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Acute and chronic behavioral effects of kelp gull micropredation on southern right whale mother–calf pairs off Península Valdés, Argentina

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ABSTRACT: Kelp gulls *Larus dominicanus* (KG) feed on the skin and blubber of living southern right whales *Eubalaena australis* (SRWs) off Península Valdés (PV), Argentina. The whales respond strongly to KG micropredation by changing their immediate (acute) behavior during attacks and their overall (chronic) surfacing pattern and body posture to minimize gull exposure. The energetic and large-scale behavioral consequences of these attacks are unknown. To address this knowledge gap, we quantified the effect size of both acute (during attacks) and chronic (not during attacks) responses by comparing the respiration rates, swim speed, and nursing behavior of PV SRWs to undisturbed (control) SRW mother–calf pairs in Head of Bight, Australia, using unmanned aerial vehicle focal follows. Even when gulls were not attacking, PV SRW mothers and calves demonstrated ~50 and ~25% higher respiration rates, respectively, than whales in Australia. During attacks, PV calf respiration rates increased by an additional 10%. PV SRW mothers also frequently (>76% of respirations) exhibited irregular breathing postures, causing the whales to potentially expend extra energy by working against their natural buoyancy. Despite no significant increase in average maternal swim speed, 76 and 90% of gull attacks elicited strong behavioral reactions from mothers and calves, respectively. Overall, PV calves spent less time nursing during individual bouts compared to those in Australia but entered suckling position more frequently. Furthermore, kelp gulls seemed to show a preference for attacking previously wounded calves and at a higher rate. These chronic and acute behavioral effects may carry energetic costs, which could have long-term consequences for SRW survival and reproduction.

KEY WORDS: Behavioral disturbance · Micropredation · Respiration rate · Nursing · Swim speed · Unmanned aerial vehicle · Seabird–cetacean interactions

1. INTRODUCTION

Micropredation occurs when a predator feeds upon its victims without immediately killing them, e.g. sanguivorous organisms such as leeches *Hirudo* spp., mosquitoes *Anopheles* spp., vampire bats *Desmodus* spp., and ticks *Ixodida* spp; or creophagous organisms such as cookie-cutter sharks *Isistius brasiliensis* (Lafferty & Kuris 2002, Poulin 2011). Such attacks are transitory, where the predator takes a small amount of

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tissue from the prey and then moves on to the next victim (Poulin 2011). Micropredators can attack more than one victim and are not infectious per se but can act as vectors (mechanical or otherwise) for infectious pathogens (Lafferty & Kuris 2002, Buck 2019). The fitness cost from micropredation can be minimal if the pre-existing condition of an organism is good. However, if an organism is already in poor condition, micropredation can have a significant impact on its survival. Micropredators can also indirectly affect prey by increasing stress levels or creating open wounds (Poulin 2011). The effects of micropredation are intensity-dependent, with negative biological consequences increasing with the frequency of attacks (Lafferty & Kuris 2002). If micropredation events or subsequent avoidance strategies occur frequently or with high intensity, they can reduce prey growth, fitness, fecundity, or survival over time (Penfold et al. 2008), which in turn could have long-term population-level consequences.

There are few examples of birds exhibiting micropredatory behavior (Bowman & Billeb 1965, Attwell 1966, Schluter & Grant 1984, DeRoy 1986, Towers & Gasco 2020). While birds have been known to feed on dying cetaceans, as well as carcasses and afterbirths (Thomas 1988), interactions are typically mutualistic or commensalistic (Evans 1982). However, some seabirds such as giant petrels *Macronectes* spp. have learned to occasionally feed on the flesh of live sperm whales *Physeter macrocephalus* in sub-Antarctic waters (Towers & Gasco 2020), and silver gulls *Larus novaehollandiae* have been seen pecking the skin of live humpback whale *Megaptera novaeangliae* mother–calf pairs off Western Australia (Harkness & Sprogis 2020). Likewise, yet on a much longer timescale, kelp gulls *Larus dominicanus* (KG) have learned to gouge skin and blubber from the backs of southern right whales *Eubalaena australis* (SRW) off Península Valdés (PV), Argentina (Thomas 1988, Rowntree et al. 1998). When this behavior was first observed in the 1970s, it was believed to be less harmful to the whales because it appeared that the gulls were occasionally peeling skin and/or cyamids (Cummings et al. 1972). However, Thomas (1988) defined this behavior as parasitic and reported that the gulls were, in fact, eating skin and blubber from the dermal and subdermal layers of the whales' backs, causing large open wounds to form (McAloose et al. 2016). Hence, KGs could be considered micropredators of SRWs.

KG harassment on SRWs off PV has accelerated with the increased number of open waste-disposal sites, a food source for the gulls, and an increase in KG populations at PV (Rowntree et al. 1998, Sironi et al. 2009, IWC 2010). It is possible that human-driven land use and changes in resource availability created the environment in which KGs began using SRWs as a food source 50 yr ago. With a larger population of KGs at PV (Lisnizer et al. 2011, Yorio et al. 2016), the micropredatory behavior has become widespread, and the frequency and severity of lesions on mothers and calves has increased exponentially. Marón et al. (2015) reported that the percentage of SRW mothers and calves with gull lesions increased from 2% in the 1980s to 99% in the 2010s. In accordance with this increase in the severity of lesions, KGs have shown a preference for attacking preexisting lesions (Thomas 1988, Rowntree et al. 1998, Marón et al. 2015), particularly in previously wounded calves (M. M. Urhart, M. Sironi, and C. F. Marón pers. obs.). Calves have become the focus of gull attacks in recent years (Sironi et al. 2009, Marón et al. 2015). This could be because they have softer skin, spend more time at the surface (Sironi & Rowntree 2013), or are unable to avoid KG attacks effectively (Marón et al. 2015). Since PV SRWs experienced the highest known calf mortality of any baleen whale (Rowntree et al. 2013, Sironi et al. 2018), our study aimed to better understand the potential effects of KG harassment, which has been proposed as a potential contributing factor to calf mortality (Uhart et al. 2008, IWC 2010, 2018, Thomas et al. 2013, McAloose et al. 2016, Fernández Ajó et al. 2018).

Like predators, micropredators elicit avoidance strategies or behavioral reactions from their prey (Hart 1990, Grutter 1995). In response to gull attacks off PV, SRWs show a variety of acute and chronic behavioral reactions. Acute behaviors were first documented in the 1980s and include flinching, rolling, tail and fin slapping, and rapid travel immediately during or after an attack (Thomas 1988, Rowntree et al. 1998). Chronic avoidance behaviors occur both during attacks and when attacks are not occurring. One prominent example is a new respiration mode known as 'oblique breathing', in which the whale emerges with only its head and blowholes exposed to breathe, while the rest of the body remains below the water's surface (Fazio et al. 2015). Mother SRWs also frequently rest in an abnormal 'galleon' posture in which their backs are submerged below the water's surface, while their tails and blowholes remain above, potentially minimizing exposure to gulls (Thomas 1988, Rowntree et al. 1998, Sironi et al. 2009). These irregular postures cause the whales to work against their natural buoyancy by keeping most of their body submerged while surfacing (Nowacek et al. 2001), which is believed to carry energetic costs for mothers and calves (Thomas et al. 2013, Marón et al. 2015). Gull attacks could also be affecting the whales in a multitude of other ways, including causing pain or discomfort, disrupting nursing bouts, inducing a re-allocation of energy for wound healing, increasing stress levels, limiting the whales' ability to rest, and decreasing energy transfer from mother to calf (Thomas et al. 2013, Fernández Ajó et al. 2020). All these effects have the potential to impede calf growth and survival.

