 0.18 [0.09, 0.30] as annual GAF increased from 0.11 to 0.27 attacks h^{-1} .

GAPM increased the probability of calves dying approximately 8 times more than did GAPC when considering both gulfs together. Calf mortality increased by 0.03 [−0.04, 0.08] units when GAPC

increased from 0.34 to 3.99 attacks h^{-1} (minimum and maximum observed values of GAPM). However, the same increment in GAPM increased mortality by 0.24 [0.08, 0.41] units. Predictions for each gulf separately are shown in Table S5.

Calf mortality in a year of average attack intensity and frequency was 2.26 [1.22, 4.35] times as high as in a hypothetical year without attacks (indicating a 126% increase; $\Pr[q > 1]$), averaging predictions of the 3 models. Based on the GAPM model, calf mortality in a year of average GAPM was 1.84 [1.22, 2.70] times as high as in a hypothetical year without attacks ($\Pr[q > 1] = 1$). Fixing the 3 attack indexes at their means, calf mortality in an average year was 0.21 [0.17, 0.25] in Golfo Nuevo and 0.13 [0.10, 0.16] in Golfo San José. In contrast, in a hypothetical year without attacks, calf mortality in Golfo Nuevo would have been 0.11 [0.06, 0.19] and 0.07 [0.04, 0.13] in Golfo San José. In both scenarios, calf mortality was higher in Golfo Nuevo than in Golfo San José, with a

