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Lower marine productivity increases agonistic interactions between sea lions and fur seals in Northern Pacific Patagonia

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Abstract

Interspecific interactions are key drivers of individual and population-level fitness in a wide range of animals. However, in marine ecosystems, it is relatively unknown which biotic and abiotic factors impact behavioral interactions between competing species. We assessed the impact of weather, marine productivity, and population structure on the behavioral agonistic interactions between South American fur seals (SAFSs), *Arctocephalus australis*, and South American sea lions (SASLs), *Otaria byronia*, in a breeding colony of SAFS. We hypothesized that agonistic interactions between SAFSs and SASLs respond to biotic and abiotic factors such as SAFS population structure, marine productivity, and weather. We found that SASL and SAFS interactions almost always resulted in negative impacts on the social structure or reproductive success of the SAFS colony. SASL adult males initiated stampedes of SAFS and/or abducted and predated SAFS pups. Adult SAFS males abundance and severe weather events were negatively correlated with agonistic interactions between species. However, proxies for lower marine productivity such as higher sea surface temperature and lower catches of demerso-pelagic fish were the most important predictors of more frequent agonistic interactions between SAFS and SASL. Under the current scenario of decline in marine biomass due to global climate change and overfishing, agonistic interactions between competing marine predators could increase and exacerbate the negative impacts of environmental change in these species.

Key words: interspecific interactions, climate change, Guafo Island, sea surface temperature, South American fur seal, South American sea lion.

Interspecific interactions are key drivers of individual and population-level fitness in a wide range of animal species (Laidre et al. 2008). However, the biotic and abiotic factors that mediate beneficial or agonistic interactions between species are not always clear, especially in long-living mammals. Abiotic factors such as temperature and precipitation impact species abundance and sometimes behavior, potentially influencing interactions between species (Mason-Romo et al. 2018). Similarly, biotic factors such as food availability also impact on population density and behavior, influencing interspecific interactions (Selonen et al. 2020). In some circumstances, biotic and abiotic elements synergistically modify the ecosystem and the behavioral responses of species, eliciting a cascade of events that can have significant impacts on the structure of animal populations. For instance, in South Africa, drought or severe winter leads to starvation in large predators (such as wild dog *Lycaon pictus* and cheetah *Acinonyx jubatus*) forcing them to attempt the capture of nonconventional prey species (Fuller et al. 2021). Similarly, in the Mediterranean basin, scarce spring–summer rainfall reduces grass abundance, increasing the spatial overlap between deer and other herbivores, facilitating competition and aggression between species (Ferretti and Fattorini 2021). In Southern Chile, decline in the availability of animal carcasses leads black vultures *Coragyps atratus* to shift from scavenging to predation of live South American sea lion (*Otaria byronia*; SASL) pups (Pavés et al. 2008). Although these phenomena have been documented, there is still little mechanistic understanding on how these responses develop and what are the most important drivers of agonistic interactions, especially in environments with more limited knowledge of behavioral responses such as marine ecosystems. However, a better synthesis of the impact of biotic and abiotic factors on agonistic interactions between species is crucial under the current scenario of accelerated climate change and degradation of ecosystems, particularly in the marine environment.

In large vertebrates, such as marine mammals, the most common interactions between species include predation (Gentry and Johnson 1981; Schmitz 2007; Söffker et al. 2015) and competition (Baird et al. 1992; Clapham and Brownell 1996; Fitzpatrick et al. 2012). These interactions may negatively impact survival, growth, and the community dynamics of certain species; however, depending on the local biotic and abiotic conditions, the frequency and strength of these interactions as well as their impacts can be variable (Forsman et al. 2002; Ørsted et al. 2017; Silknetter et al. 2020). For instance, increase in global temperatures has led to the reduction of the permanent ice shelf in the Arctic, causing a decline in the availability of prey for polar bears *Ursus maritimus*, which boosts intraspecific predation and cannibalism (Amstrup et al. 2006). In the Galapagos Archipelago, El Nino Southern Oscillation (ENSO) events lead to decline in marine productivity and fish abundance, boosting competition between Galapagos sea lion *Zalophus wollebaeki* and Galapagos fur seals *Arctocephalus galapagoensis* due to the scarcity of food resources (Páez-Rosas et al. 2021). Therefore, since biological interactions are involved in structuring community composition, they are probably very important for the community response to changing environmental conditions.