The aim of this study was to quantify both the acute and chronic behavioral responses of SRW mothers and calves to KG attacks off PV. We did this by comparing the behavior of SRWs off PV with seemingly undisturbed SRWs at the Head of Bight (HoB) breeding ground in Australia. HoB is an ideal location as it is remote, vessel traffic is prohibited during the breeding season (DSEWPaC 1999), and whales are not known to experience bird attacks (Christiansen et al. 2018, Charlton et al. 2019, Nielsen et al. 2019); therefore, the site can be used as a control for comparison to PV. To be able to infer energetic effects from gull attacks on SRWs, our response variables included respiration rates (effects on energy expenditure), swim speed (influences respiration rates and hence energy expenditure), and nursing behavior (effects on energy transfer between mother and calf). We also investigated the relationship between gull attacks and calf lesions to determine if KGs preferred attacking previously wounded calves.

2. MATERIALS AND METHODS

2.1. Study species and sites

The frequency of KG attacks and SRW behavioral data were collected off PV, Argentina (42° 23′ S, 64° 03′ W) (Fig. 1A), from 8 September to 12 November 2018 and 18 August to 5 October 2019. PV extends from the South American continent as a cape that forms 2 protected gulfs, Golfo San José and Golfo Nuevo, used by SRWs to calve and nurse their young from April to December each year (Whitehead & Payne 1981, Rowntree et al. 2001, Crespo et al. 2019). These gulfs vary in depth and can be as shallow as 5 m, which is the preferred depth used by SRW mother–calf pairs (Payne 1986). Whale-watching and recreational boating is permitted with restrictions in some areas of Golfo Nuevo (Chalcobsky et al. 2020). SRW behavioral data were also collected at HoB in South Australia (31° 29′ S, 131° 08′ E) (Fig. 1B) from 13 July to 25 September 2017 (Nielsen et al. 2019). HoB is a shallow (<20 m) coastal area used by SRWs to nurse their young from June to October each year (Charlton et al. 2019). At HoB during the breeding season, vessel traffic is not permitted (DSEWPaC 1999), and there have been no recorded occurrences of any bird species harassing or attacking SRWs since cliff-based surveys began in 1992 (Charlton et al. 2019). The Australian SRW population currently numbers >2500 animals (Bannister 2018), while the PV population was estimated at ~4000 individuals in 2010 (Cooke 2012) and ~5500 individuals in 2020 (M. Agrelo pers. comm.).

2.2. Unmanned aerial vehicle and focal follow procedures

At PV, a DJI Mavic Pro Platinum quadcopter unmanned aerial vehicle (UAV) (diameter without propellers: 33.5 cm; weight: 743 g) was used to conduct behavioral focal follows on SRW mother–calf pairs. A 12.35 megapixel sensor captured video in 4K (ultra-high definition), using a 26 mm (35 mm format equivalent) *f*/2.2 lens. In HoB, a DJI Phantom 3 Professional UAV (diameter without propellers: 35 cm; weight: 1280 g) was flown. A 12.4 megapixel camera captured video in 4K (ultra-high definition), using a

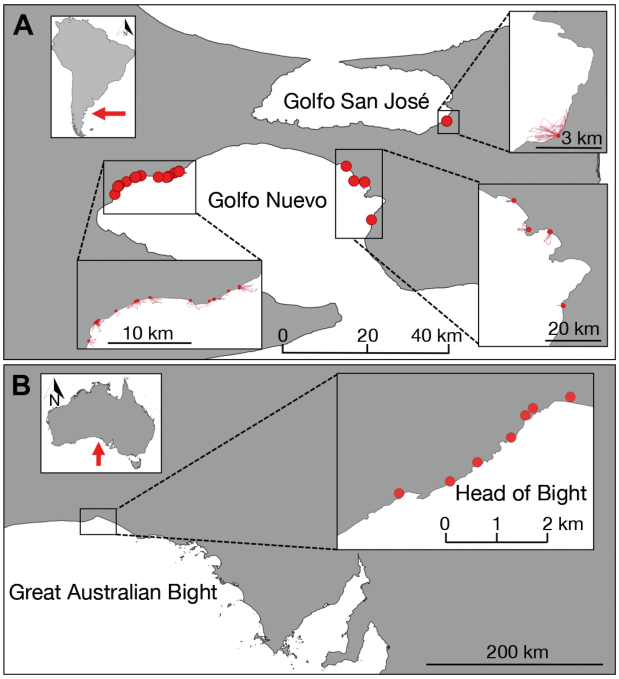

Fig. 1. Study sites at (A) Península Valdés (42° 23′ S, 64° 03′ W), Argentina, and (B) Head of Bight (31° 29′ S, 131° 08′ E), South Australia. Red dots: launch sites used to conduct unmanned aerial vehicle (UAV) behavioral focal follows on southern right whales

20 mm (35 mm format equivalent) *f*/2.8 lens. In both study areas, behavioral focal follows were performed on individual mother–calf pairs for ≥1 consecutive flight (following the protocol of Nielsen et al. 2019). The UAV was flown above the whales at an altitude of ~20 m (range: 20 to 100 m) with the UAV continuously oriented north, and the camera pointing vertically down at a 90° angle with the center of the frame on the focal mother. At this altitude, the noise of the UAV cannot be heard by the whales while close to the surface or underwater (Christiansen et al. 2016), and SRW mother–calf pairs do not respond behaviorally to the presence of the UAV, even at low altitudes (e.g. 5 m; Christiansen et al. 2020). Once the UAV was correctly positioned, a live feed of the video recording was transmitted to an iPad Air tablet which was used to maintain the position of the UAV. The UAV remained positioned above the focal mother, even if the calf swam out of frame. Each mother was identified by the unique callosity pattern on her head (Payne et al. 1983) to ensure flights in the same follow were being made over the same mother–calf pair. UAV flights were only conducted during good weather conditions (i.e. wind speeds <15 knots and no precipitation). UTC time and GPS positioning data were recorded by the UAV every 100 ms.

2.3. Video analysis

UAV videos were processed in the open source software Solomon Coder (https://solomon.andraspeter.com/). Instantaneous (i.e. a count of a zero-duration, pre-defined behavioral event) and continuous behaviors (i.e. a pre-defined behavioral event with a start and end time) (Altmann 1974) were noted during video playback (Table 1). For each video, water turbidity was scored as 0, 1, 2, or 3, with 0 signifying excellent visibility (e.g. whales clearly visible and all behaviors likely observable) and 3 signifying poor visibility (e.g. whales only visible when at the surface of the water) (Nielsen et al. 2019). In situations where the mother or calf was absent or could not be located (e.g. post-submersion in turbid water or the calf swam out of frame), it was noted for the individual and subtracted from the duration of the video before analysis. Calf body length (in pixels) was measured from still frames taken from UAV recordings and compared to maternal body length (hereafter 'ML', in pixels) to determine relative calf body length, following the methods of Christiansen et al. (2018).