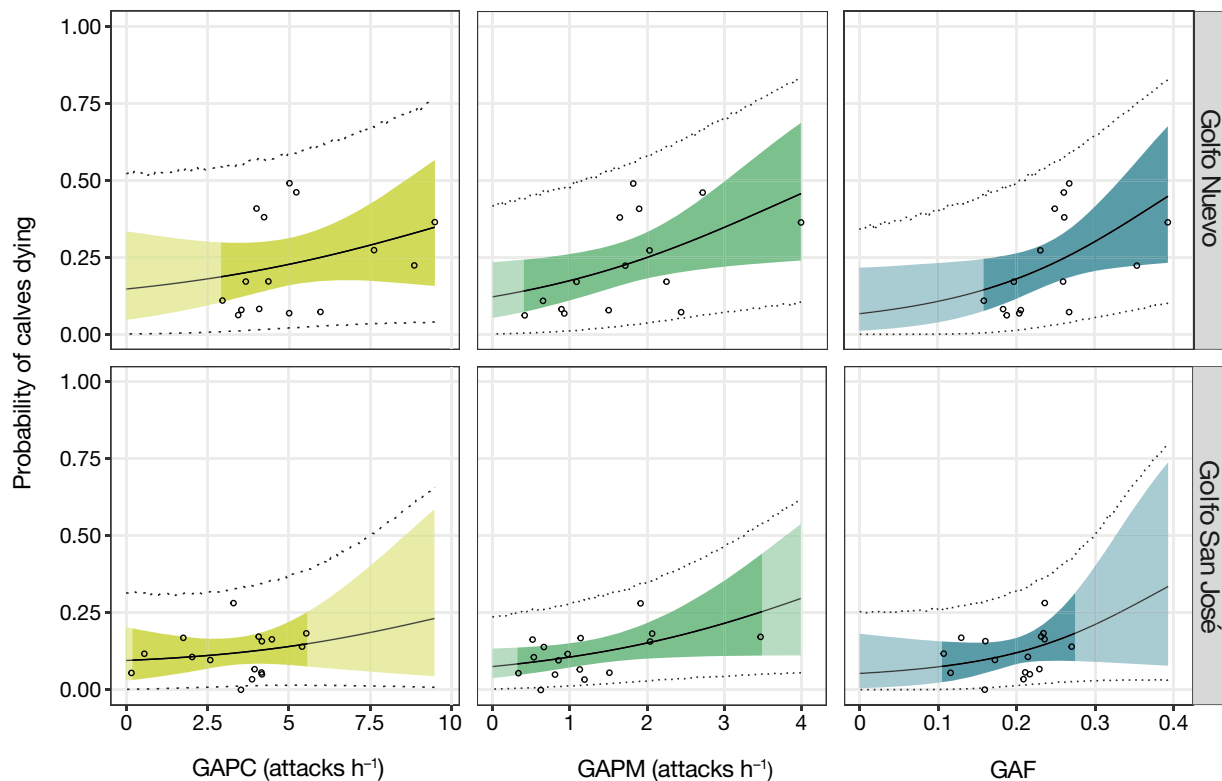


Fig. 3. Probability of calves dying increases with gull attacks. The probability of dying should be read as the probability for an average calf or a pool of calves dying (i.e. calf mortality) in its first months of life at Península Valdés given the attack index values (GAPC: gull attack pressure on calves; GAPM: gull attack pressure on mothers; GAF: gull attack frequency). Black lines: posterior means of the estimated probability of calves dying in an average year; coloured ribbons: 95% credible intervals. The intensity of the black lines and the ribbons indicate whether the estimations were made for the ranges of observed values of the gull attack indexes (darker) or outside of those ranges (lighter). Dotted ribbons: 95% prediction intervals; points: observed calf mortality in each gulf. Note that the ranges of the attack indexes are different (hence, their effects are not directly comparable in this graph). In all cases, the sea surface temperature anomalies in Islas Georgias del Sur/South Georgia were fixed at their mean values

posterior probability of 1 in the average attack scenario and 0.9 in the zero-attack scenario. Single model predictions and estimates of probabilities of calves dying per year and gulf are available in Tables S2–S4, S6 & S7.

SST anomalies in Islas Georgias del Sur/South Georgia had no effect on the probability of calves dying in any of the 3 models ($\Pr[\beta < 0]_{\text{GAPC}} = 0.75$, $\Pr[\beta < 0]_{\text{GAPM}} = 0.73$ and $\Pr[\beta < 0]_{\text{GAF}} = 0.86$ in the GAPC, GAPM and GAF models, respectively). For Golfo Nuevo, the GAPM model estimated a decrease in calf mortality from 0.25 [0.13, 0.39] to 0.20 [0.11, 0.29] with increasing SST anomalies from -0.72 to 0.65 (minimum and maximum values observed; Fig. S5). Mortality also decreased from 0.26 [0.13, 0.42] to 0.2 [0.1, 0.3] in the GAPC model and from 0.27 [0.14, 0.41] to 0.17 [0.09, 0.27] in GAF models with the same SST anomaly values (Fig. S5). The results for Golfo San José were similar and are shown in Fig. S5. The credible intervals associated with all the predictions were wide enough to consider a zero effect of SST anomalies on calf mortality (Fig. S5).

Extreme mortality was not explained by GAPC, GAPM, GAF or SST anomalies. The extremely low calf mortality did not necessarily occur during years of extremely low values of GAPC, GAPM, GAF or SST anomalies (Fig. 3; Fig. S5). Likewise, the extremely high calf mortality registered in 2007, 2008 and 2012 in Golfo Nuevo did not occur during years of extremely high values of GAPC, GAPM, GAF or SST anomalies (Fig. 3; Fig. S5). Consequently, the probability of dying exhibited unexplained inter-annual variability, particularly in Golfo Nuevo. This is indicated by the width of the prediction intervals (wider bands in Fig. 3 & Fig. S3) and the dispersion of the data (Fig. 3). Correspondingly, Bayesian R^2 values for the 3 models were low or moderate: 0.30 [0.18, 0.67] for the GAPC model, 0.43 [0.09, 0.54] for GAPM and 0.40 [0.15, 0.64] for GAF, indicating that the covariates included in this study only explained between 30 and 43% of the variation in mortality.

3.3. Gull attacks and late-season calf deaths

Calves found dead at PV in 2003–2019 ranged from newborns to older calves (2.18–9.83 m in length; Uhart et al. 2009, Sironi et al. 2014). Half of the calves presented an open umbilicus ($n = 416$), and half had a healed umbilicus ($n = 414$). The average length of dead calves in each month was positively correlated with their month of death ($r = 0.98$, $p < 0.0001$; Fig. 4A). Also, the relative frequency of dead calves with healed

umbilici increased over the months ($r = 0.95$, $p < 0.0001$), while the frequency of calves with open umbilici decreased ($r = -0.95$, $p < 0.0001$; Fig. 4B). Both patterns were more evident in high mortality years.