Among marine mammals, otariids (sea lions and fur seals) are broadly distributed across the world's oceans, with many species coexisting sympatrically with other otariid species in most of their distribution (Antonelis et al. 1990; Dellinger and Trillmich 1999; Waite et al. 2012; Villegas-Amtmann et al. 2013). In South America, the SASL and the South American fur seal (*Arctocephalus australis*; SAFS), two of the otariids species with the widest range in the region, overlap in most of their distribution (Sielfeld 1999; Bombau and Szteren 2017). However, in the Southern Pacific Ocean, SASLs have substantially increased their numbers during the last decades, whereas SAFS have not recovered their historical numbers after an 80% population decline in the second half of the 20th century (Cardenas and Oliveira 2015; Seguel and Pavés 2018). As a consequence of this phenomenon, Guafo Island, in the Northern Chilean Patagonia, has become one of the few areas in the Southern Pacific Ocean where numerous rookeries of both species coexist (Pavés and Schlatter 2008; Seguel and Pavés 2018). For SASLs and SAFSs, aggressive intraspecific or interspecific interactions are usually considered an expression of individuals competing for resources, such as shelter, food, or mates (Bohórquez-Herrera et al. 2014). Therefore, giving the high variation of resources in marine ecosystems, agonistic interactions between SASL and SAFS are common in SAFS colonies (Harcourt 1992; Cassini 1998). Among these agonistic behaviors, aggression and predation from SASL toward SAFS are the most common and are directly linked to negative consequences for one of the otariids species (Harcourt 1992; Cassini 1998). Landscape spatial heterogeneity can mediate these interactions and facilitate species coexistence (Fisher et al. 2014). Despite the evidence of predation and competition between SASL and SAFS, how the presence of sea lions affects fur seal populations in the Southern Pacific Ocean is poorly understood, mainly because these interactions occur primarily during particular times (e.g., reproductive season) in remote locations, making the recording and quantification of these phenomena difficult.

Environmental factors can drive resource availability, ultimately influencing competitive interactions between individuals. Competitive asymmetries between species that overlap in the use of resources may result in the displacement of competitively inferior species from breeding habitats if these become scarce (Kodric-Brown and Mazzolini 1992; Bruno et al. 2003). In the case of otariids, their reproductive colonies are strategically located in areas that provide shelter from storms and predators while offering thermoregulatory options through access to shade and pools (Pavés et al. 2005; Seguel and Pavés 2018). Additionally, due to their reproductive ecology (i.e., income breeding) with prolonged lactation periods (6 months to 1 year), these colonies are usually located in regions with easy access to prey for the nursing female (Raum-Suryan et al. 2002; Sinclair and Zeppelin 2002). Therefore, coastal areas that meet these requirements can become highly valuable for sea lions and fur seals, and the use of the same rookery by the 2 species is common (Seguel and Pavés 2018). However, the use of a common space increases the chances of agonistic interaction between species, especially if certain resources become scarce. In the Southern Pacific Ocean, sea surface warming reduces marine productivity and biomass, putting an energetic constraint on otariid species (DeRango et al. 2019). Similarly, storms can lower the quality of previously suitable reproductive habitat for otariid species (Schumann et al. 2013; Briscoe et al. 2018; Sepúlveda et al. 2020). These 2 types of events, sea surface warming and extreme weather events, are expected to occur with higher frequency due to climate change (Frölicher and Laufkötter 2018; Xiu et al. 2018). This could have indirect consequences for the interactions between otariid species if their habitats are significantly disturbed. Thus, it is crucial to understand the potential role of interspecific interactions on the population dynamics of otariids in the Southern Pacific Ocean and how this phenomenon might be impacted by environmental disturbances. Biotic and abiotic elements of the environment can significantly impact the distribution and behavioral patterns of mammals

(Svenning et al. 2014), and within this context, alterations of the local environment could generate changes in reproductive events and behaviors of SASL and SAFS.