To measure chronic effects of gull attacks, respiration events of SRW mothers and calves were re-

Table 1. Events (instantaneous and continuous) recorded during unmanned aerial vehicle (UAV) focal follows of southern right whale mother–calf pairs off Península Valdés, Argentina, and Head of Bight, Australia

Event	Sampling type	Definition
Respirations		
Regular respiration	Instantaneous	The animal exposes its back and blowholes above the surface and breathes. Can be identified with the clear vapor expelled, or by clearly observing the blowholes open and close while at the surface
Irregular respiration	Instantaneous	The animal exposes its head and blowholes, while keeping the back and body submerged. Usually emerges vertically or at a 45° angle. Also known as oblique breathing (Fazio et al. 2015)
Mother–calf interaction		
Apparent nursing	Continuous	Any time a calf is under the mother and is observed with its head close to the mammary gland area (Nielsen et al. 2019). Due to the vertical position of the UAV above the whale, direct transfer of milk could not be confirmed (Whitehead & Mann 2000), and the behavior was therefore recorded as 'apparent nursing'. This definition of nursing may represent an overestimation of actual time spent suckling (Nielsen et al. 2019)
Gull interactions		
Successful attack	Instantaneous	An instance in which a kelp gull initiated an attack, and the bill of the gull contacted the body of the SRW (Sironi et al. 2009)
Unsuccessful approach	Instantaneous	An instance in which a kelp gull approached a whale, but the whale submerged before the gull could reach it (Sironi et al. 2009)
Reaction to a gull interaction (successful or unsuccessful)	Continuous	The duration of an observed reaction to a successful attack or unsuccessful gull approach. Typical reactions include flinching (i.e. a rapid 'startled' submersion), submerge (i.e. individual immediately descends from surface of water), acceleration (i.e. initiated forward motion or increased speed), tail or fin slapping, and rolling (i.e. individual rolls on longitudinal axis, submerging dorsal surface) (Thomas 1988, Rowntree et al. 1998)

corded and categorized as 'regular' or 'irregular', where instances of 'oblique breathing' (Fazio et al. 2015) were classified as 'irregular' (Table 1). To measure acute effects, gull interactions were recorded and categorized as 'successful attacks' (i.e. any time in which the bill of a KG contacted the body of the SRW) or 'unsuccessful approaches' (i.e. any time in which a KG approached or targeted a whale, but the whale submerged before the gull could reach it) (Sironi et al. 2009, Table 1). Interactions (attacks or approaches) with mothers and calves were recorded separately, and the duration of an observable reaction (i.e. flinching, rolling, or rapid submersion or acceleration; Thomas 1988, Table 1) was noted.

'Apparent nursing' was recorded as a continuous variable starting at the time a calf was positioned underneath its mother with its head close to the mammary gland area (Nielsen et al. 2019) (our Table 1). Due to the vertical position of the UAV above the whale, direct transfer of milk could not be confirmed (Whitehead & Mann 2000); therefore, the behavior was recorded as 'apparent nursing'. This definition of nursing may represent an overestimation of actual time spent suckling (Nielsen et al. 2019).

2.4. Consolidation and classification of flight data

Consecutive flights over the same mother–calf pair in one sample period (typically over a period of a few hours) were combined to establish one continuous focal follow. Each follow was classified into one of 3 gull conditions: 'HoB', which represented the undisturbed SRW population in Australia with no known bird attacks (control), 'PV-A', which were flights from PV with no recorded gull interactions, and 'PV-P', which were flights from PV with recorded gull interactions. If a gull attack occurred at any point within a focal follow, the time before the attack was considered PV-A, and the rest of the follow was considered PV-P. Additionally, any consecutive flights post-attack were considered PV-P.

2.5. Response variables

We investigated the effect of gull condition ('HoB', 'PV-A', or 'PV-P') on maternal respiration rate, calf respiration rate, maternal swim speed, and time spent in apparent nursing. The mean value of each behavioral variable was calculated for each condition within a follow.

2.5.1. Respiration rate. Respiration rates (breaths min^{-1}) were calculated as the total (both 'regular' and 'irregular') number of breaths that occurred under a given condition during the follow divided by the time spent under that condition in the follow. Focal follows of short duration can lead to an over- or underestimation of cetacean respiration rates (Williams & Noren 2009, Christiansen et al. 2014). By systematically removing shorter follows, at increments of 1 min, and fitting a linear model (LM) between respiration rate and follow duration, it was possible to identify this minimum threshold in duration (where the slope parameter is zero) (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m668p133_supp.pdf). All follows below this duration (5 min for both mothers and calves; Fig. S1) were removed from analyses.

2.5.2. Swim speed. The horizontal distance traveled by the UAV was used as a proxy for the distance traveled by the focal mother due to the continuous positioning of the UAV above the mother for the duration of the focal follow. The UAV positions were recorded by an iPad Air tablet and converted into a .csv file for analysis. We sub-sampled the positional data to one position every 15 s to avoid overestimating distance due to small corrective movements made by the UAV during flights. Swim speed was then calculated by dividing the total distance traveled by the mother by the total duration of the time spent under a condition in a follow. To remove erroneous data, swim speed measurements exceeding $3\ \text{m s}^{-1}$ ($10.8\ \text{km h}^{-1}$) were excluded as no SRW has ever been recorded swimming above this limit (Nielsen et al. 2019, Mackay et al. 2020). Visual inspections of histograms of maternal swim speed confirmed that the majority (98.3%) of swim speed measurements were below this threshold, with 95.9% of swim speeds being below $1\ \text{m s}^{-1}$ (Fig. S2). Calf swim speed was not examined, as its speed was dependent on the mother and the UAV focal follow was focused on the mother.

2.5.3. Nursing. Effects of gull micropredation on energy transfer were identified by estimating the nursing rate (number of nursing bouts min^{-1}) and the nursing bout duration (average duration of individual nursing bouts). Apparent nursing (the proportion of time spent nursing) was calculated by multiplying the nursing rate by the nursing bout duration.

2.6. Calf lesions

To determine if KGs showed a preference for attacking calves with existing lesions on their backs, we investigated the relationship between the rate of attack and the area of lesions on the calf's back. We used the same approach as Marón et al. (2015) to estimate the percentage of the calf's back that was damaged by lesions. First, a still frame was extracted from each focal follow in which the dorsal surface of the calf was clearly visible. Only images in which more than 50% of the whale's back was visible above the surface were used for examination. ImageJ (https://imagej.nih.gov/ij/) was then used to measure the pixel area on the whale's back covered by lesions. Using the same image, we also measured the total back area of the calf, from immediately behind the blowhole to the beginning of the tail stock. The percentage of the area of the back that was covered by lesions was then calculated (for details, see Marón et al. 2015).

2.7. Statistical analysis

All statistical analyses were carried out using R v.3.5.3 (R Core Team 2019). Calf length relative to its mother has been shown to influence all 3 response variables (Taber & Thomas 1982, Thomas & Taber 1984, Nielsen et al. 2019) and was therefore included as an explanatory variable in the respiration rate, swim speed, and nursing analyses. In all models, maternal ID was included as a random effect to account for temporal autocorrelation between flights over the same mother–calf pair and individual variation in behavior.

2.7.1. Respiration rate. The effect of gull condition ('HoB', 'PV-A', or 'PV-P') on mother and calf respiration rates was investigated using linear mixed effects models (LMMs) ('nlme' package; Pinheiro et al. 2020). Since respiration rates in whales are positively correlated with swim speed (Williams & Noren 2009, Christiansen et al. 2014), maternal swim speed was also included as an explanatory variable. Mean respiration rates were calculated with mothers swimming at an average speed of 0.35 m s^{-1} and with an average-sized calf of 45% ML. Effect of day-of-the-year on the proportion of irregular breathing for both mothers and calves was also examined, using a binomial generalized linear model (GLM) ('nlme' package; Pinheiro et al. 2020).