Calves died later in the calving season — closer to October than to August — in years with higher attack index values. In Golfo Nuevo, the average month of death was later in the season when GAF, GAPC and especially GAPM were high (Fig. 4C; $\Pr[\beta > 0]_{\text{GAPC}} = 0.81$, $\Pr[\beta > 0]_{\text{GAPM}} = 0.98$, $\Pr[\beta > 0]_{\text{GAF}} = 0.95$). Conversely, most calf deaths occurred during the months of maximum calf abundance — closer to August and September — in years of low values of GAPC, GAPM and GAF in Golfo Nuevo. As for Golfo San José, a weak and uncertain relationship was found between the month of death and GAPM ($\Pr[\beta > 0] = 0.77$), and no relationship was detected for the other 2 attack indexes ($\Pr[\beta > 0]_{\text{GAPC}} = 0.3$ and $\Pr[\beta > 0]_{\text{GAF}} = 0.4$). Unexplained inter-annual variation in the average month of death was higher (wider ribbon in Fig. 4C) in years when calf mortality was extremely high (denoted by lighter points in Fig. 4C). This was reflected in relatively low Bayesian R^2 values: 0.19 for the GAPC model, 0.28 for the GAPM model and 0.24 for the GAF model (posterior means; 95% credible intervals were [0.02, 0.46], [0.06, 0.54] and [0.03, 0.5], respectively).

4. DISCUSSION

Our results suggest that kelp gull attacks increased SRW calf mortality at PV during 1995 and 2005–2019, contributing to the high calf mortality observed on this calving ground in the 2000s. Our analyses relate long-term temporal and spatial changes in the dynamics of attacks to the probability of calves dying during their time at PV. Specifically, mortality appears to have doubled as a consequence of attacks, and attacks on mothers explain most of this increased mortality. We also found evidence that such attacks may have contributed to late-season deaths of older calves, as gull micropredation degrades the health of the calves through the calving season.

The intensity and frequency of attacks changed throughout the study period. Overall, the attacks showed a sharp increase from 1995 to the 2000s, and 3 main periods of change from 2004 to 2019 were detected. The 2 increases observed from 1995 to 2010 overlapped with 2 periods of population growth in the kelp gull colonies of northern Patagonia (Lisnizer et al. 2011), while the third period from 2014 to 2019, when gull attack indexes decreased or remained stable