In this study, we assessed the impact of weather, marine productivity, and population structure on the behavioral agonistic interactions between sea lions and fur seals in the Southern Pacific Ocean. We hypothesized that agonistic interactions between SAFS and SASL increase in response to decreased marine productivity. Additionally, we predicted that higher number of reproductive male SAFS (mSAFS) and severe weather could decrease agonistic interactions by impeding intrusion of SASL into SAFS breeding grounds.

Materials and Methods

Study site
The study was completed in the breeding colony of SAFS at Guafo Island, Northern Chilean Patagonia (43° 35′ 34.9″ S, 74° 42′ 48.53″ W). This colony is composed of approximately 3,000 SAFS (including pups) in a $0.077\,km^2$ (Pérez-Venegas et al. 2017). The presence of SASLs is not permanent in the colony; however, there is a major reproductive colony of approximately 5,000 SASLs on the same island, 13.7 km south from the SAFS colony. Intromissions of SASLs within the SAFS colony are occasionally observed. Field observations spanned 4 breeding seasons: 8 November 2004 to 30 March 2005; 10 December 2005 to 20 March 2006; 26 December 2006 to 20 March 2007; and 14 December 2016 to 4 March 2017.

Quantification of agonistic interactions
Daily observations of animals were conducted from elevated points in the rookery using binoculars for 12 h (between 8:00 and 20:00 h) by ad libitum sampling (Altmann 1974), resulting in a total of 784 h of observation across the 4 seasons.

To quantify behaviors of SASL, the following variables were recorded: date of sighting age and sex class (e.g., "adult male"), number of individuals, time of entry, and departure to the SAFS colony. Agonistic interactions (i.e., interactions where SAFS or SASL individuals can be harmed) between SAFS and SASL were classified based on the definitions used in previous studies (Fernández-Juricic and Cassini 2007; Jacobs et al. 2008; Young et al. 2008). Agonistic interactions were classified as: *threat*, an open-mouth threat, where the individual opens its mouth and shows its teeth while facing the direction of the opponent (i.e., SASL) and usually may be accompanied by a growl; *bite*, a contact between the individual's open mouth and the opponent's body (i.e., SAFS); *stampedes*, defined as a sudden panicked rush of a number of SAFS individuals; and, *abductions*, situations where a SASL kidnap a SAFS pup. These interactions usually occurred as an escalation of SASL aggressive behavior toward SAFS, with SASL entering the colony and causing a stampede, followed by threatening, which was sometimes followed by bites and rarely abductions of pups. Therefore, we grouped all these interactions under the category "agonistic interactions" considering that this metric better encompassed the true level (or score) of interaction between SASL and SAFS at different sampling seasons and periods (Hughes et al. 1997). To avoid underestimation of interactions in seasons with lower sampling effort, we divided the number of interactions by the number of continuous hours of observation.

Density, trophic indicators, and environmental factors
Weekly censuses of the SAFS colony were completed following previously described methods (Pavés et al. 2005; Pérez-Venegas et al. 2017). Data collected from censuses was used to calculate the number of territorial males of both species and the animals per square meter to measure the effect of population density over agonistic interactions. During the same study period, demographic data for the SASL colonies at Guafo Island were extracted from previously published reports (Oliva et al. 2012; Seguel and Pavés 2018).