2.7.2. Swim speed. A LMM was used to investigate the effect of condition on maternal swim speed.

2.7.3. Apparent nursing. To explore the effect of gull condition on time spent nursing, 2 separate LMMs were used. In the first model, the effect of condition on the rate of nursing bouts in a follow was investigated. In the second model, the effect of condition on the average duration of nursing bouts was investigated. Nursing bout duration was log transformed to conform to the assumptions of the LMM. The effect of gull attacks on the time spent nursing was then calculated by multiplying the nursing bout rate with the average nursing bout duration for each condition separately. For both LMMs, relative calf body length was included as an explanatory variable (Nielsen et al. 2019). For videos in which turbidity was classified as ≥2, nursing was excluded from analysis due to the inability to identify the calf in nursing position.

2.7.4. Calf lesions. A binomial GLM ('nlme' package; Pinheiro et al. 2020) was used to examine the probability of a calf being attacked by KGs during a focal follow, as a function of the percentage of the back covered by lesions. For follows which included one or more attacks on a calf, the rate of attack (number of attacks $\min^{-1}$) as a function of the percentage of lesions on the calf's back was investigated using a LM. To bind the response variable to positive values, the rate of KG attacks was log transformed. We also investigated if there was an effect of day-of-the-year on the frequency of attacks, using a LM. Visual inspections of scatterplots revealed a positive bias in attack rates for shorter videos. To remove this bias, we systematically removed shorter follows, at increments of 1 min, and fitted LMs between gull attack rates and follow duration for mothers and calves separately (Fig. S3). The minimum thresholds were identified as the duration at which the slope parameters of the LMs were zero and there was no longer a bias in attack rates due to follow duration. This occurred at 8 and 6 min duration for mothers and calves, respectively (Fig. S3). All follows below these durations were removed from analyses.

For all analyses (respiration rate, swim speed and apparent nursing), model selection was performed using Akaike's information criteria (AIC). Using the 'MuMIn' package (Barto 2018), the marginal (R^2_m) and conditional (R^2_c) R^2 of the model fit of the LMM were obtained. R^2_m is the variance explained by the fixed effects, and R^2_c is the variance explained by both the fixed and random effects (i.e. the entire model) (Nakagawa & Schielzeth 2013). Model validation tests were conducted to identify potential violations of the assumptions of the model. Homogeneity in residuals was inspected in scatterplots of residuals versus fitted values and against each explanatory variable in the model. Normality of residuals was interpreted from residual histograms. All model assumptions were fulfilled.

3. RESULTS

3.1. Sample size

Off PV, fieldwork was conducted on 23 days in 2018 and 12 days in 2019, within a sampling period of 65 d (8 September to 12 November) in 2018 and 48 d in 2019 (18 August to 5 October). There were 35.9 h of usable footage from 132 flights (2018: 98; 2019: 34) which were conducted over 69 mother–calf pairs (2018: 52; 2019: 17). The individual flight time ranged from 2.4 to 30.8 min (mean ± SD: 16.3 ± 4.81 min). The number of flights over the same mother–calf pair (i.e. a focal follow) ranged from 1 to 3 (median: 2; mean duration: 31 min).

In HoB, fieldwork was conducted on 35 days, within a sampling period of 75 d (13 July to 25 September) in 2017. A total of 281 flights were conducted over 51 individual mother–calf pairs, amounting to approximately 58.7 h of usable footage. The individual flight time ranged from 0.42 to 20.1 min (12.5 ± 3.22 min). The number of flights over the same mother–calf pair (i.e. a focal follow) ranged from 1 to 16 (median: 4; mean duration: 72 min). In both areas, calf relative body length ranged from 29 to 60% of ML.

3.2. Gull attacks

Off PV, there were a total of 132 flights: 64 (48.5%) included ≥1 gull interaction (successful attack or unsuccessful approach) on either the mother, calf, or both, and 68 (51.5%) did not record any gull interaction. Of the 64 flights where interactions were recorded, successful attacks on the mother were recorded in 26 (40.6%), while successful attacks on the calf were recorded in 59 (92.2%). In total, there were 409 recorded interactions. Of these interactions, 68 (16.6%) were aimed at the mother, with 37 (54.4%) successful attacks and 31 (45.6%) unsuccessful approaches. In a total of 341 (83.4%) attacks targeting the calf, 222 (65.1%) were successful attacks and 119 (34.9%) were unsuccessful approaches. In many cases, both mother and calf were attacked in the same follow.

Across all focal follows off PV, SRW mothers experienced a successful gull attack on average every 56.8 ± 8.0 min while calves were successfully attacked on average every 8.4 ± 3.4 min (total number of successful attacks / total duration of all PV-P and PV-A follows). In response to these attacks, behavioral reactions (i.e. flinching, rolling, or rapid submersion or acceleration; Table 1) by the mother were recorded on 28 occasions (75.7%), while 198 reactions (89.2%) were recorded for calves. The mean duration of a reaction by the mother was 8.1 ± 7.8 s (range: 2.4–42.4 s) and 17.0 ± 16.6 s (range: 1.6–77.0 s) for calves.

The rate of gull attacks did not vary throughout the season (as a function of day-of-the-year) for mothers (LM: $F_{1,118} = 0.455$, $p = 0.501$), and marginally decreased through the season for calves (LM: $F_{1,117} = 3.853$, $p = 0.052$) at a rate of −0.002 attacks d^{-1} (SE = 0.001) (Fig. S4, Table S1). With the relative calf body length increasing with day-of-the-year (LM: $F_{1,192} = 31.713$, $p < 0.001$; Fig. S5A, Table S1) at a rate of 0.091% ML d^{-1} (SE = 0.016), we also found a negative effect of calf body length on the rate of gull attacks off PV (LM: $F_{1,117} = 8.803$, $p = 0.004$; Fig. S5B, Table S1) at a rate of −0.131 (SE = 0.044) attacks for every 10% increase in relative calf body length.

3.3. Oblique ('irregular') respiration posture

A total of 76.1% of all breaths from PV mothers were irregular, while 41.8% of all breaths from calves were irregular. The proportion of irregular breaths showed no variation based on day-of-the-year for mothers (binomial GLM: $z = -1.499$, $p = 0.134$, $n = 178$) (Fig. S6A, Table S1). For calves, the proportion of irregular breaths decreased through the season (binomial GLM: $z = -2.732$, $p = 0.006$, $n = 193$) from 54.1 to 21.9% from day 229 (17 August) to day 315 (11 November) (Fig. S6B, Table S1).