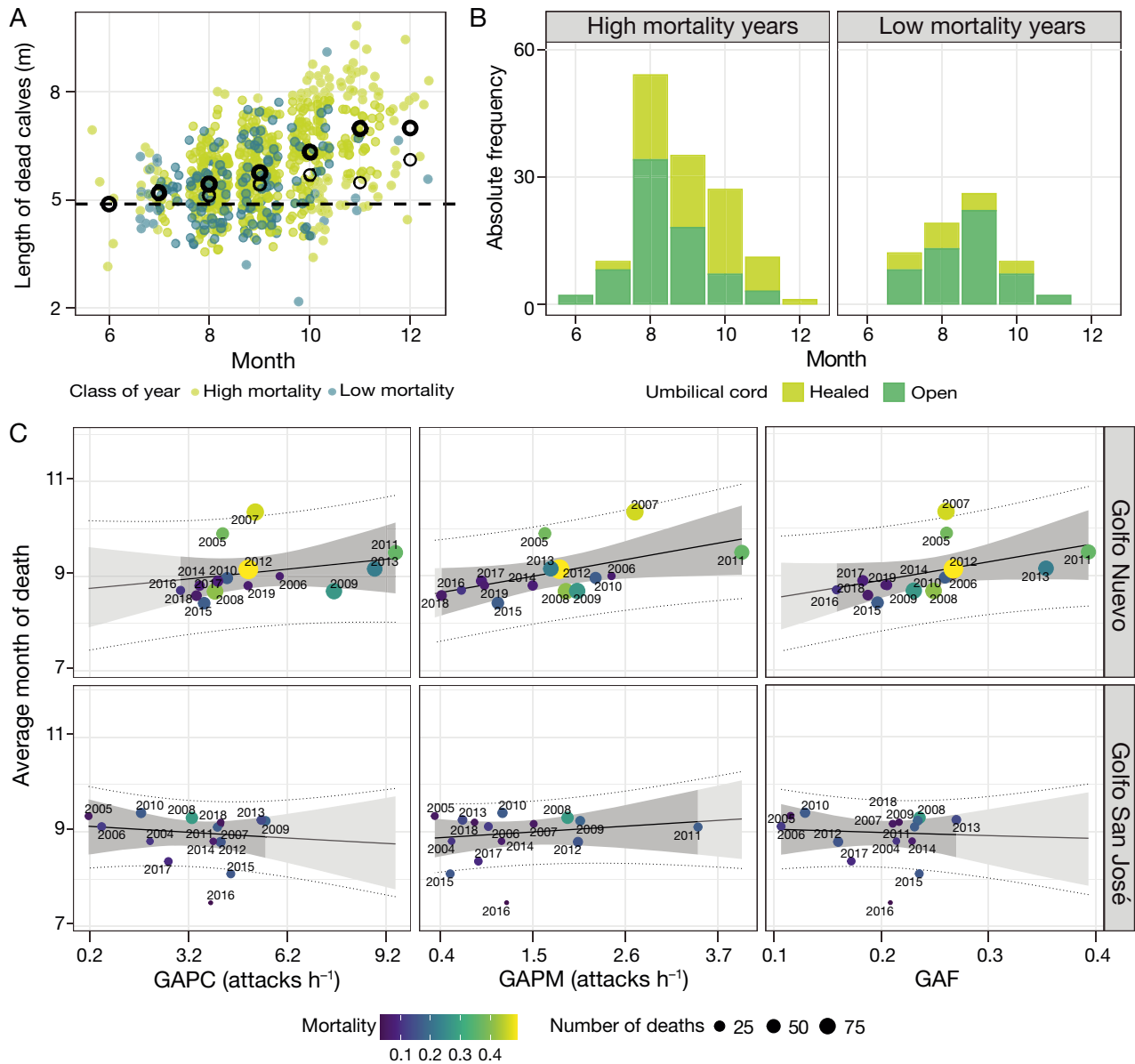


Fig. 4. Gull attacks and timing of calf deaths. (A) Length of dead calves over the calving season. Coloured dots: observed length (colour indicates high or low mortality years: light: high, dark: low; Marón 2015), jittered on the x-axis to improve visibility. Thick circles: observed monthly means of calves' lengths in high-mortality years; thin circles: calves' lengths in low-mortality years; dashed line: estimated average length at birth of southern right whale calves (Christiansen et al. 2022). (B) Umbilicus condition of dead calves across months in high- and low-mortality years. (C) Average month of calf deaths as a function of the 3 gull attack indexes (GAPC: gull attack pressure on calves; GAPM: gull attack pressure on mothers; GAF: gull attack frequency) and the gulf. Dots show the average month of death by year and gulf, with colour denoting observed mortality and size indicating the number of deaths. Solid lines: posterior means of the average month of death in an average year; coloured ribbon: 95% credible interval; dotted ribbon: 95% prediction interval considering yearly variation. The brightness of the ribbon indicates whether the estimates were made within the observed range of the attack indexes (darker grey) or outside of this range (lighter grey)

at lower values, partially coincides with the implementation of a pilot kelp gull culling program by the provincial government of Chubut (Bertellotti et al. 2015). The program was restricted to a small area in Golfo Nuevo, near our study site. However, no specific ana-

lyses could be carried out to test whether the control effort caused a reduction in gull attacks, as few details about the results of the culling program are available.

Gull attack intensity and frequency differed between gulfs, with most of the attacks occurring in

Golfo Nuevo. Golfo Nuevo has 2 human settlements on its coast: the city of Puerto Madryn with a port for large ships, and the tourist town of Puerto Pirámides. Golfo San José, by contrast, is a protected marine reserve with relatively little human activity. Gulls congregate in large numbers in Golfo Nuevo (P. Yorio pers. comm) and are mainly attracted by fishery discards (Yorio et al. 2016) and anthropogenic food subsidies (Giaccardi & Yorio 2004). For instance, more than 4669 kelp gulls were counted at waste disposal sites in 1996 and 1997 (Giaccardi & Yorio 2004). Consequently, if gull abundance were higher in Golfo Nuevo, then a higher likelihood of attacks on whales could be expected relative to Golfo San José.