3.4. Maternal respiration rate

Maternal respiration rate differed significantly between gull conditions ('HoB', 'PV-A', or 'PV-P') (LMM: $F_{2,198} = 19.0$, $p < 0.001$) and was also affected by relative calf body length (LMM: $F_{1,198} = 13.7$, $p < 0.001$) and maternal swim speed (LMM: $F_{1,198} = 38.1$, $p < 0.001$, (Table S1). The variance explained by the fixed effects (R^2_m) was 28.1%, whereas the variance explained by both the fixed and random effects (R^2_c) was 36.5%. The mean respiration rate for HoB mothers was 0.46 (SE = 0.019) breaths min^{-1}, for PV-A mothers respiration rate was 0.69 (SE = 0.039) breaths min^{-1}, and for PV-P mothers it was 0.68 (SE = 0.041) breaths min^{-1} (Fig. 2A). Maternal respiration rate decreased with relative calf body length at a rate of −0.093 (SE = 0.0252) breaths min^{-1} per 10% increase in relative calf body length (Fig. 2B). Maternal

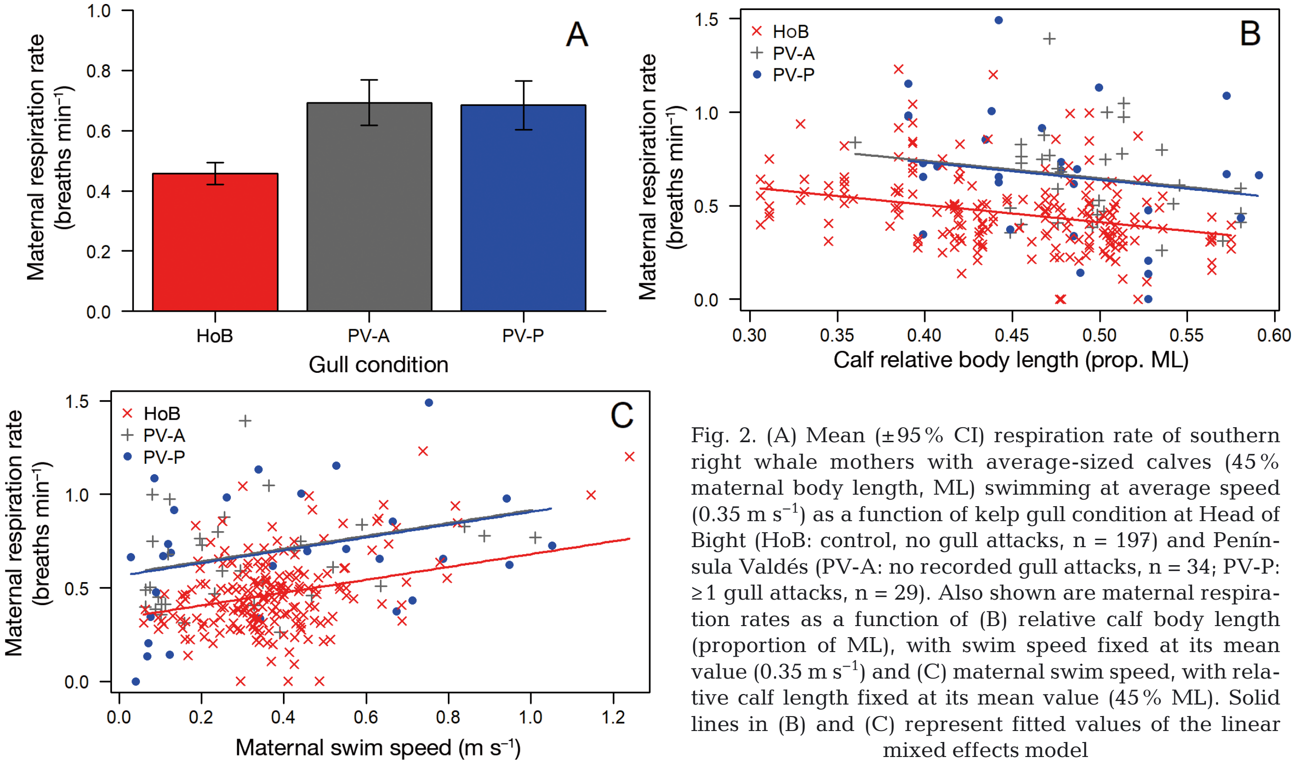

Fig. 2. (A) Mean (±95% CI) respiration rate of southern right whale mothers with average-sized calves (45% maternal body length, ML) swimming at average speed (0.35 m s^{-1}) as a function of kelp gull condition at Head of Bight (HoB: control, no gull attacks, n = 197) and Península Valdés (PV-A: no recorded gull attacks, n = 34; PV-P: ≥1 gull attacks, n = 29). Also shown are maternal respiration rates as a function of (B) relative calf body length (proportion of ML), with swim speed fixed at its mean value (0.35 m s^{-1}) and (C) maternal swim speed, with relative calf length fixed at its mean value (45% ML). Solid lines in (B) and (C) represent fitted values of the linear mixed effects model

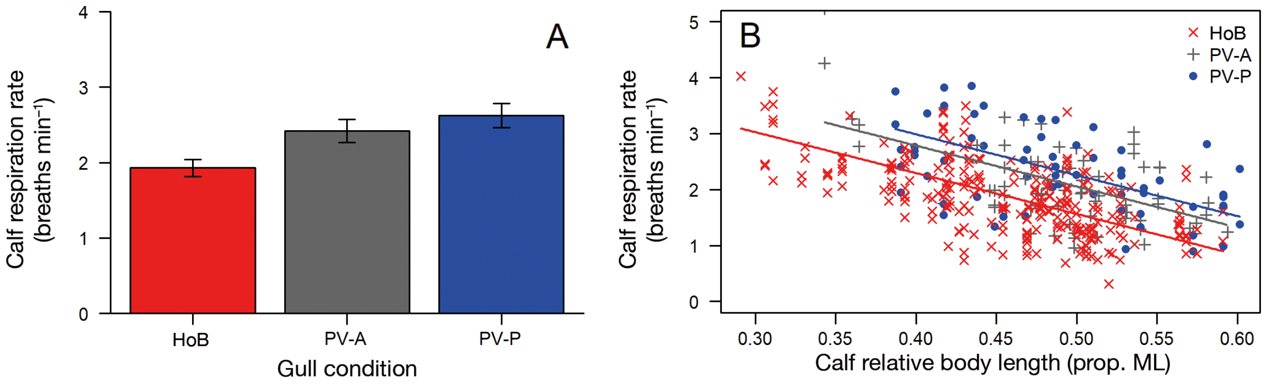

Fig. 3. (A) Mean (±95% CI) respiration rate of an average-sized southern right whale calf (45% maternal length, ML) as a function of kelp gull condition and (B) calf respiration rate as a function of relative calf body length. Solid lines: fitted values of the linear mixed effects model (see Fig. 2 for abbreviations. HoB, n = 266; PV-A, n = 69; PV-P, n = 62)

respiration rate increased at a rate of 0.343 (SE = 0.067) breaths min^{-1} per m s^{-1} increase in maternal swim speed (Fig. 2C).

3.5. Calf respiration rate

Calf respiration rate differed significantly between gull conditions (LMM: $F_{2,327} = 22.9$, $p < 0.001$) and was also affected by relative calf body length (LMM: $F_{1,327} = 193.1$, $p < 0.001$) (Table S1). R^2_m was 42.3%, whereas R^2_c was 62.5%. The mean respiration rate for HoB calves was 1.93 (SE = 0.057) breaths min^{-1}, for PV-A calves it was 2.42 (SE = 0.077) breaths min^{-1}, and for PV-P calves it was 2.62 (SE = 0.082) breaths min^{-1} (Fig. 3A). Calf respiration rate decreased at a rate of −0.73 (SE = 0.053) breaths min^{-1} per 10% increase in relative calf body length (Fig. 3B). There was no significant effect of maternal swim speed on calf respiration rate.

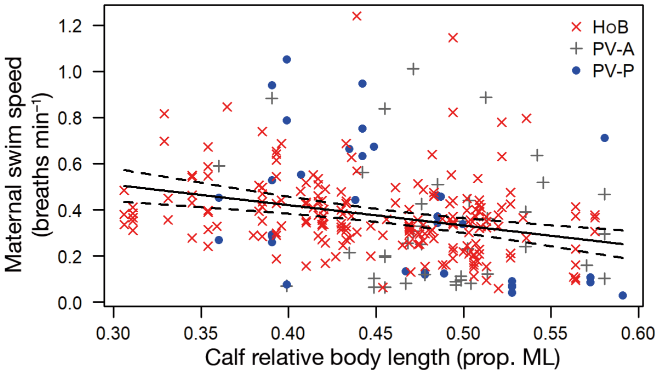

Fig. 4. Southern right whale maternal swim speed as a function of relative calf body length (see Fig. 2 for abbreviations; HoB, n = 202; PV-A, n = 39; PV-P, n = 34). Solid line: fitted value of the linear mixed effects model; dashed lines: 95% CIs (n = 275)

3.6. Swim speed

There was no effect of condition on maternal swim speed. The only variable affecting swim speed was relative calf body length (LMM: $F_{1,215}$ = 18.1, $p < 0.001$) (Table S1). The variance explained by relative calf body length (R^2_m) was 7.7%, whereas R^2_c was 14.9%. Maternal swim speed off PV decreased at a rate of −0.088 (SE = 0.021) m s^{-1} for every 10% increase in calf body length (Fig. 4).

3.7. Apparent nursing

There was a marginally significant effect of condition on apparent nursing rate (LMM: $F_{2,145}$ = 3.00, p = 0.053) (Table S1). R^2_m was 2.9% whereas R^2_c was 20.7%. The nursing rate in PV-A was 0.239 (SE = 0.043) bouts min^{-1}, which was higher than in PV-P and HoB where the nursing rates were 0.104 (SE = 0.053) and 0.137 (SE = 0.023) bouts min^{-1}, respectively (Fig. 5A). There was no significant difference in nursing rate between PV-P and HoB (Fig. 5A). Nursing bout duration also differed between conditions (LMM: $F_{2,80}$ = 5.31, p = 0.007) (Table S1). R^2_m was 8.3% whereas R^2_c was 10.1%. The average nursing bout duration in HoB was 0.596 min (95% CI: 0.51–0.69 min), which was significantly higher than PV-A, which was 0.341 min (95% CI: 0.25–0.46 min) (Fig. 5B). The nursing bout duration in PV-P was 0.505 min (95% CI: 0.34–0.74 min) and did not differ significantly from PV-A and HoB (Fig. 5B). Multiplied together, the mean proportion of time spent nursing was 8.2% in HoB, 8.1% in PV-A, and 5.3% in PV-P (Fig. 5C).

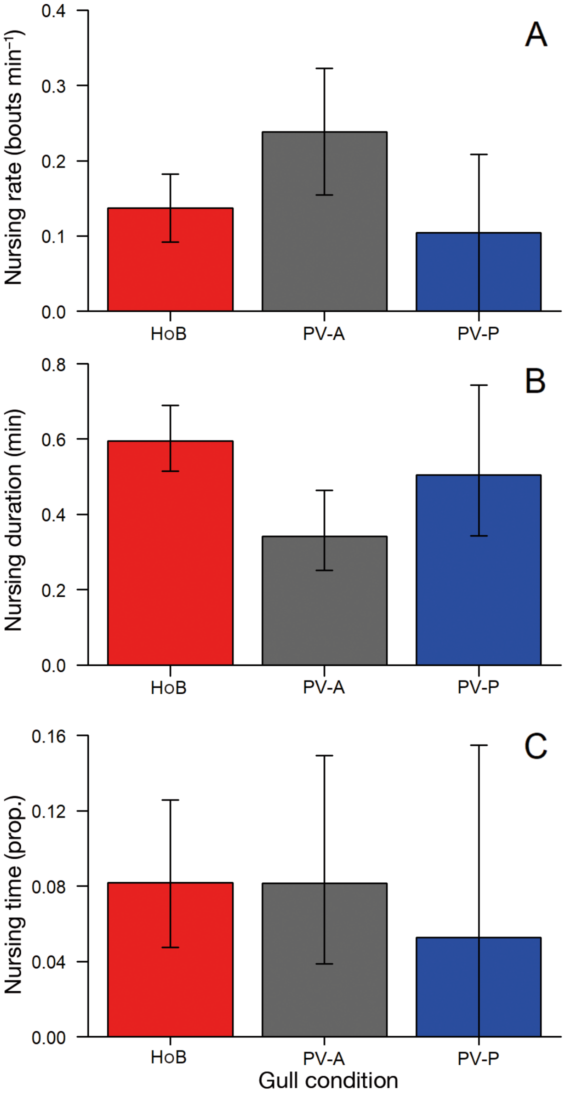

Fig. 5. Mean (±95% CI) southern right whale (A) nursing rate (HoB, n = 149; PV-A, n = 27; PV-P, n = 19), (B) nursing bout duration (HoB, n = 88; PV-A, n = 19; PV-P, n = 12), and (C) calculated mean proportion of time spent nursing as a function of kelp gull condition (see Fig. 2 for abbreviations)

3.8. Calf lesions

The area of the calves' backs covered by lesions had a significant effect on both the probability of a gull attack (binomial GLM: z = 2.235, p = 0.025, n = 42) and the rate of attacks (LM: t = 3.576, p = 0.006, n = 11; Table S1). The probability of an attack increased from ~10.5 to ~68.7% and the rate of attacks increased from ~0.108 to ~0.948 attacks min^{-1} as the area of lesions on the calves' backs increased from 0 to 13.3% (Fig. S7) (see Table S1 for model parameter values).

4. DISCUSSION

Southern right whale mother–calf pairs off PV exhibited both acute and chronic behavioral changes in response to KG attacks. By comparing their behavior to SRW mothers and calves in HoB, Australia, where no bird species are known to attack SRWs, we were able to distinguish and quantify the effect sizes of the behavioral changes displayed by PV SRWs. Acute (PV-P) effects included post-attack reactions (i.e. flinching, rolling, or rapid submersion or acceleration; Thomas 1988, our Table 1), an immediate increase in respiration rate of calves (PV-P vs. PV-A) during and after attacks, and a decrease in the proportion of time spent nursing. Gull attacks also caused chronic effects on PV SRWs, including consistent irregular breathing posture and an overall increase in respiration rates of both mothers and calves off PV, even when gull attacks were not occurring (PV-A vs. HoB). Calves in PV also displayed shorter but more frequent nursing bouts (PV-A vs. HoB) as well as a decrease in overall time spent nursing during gull attacks (PV-P vs. PV-A).