GAPC was notably higher in the 2000s than in 1995, and almost 3 times higher than GAPM in 2004–2019. GAPM increased less from 1995 to the 2000s and was even lower in 2014–2019 than in 1995. This is consistent with results on the severity of kelp gull lesions on mothers and calves (Marón et al. 2015). The area of lesions on calves in the 2000s was twice as high as in the 1990s and 3 times the area than that on mothers (Marón et al. 2015). On the mothers, the area of lesions increased by 40% from the 1990s to the 2000s (Marón et al. 2015). Thus, our findings confirm an apparent shift in the dynamics of attacks during the 1990s, when calves were becoming preferred targets of the gulls. This change in gulls' preference might be explained by the increasing number of gulls in northern Chubut (Lisnizer et al. 2011) and the mothers learning avoidance behaviours to reduce attacks during the 2000s (Rowntree et al. 1998, Fazio et al. 2015, Azizeh et al. 2021). Attack-evasive behaviour patterns such as the 'galleon' posture — with the back strongly arched, hiding it from the gulls (Thomas 1988, Sironi et al. 2009) — and oblique respiration — with only blowholes exposed — became frequent in mothers in the 2000s and widespread in the late 2010s (Fazio et al. 2015, Azizeh et al. 2021), reducing the opportunity for attacks on the mother's back. However, calves have never been observed in the galleon posture, and until 2013, oblique respiration was not as frequently observed as it was in adults (Fazio et al. 2015). Consequently, calves may have become more frequent targets of attacks that had previously been aimed at their mothers, as the mothers became more adept at evading such attacks. This is concerning, given the consequences of micropredation on calf health and well-being (Marón et al. 2015, Fiorito et al. 2016, McAloose et al. 2016, Fernández Ajó et al. 2018). Long-term analyses of the effects of gull attacks on mother and calf behaviour are underway and may reveal how behaviour has changed since the 1990s and how these

changes may have affected gull attack dynamics and calf mortality.

Gull micropredation increases the probability of calves dying during their first months of life at PV. The first and second periods of increasing and fluctuating attack index values coincided with high calf mortality years, and the period of reduced attack index values with reduced mortality (Fig. 2). Hence, changes in the attack dynamics may explain changes in calf mortality. As a consequence, a year with an average rate of attacks had more than twice the calf mortality — 126% more — than a hypothetical year without attacks. However, the considerable uncertainty associated with our models' predictions and the complexity of the natural system indicate that gull harassment may be a factor contributing to calf mortality, but not the only and maybe not even the main cause (Thomas et al. 2013, IWC 2016, Fernández Ajó et al. 2020). Mothers and calves are exposed to gull attacks from the beginning of the calving season in June (Fazio et al. 2012). By October, they have accumulated a maximum number of gull lesions (Marón et al. 2015), as the highest attack rates are recorded during August and September (Sironi et al. 2009, Fazio et al. 2012). The attacks open and enlarge pre-existing gull lesions on the whales' backs (Thomas 1988, Rowntree et al. 1998) and cause chronic stress (Fernández Ajó et al. 2018, 2020, Azizeh et al. 2021). Wounds can provide an entry for pathogens and facilitate systemic infections (Fiorito et al. 2016, McAloose et al. 2016), while elevated glucocorticoids for prolonged periods can inhibit immune function (Dhabhar 2014, McAloose et al. 2016, Romero & Wingfield 2016). In severely wounded calves that were found dead, glucocorticoids dropped near the time of death, suggesting adrenal failure in these cases (Fernández Ajó et al. 2018). Thus, repeated attacks could chronically stress calves, such that they become more vulnerable to other factors that could trigger their deaths.

Our analysis indicates that gull attacks contribute to calf death towards the end of the calving season, around October. The length of dead calves and the frequency of dead calves with healed umbilici increased over time, especially during years of high calf mortality. Therefore, most of the calves that died towards the end of the season in those years were not newborns or neonates (Fig. 4A). We also found a positive relationship between gull attack pressure and frequency and the month of the year when most dead calves were recorded. This implies that calves tended to die later in the season following high values of GAPC, GAPM or GAF in September (see Section 2.1.1). A previous study reported that the area of lesions

increases with calf length (Marón et al. 2015). Older wounded calves that died in October might have been born between July and September and exposed to the peak attack months (Fazio et al. 2012). They might have accumulated lesions through the season, suffered chronic physiological stress and eventually died months after their birth. Our results thus provide evidence supporting the hypothesis that attacks have cumulative effects, aligning with findings from other recent studies. For instance, a capture–recapture analysis of individually identified calves found that more and larger gull-inflicted lesions reduced the probability of their first-year survival. The initial sightings used in those models were made in September, before any late-season deaths. If calves died at any time after they were recorded alive with gull-inflicted lesions, they would not be re-sighted in subsequent years, and the estimated first-year survival would be reduced. Our findings on local and late-season deaths complement those of Agrelo et al. (2023), and when considered together, these findings strengthen the evidence that gull attacks contribute to calf mortality.