4.1. Acute effects

Gull attacks elicited a behavioral response 76 and 90% of the time for mothers and calves, respectively. For more details about the behavioral reactions of SRWs to gull attacks, see Thomas (1988), Rowntree et al. (1998), Sironi (2004), Sironi et al. (2009), Thomas et al. (2013), IWC (2010, 2015) and Fazio et al. (2015). Although we documented no significant increase in average maternal swim speed off PV compared to HoB, mothers and calves often accelerated rapidly in response to a successful gull attack to avoid further injury. Thomas & Taber (1984) found that mothers with newborn calves swam faster than mothers with larger calves, and the same was shown at both PV and HoB (Nielsen et al. 2019). Neonate calves (≤1 mo) are thinner, and hence less buoyant, than larger (1 to 3 mo) calves (Christiansen et al. 2018). This might require neonates, and consequently their mothers, to swim at a faster pace to stay afloat. Nielsen et al. (2019) further proposed that SRW mothers might reduce their swim speed as the calves grow larger to compensate energetically for the concurrent increase in metabolic rate (Christiansen et al. 2018). By swimming slower, females can reduce their own energy expenditure and maintain a steady linear decrease in body volume (and mass) through the breeding season (Christiansen et al. 2018).

The respiration rate of calves off PV increased by an additional 10% when gull attacks occurred (PV-P vs. PV-A). Because respiration rates of cetaceans are positively correlated with metabolic rates (Yazdi et al. 1999), this could represent an increase in the energy expenditure due to immediate post-attack responses. Gull attacks also led to a reduction in time spent apparently nursing by 35% (PV-P vs. PV-A), which suggests that energy transfer between mother and calves could be negatively affected.

4.2. Chronic effects

Even when gull attacks were not occurring (PV-A), the average respiration rates of SRW mothers and calves off PV were 50 and 25% higher than in HoB, respectively. This may denote an increase in energy expenditure, but since the respiratory physiology of free-ranging cetaceans is poorly understood (Wahrenbrock et al. 1974, Kooyman et al. 1975, Sumich 2001, Fahlman et al. 2016), it is possible that SRWs off PV are compensating by altering their breathing behavior. For example, if PV SRWs are taking more frequent breaths of smaller volumes, then the observed increase in respiration rate may not necessarily represent an increase in energy expenditure. However, if we assume that the amount of air intake per breath is constant, as many other studies of baleen whales do (Sumich 1983, Armstrong & Siegfried 1991, Folkow & Blix 1992, Blix & Folkow 1995, Christiansen et al. 2014), then we can expect the higher respiration rates off PV of 50 and 25% for mothers and calves, respectively, to reflect an increase in energy demand due to gull harassment. To put the magnitude of this behavioral effect into context, Christiansen et al. (2014) found that minke whales *Balaenoptera acutorostrata* experienced a ~27% (0.88 to 1.12 breaths min^{-1}) increase in respiration rates in response to whale-watching boats, which corresponded to an equal 27.6% increase in estimated energy expenditure. This could suggest that the 25 and 50% increases in respiration rates demonstrated by PV SRWs when gull attacks are not occurring (HoB vs. PV-A) may have similar or higher energetic consequences, which could negatively affect individual body condition (energy reserves) and vital rates (survival and reproductive success). Since SRW mothers on the breeding ground rely on stored energy reserves to cover both their own energy requirements and that of their dependent calf, the observed increase in energy expenditure due to gull harassment constitutes a significant increase in the overall energetic costs of

SRW mothers. Although a SRW mother could potentially offset some of these added costs by reducing their own activity level (swim speed) (Nielsen et al. 2019), this was not evident from our swim speed analyses. Hence, gull harassment is likely to lead to a reduction in maternal body condition, which could negatively affect energy transfer to the calf and, consequently, calf growth rates (Christiansen et al. 2018) and possibly survival. Research into the body condition of SRW mother–calf pairs in relation to gull attack rates (i.e. the area of the lesions on their backs) and calf survival is therefore urgently needed to quantify the relationship between gull harassment and SRW vital rates (survival and reproduction).

It is possible that oceanographic differences between Argentina and Australia, which vary in sea surface temperature (11 vs. 15°C, respectively), could influence heat loss and hence energy expenditure, especially in young calves which might lack sufficient blubber insulation. This could be exacerbated by the loss of skin experienced through kelp gull wounding, which may compromise thermoregulation, disrupt homeostasis, and increase loss of body fluids (Namdar et al. 2010, Thomas et al. 2013, Fernández Ajó et al. 2020). Another factor to consider is that the higher chronic respiration rates of calves at PV (PV-A vs. HoB) may be the result of overall higher stress levels due to frequent gull harassment (Fernández Ajó et al. 2018, 2020). Chronic, disturbance-induced high stress levels have been shown to affect metabolic processes in northern resident killer whales *Orcinus orca* (Williams et al. 2006) and respiration rates in minke whales (Christiansen et al. 2014), as well as in terrestrial animals (Willner 1997, Creel et al. 2002, Grippo & Johnson 2009, Dulude-de Broin et al. 2020). Consequently, increased metabolic rates can lead to long-term health issues and suppressed immune functions (Dhabhar 2009, 2014, Fernández Ajó et al. 2020). To better understand the relationship between gull-induced stress and respiration rates (i.e. possible increase in metabolic rates), a comparison of calf respiration rates between PV and other areas without gull attacks along the coast of Argentina and Uruguay should be undertaken.

The increasing KG attack rates off PV have led to SRWs adopting irregular resting and breathing postures, including 'oblique breathing' in both adults and calves (Fazio et al. 2015) and the 'galleon' position in adults (Thomas 1988, Rowntree et al. 1998, Sironi et al. 2009). 'Oblique breathing' has not been documented in other SRW calving grounds globally (Fazio et al. 2015) including HoB and therefore can be interpreted as a gull avoidance strategy adopted by SRWs that use the PV calving ground. Fazio et al. (2015) reported that this unique breathing posture likely evolved in SRWs off PV around 2008 or 2009 and was observed in as many as 77% (n = 284) of sightings on the western side of Golfo Nuevo in 2013. This is supported by our study, where >76% of respirations by mother SRWs were oblique, while calves performed this avoidance behavior only 41% of the time. Newborn calves have higher respiration rates than adults (Nielsen et al. 2019), and hence spend more time near the surface where they are exposed to gull harassment (Sironi & Rowntree 2013). Also, calves may not consistently practice avoidance techniques, such as oblique breathing, while mothers have had years off PV to learn these tactics (Marón et al. 2015). This is supported by our data, which shows that SRW mothers off PV experienced a constant rate of gull attacks through the season and maintain the same frequency of oblique breathing. In contrast, the rate of gull attacks decreased for calves through the breeding season, as did the proportion of irregular breaths. The reduction in gull attacks on SRW calves is likely a result of KGs starting to nest in October each year, which results in them remaining nearer to their colony (Bertellotti & Yorio 1999). That no reduction in attack rate was observed for SRW mothers is likely due to the already low attack rate on mothers.

Nowacek et al. (2001) showed that right whales exhibit positive buoyancy near the water's surface, and Christiansen et al. (2019) showed that the average density of adult SRWs (755 kg m^{-3}) is below that of sea water. Hence, when performing irregular surfacings, SRWs are working against their natural buoyancy, which might be energetically costly (Fazio et al. 2015). Calves performed irregular surfacings less than half of the time. This could be because they are smaller and/or more buoyant compared to adults and may therefore struggle to submerge their backs deeply enough to avoid gull attacks (Sironi et al. 2009, Marón et al. 2015). Furthermore, Rowntree et al. (1998) observed a recovery time of at least 30 min, but closer to 60 min, before SRW mother–calf pairs returned to typical behaviors post-attack. Since the total focal follow duration over a single whale off PV seldom exceeded 30 min, this suggests that the whales most likely did not return to undisturbed behavior at any point during our focal follows once they were observed to have been attacked. Moreover, these recovery times were calculated when avoidance behaviors, such as oblique breathing and galleon position, were rare (Rowntree et al. 1998) and gull attacks were less frequent (Sironi et al. 2009, IWC 2015, Marón et al. 2015). These behaviors, especially oblique breathing, are now much more common, and SRWs face more intense attack rates. At the same time, adults adapting the galleon position have likely reduced their individual exposure to gull attacks over the years (Fazio et al. 2015). Additionally, the intensity of gull attacks likely differs spatially within the PV study area. Recovery time should hence be re-estimated to assess the total time SRWs spend under gull-induced disturbance off PV, as well as avoidance tactics used by different reproductive classes and potential spatial differences in attack rates.

We observed calves off PV spending less time apparently nursing in the presence of gulls. Additionally, even at times when gull attacks were not occurring (PV-A), SRW calves off PV spent less time nursing during a specific nursing bout compared to calves in HoB. To potentially compensate for the reduced nursing bout durations, calves off PV instead initiated nursing bouts at a higher frequency compared to HoB. Calves in PV may also be compensating by nursing at night, when it is presumed that gulls are attacking less frequently or not at all. In both sites, however, nursing may have been over- or underestimated due to the difficulty of confirming the direct transfer of milk between mother and calf (Whitehead & Mann 2000) when using an UAV (Nielsen et al. 2019). Nursing could also have been overestimated because calves will often position themselves under their mothers during an attack (Nielsen et al. 2019), and it is difficult to differentiate this behavior from apparent nursing from an aerial view. During the calving season, SRW mothers need to transfer large amounts of energy to their calf to sustain their rapid growth (on average 3.2 cm d^{-1} in length and 0.081 m^3 d^{-1} in volume) during the first 3 to 4 mo of life (Christiansen et al. 2018). The cumulative energetic effects of increased energy expenditure and reduced nursing due to gull harassment could compromise the growth rate of the calves, which could ultimately influence weaning time and survival (McMahon et al. 2000, Miller et al. 2011, Christiansen et al. 2018). However, Marón et al. (2021) found no decline in blubber and lipid measures of dead SRW calves in high-mortality years and no differences in fatty acid composition between living and dead calves (Marón et al. 2020). Additionally, there was no difference in the area of lesions on dead SRW calves in high- and low-mortality years (Marón et al. 2015). This suggests that maternal energy and nutrient transfer to calves is not compromised. Additionally, despite the fasting that is generally associated with the calving ground and the low concentrations of zooplankton (Hoffmeyer et al. 2010), PV SRWs feed opportunistically on zooplankton at the sea surface, and later in the season, at deeper depths to access higher densities of prey (D'Agostino et al. 2016). This could potentially be an attempt to compensate for increased energy expenditure. Future studies could utilize video tag-based research methods (e.g. CATS tags) (Cade et al. 2016, Tackaberry et al. 2020) to identify 'known nursing' bouts, determine the efficacy of nursing, and estimate maternal energy transfer at both PV and HoB.

4.3. Calf lesions and mortality

In agreement with earlier studies (Sironi et al. 2009, Marón et al. 2015), we found that calves were the main target of gull attacks off PV. We further found that KGs were more likely to attack calves with a larger surface area of existing lesions and at a higher rate, which is consistent with observations in previous studies (Thomas 1988, Rowntree et al. 1998, Marón et al. 2015). This means that the relative disturbance of KGs to SRW calves off PV is heterogeneous, with some calves (potentially those that are less effective at practicing avoidance behaviors) experiencing considerably more harassment than others. The increase in attack rate and intensity on previously wounded calves most likely exacerbates existing negative effects from gull attacks. The correlation between cortisol, a proxy for stress, and degree of wounding in the baleen of dead calves in PV showed that highly wounded calves had increased cortisol levels (Fernandez Ajó et al. 2020). While calf hormone levels may reflect calf-produced and maternally transferred cortisol (Fernández Ajó et al. 2018), this has not yet been tested. Notwithstanding, calves must reallocate precious time and energy needed for development, growth, and rest into maintaining homeostasis (mitigating effects from high cortisol levels) and wound healing.

Baleen whales are *K*-selected (Pianka 1970) and have evolved to maximize adult survival by minimizing predation risks at all costs (Stearns 1992). Therefore, they often respond strongly towards even minor, non-lethal stressors, since individual costs of antipredator behaviors are significantly smaller than the potential cost of actual predation (Bouskila & Blumstein 1992, Sinclair & Arcese 1995, Christiansen & Lusseau 2014). Although KG attacks are not immediately lethal to SRWs, this micropredation stressor causes both acute and chronic behavioral effects on the PV population. The PV SRW population has experienced the highest known calf mortality of any baleen whale (Rowntree et al. 2013, Sironi et al. 2018), with gull attacks having been identified as a potential contributing factor (Uhart et al. 2008, IWC 2010, Thomas et al. 2013, McAloose et al. 2016, Fernández Ajó et al. 2018, IWC 2018). While our study shows that PV calves exhibit behaviors indicative of both increased energy expenditure and reduced energy intake (reduced energy transfer between mothers and calves) during gull attacks, further research is needed to investigate potential effects on calf survival, and ultimately, population dynamics. Although the PV population is increasing, the rate of increase has recently decelerated (Crespo et al. 2019), possibly due to environmental stressors, which could include gull harassment.

4.4. Management implications

The micropredation of KGs on SRWs off PV is believed to be a specialist foraging strategy, initially developed and practiced by a subset of the gull population (Fazio et al. 2012). At present, it is likely that most or all the KGs in the PV area exhibit this micropredatory behavior. With an increase in the KG population at PV (Lisnizer et al. 2011, Yorio et al. 2016), the attack frequency on SRWs has increased rapidly (Fazio et al. 2012), suggesting that this learned behavior has spread through the population and is being horizontally transmitted between individuals. KGs are known to feed at uncovered garbage dumps (Yorio & Giaccardi 2002) and discard from fisheries on land and at sea (González-Zevallos et al. 2017). It has been widely recognized that the KG harassment on SRWs off PV has increased in tandem with the increased number of open waste-disposal sites and an increase in KG populations at PV (Rowntree et al. 1998, Sironi et al. 2009, IWC 2010). In 2012, a pilot gull culling project was initiated by the government of Chubut. While the project had some success in reducing the number of specialized attacker KGs in some areas of PV (Bertellotti et al. 2014), the program only ran for 3 seasons (2012 to 2014) and was discontinued. The main garbage dump in PV was closed in February 2015. Nevertheless, as shown by our study, KG attacks on SRWs continue unabated. Thus, we recommend further mitigation efforts based on a suite of measures with appropriate efficacy assessments. Examples could include continuing the targeted attacker gull culling program and expanding control of KGs at breeding sites, broader stakeholder buy-in (e.g. whale-watching operators), eradication of open waste-disposal areas on land, reducing fishing discards at sea, and an updated assessment of the population status of KGs, which has been pending since 2008 (IWC 2015). This study adds to existing knowledge on the impacts of gull harassment on SRWs off PV. Increasing evidence calls for mitigation through KG population management. This study also complements existing knowledge on the impacts of gull harassment on SRWs off PV, by showing that both acute and chronic behavioral effects are causing an increase in energy expenditure for mothers and calves, and possibly a reduction in energy transfer between mothers and calves. Given the risk of long-term consequences on SRW body condition and vital rates, this increasing evidence calls for urgent mitigation through KG population management.

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