Gull attacks on the mothers have effects on the calves. GAPM increased calf mortality 8 times more than did GAPC. Consequently, calf mortality would be expected to be 84% higher in a year of average GAPM when compared to a hypothetical year with no attacks. GAPM was also the variable that was better related to calf deaths towards the end of the calving season. The early lactation period is considered the most energetically costly period of the reproductive cycle in baleen whales (Lockyer 1981, Christiansen et al. 2018). SRW mothers lose at least 25% of their body volume in the first months of lactation when they are mostly relying on energy reserves stored in the blubber (Christiansen et al. 2018). Gull attacks interrupt resting and nursing, cause stress and increase the energy expenditure of mothers and calves (Rowntree et al. 1998, Azizeh et al. 2021). These added impacts could potentially drive calf survival to a critical point at the end of the season, when the detrimental effect of the attacks has accumulated on both mother and calf and when the energy demands of calves increase as they grow and prepare for migration (Thomas & Taber 1984, Nielsen et al. 2019). SRW mothers off Australia decrease respiration rates during this period, suggesting that mothers may reduce their metabolism to support lactation (Nielsen et al. 2019). But mothers and calves at PV have on average ~50 and ~25% higher respiration rates, respectively, as a consequence of attacks compared to undisturbed pairs off Australia (Azizeh et al. 2021). Although mothers and

calves at PV are neither thin nor malnourished (Marón et al. 2015, Christiansen et al. 2020, Fernández Ajó et al. 2020), stressed mothers might plausibly reduce their levels of energy transfer near the end of the season, increasing the already chronic stress of calves and their likelihood of death.

We found that calf mortality at PV would have been similar to the calf mortality observed for other right whale populations if no attacks had occurred. In a hypothetical year without attacks, calf mortality would have been equal to 0.11 in Golfo Nuevo and 0.07 in Golfo San José. These estimated mortalities might be equivalent to calf mortality of SRWs calving off South Africa, where the average first-year calf survival was reported to be 0.852–0.988 (Brandão et al. 2018). Similarly, the average calf mortality observed for the northern right whale *Eubalaena glacialis* from 1989 to 2003 was ~0.118 (Browning et al. 2010). However, average calf mortality at PV was 0.21 in Golfo Nuevo and 0.13 in Golfo San José, and it was influenced by gull attacks. Therefore, our results suggest that gull attacks increase calf mortality to rates that exceed those reported for other right whale populations that do not experience gull micropredation at calving grounds.

However, kelp gull attacks should not be considered the only cause of the unusually high calf mortality at PV. Extremely high calf mortality did not occur during years of extremely high intensity and frequency of attacks. Also, the average month of calf death in years with extremely high calf mortality did not always relate to gull attack pressure and frequency. This means that mortality is probably affected by one or more still unknown local or regional environmental factors, with which gull attacks may interact. Likewise, SRW calf mortality at PV was not explained by SST anomalies at Islas Georgias del Sur/South Georgia, which could be due to the small proportion of the PV whales feeding in that area in recent years. Recent studies have shown that many whales migrate from PV to feeding areas in the South Atlantic other than Islas Georgias del Sur/South Georgia (Zerbini et al. 2016, Valenzuela et al. 2018, Derville et al. 2023). However, the locations of such feeding areas and their relative quality are still being studied (Vilches et al. 2023). In contrast, the probability of calves dying and the associated unexplained variability are higher in Golfo Nuevo than in Golfo San José, suggesting that some of the unknown mortality factors may be local rather than regional. Additional studies are needed to address the relationship between food density in the South Atlantic feeding grounds and reproductive success of SRWs at PV, and

to search for other local factors that might be contributing to calf mortality.

Baleen whale populations are currently threatened by anthropogenic stressors at the local, regional and global scales. Even though some populations have recovered from whaling, climate change, entanglements, pollution and maritime traffic are major threats to their conservation (Nelms et al. 2021). Other populations and species have already started to experience opportunistic seabird attacks (Groch 2001, Harkness & Sprogis 2020, Carroll et al. 2022), similar to the few cases recorded on SRWs at PV in the 1970s. As in PV, these populations may face adversity if seabird attacks progress over time or intensify. Seabird attacks on whales' calving grounds could be especially harmful to the recovery of the species, as they would occur during a sensitive stage of the life cycle of calves and mothers. Moreover, seabird micropredation could become a critical threat if it occurs on vulnerable populations such as the northern right whales, as our results suggest that frequent and intensive micropredation may have contributed to calf mortality in a SRW population. These findings highlight the need for comprehensive and long-term management actions to reduce kelp gull attacks at PV and emphasise the value of monitoring to evaluate how interactions evolve through time. Likewise, they strongly suggest that seabird and cetacean interactions should be monitored elsewhere, as chronic micropredation can undermine the health of other marine mammal populations and challenge their conservation.

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