In order to assess the impacts of marine productivity and prey abundance on agonistic interactions, proxies of primary marine productivity at Guafo Island, such as sea surface temperature (SST) and chlorophyll-a concentration, were obtained for each sampling day and each breeding season from satellite data acquired from the NASA earth observatory website (https://neo.sci.gsfc.nasa.gov). Although chlorophyll-a is a direct estimation of primary productivity, SST serves as negative predictor of marine productivity in the Southern Pacific Ocean given the negative impact of warmer waters in nutrient upwelling (Soto et al. 2004). The latitude and longitude to retrieve the chlorophyll-a and temperature data were selected to represent standard points 25–50 km west, south, north, and east of the SAFS colony at Guafo Island. Since the spatial resolution of this data is ∼11 km, the values of the different squares within the potential foraging areas were averaged for a single day. This approach was used to represent all the potential foraging areas of fur seals at Guafo Island based on the previous studies on the duration of SAFS foraging trips (Seguel et al. 2018; Montalva et al. 2019). Since the main SASL colony at Guafo Island is located ∼20 km south from the SAFS colony, these areas likely overlap with SASL foraging areas although data on the SASL foraging areas at Guafo Island are not available. Additionally, and according to the diet of SAFS and SASL around Guafo Island (Muñoz et al. 2013; Seguel et al. 2013), data of demersal-pelagic fish landings of Quellón port (the closest to Guafo Island) were obtained from the Chilean fisheries service database (SERNAPESCA, https://sernapesca.cl). Southern hake *Merluccius australis* and slender tuna *Allothunus fallai* landings were recorded every week, whereas the total landings for all demersal-pelagic fish species landings were recorded every 2 weeks or once a month. Therefore, for this last category, we used a categorical classification of landings for a given period following the criteria used by the Chilean fisheries service and Subsecretary of Fisheries (low catch; <10 tons, medium catch; 10–20 tons, high catch; >20 tons). For the study period, demersal-pelagic landings fell within the low or high categories only.

To investigate the effect of environmental variables on the social behavior of SASL and SAFS, daily data of air temperature, precipitation, and wind speed (as a proxy of the condition of the sea) were collected from the Chilean Navy meteorological station located at Guafo Island lighthouse (∼500 m from the SAFS colony). The type of substrate was classified according to the topography of the studied colony: "platform-type substrate" was defined as areas with wide surface with the presence of flat and sandy sectors, and "rocky-type substrate" was defined as zones of the colony with steep cliffs, caves, and large rocks (height >2 m).

Data analyses
Exploratory analyses were conducted to detect the presence of outliers and to test homogeneity of variance and normality of the assessed continuous traits (Zuur et al. 2010). Most traits slightly deviated from normality, except for wind speed, air, and SST. Although outliers were identified for number of agonistic

interactions, these were considered true outliers (biologically possible values) and were not removed from further analyses. The number of agonistic interactions per season was compared through Pearson's chi-square test. Several Spearman's rank correlations were done to establish associations between environmental and behavioral traits (Supplementary Table S1). Correlations were deemed significant if P-values were < 0.05 after Bonferroni's correction. To know which factors were associated with agonistic interactions, we fitted several (n = 61) negative binomial generalized linear mixed models (GLMMs) using the R package "glmmTMB" according to type (i.e., counts) and distribution of data. We used different combinations of air temperature, precipitation, wind speed, SST, landing of demersal fishes, total SAFS and SASL populations density, and mSAFS and SASL males (mSASL) density as predictors of the number of agonistic interactions were recorded in a day (details of models fitted are in Supplementary Table S2). Season was included as a random effect in all models to account for temporal separation of the data. Based on the correlation analyses, only variables with low correlation coefficient (r < 0.5) between them were included in the same model to avoid collinearity among predictors (Burnham et al. 2011). Furthermore, 2-way interactions between predictors with potential direct–indirect influence on each other were included in the same model (e.g., SST and chlorophyll-a levels). Those predictors that could encompass other indexes or indicators were treated separately in different models (e.g., density of mSASLs and density of SASLs individuals). Model homoscedasticity was assessed by visually inspecting the residuals and collinearity was assessed using the variance inflation factor calculated with the R package "performance" (Zuur et al. 2010). Models were checked for overdispersion by dividing the residuals deviance by the degrees of freedom. A ratio < 2.0 was considered acceptable (Zuur et al. 2010). Later, models with no convergence, fit, or overdispersion issues were ranked based on second degree Akaike Information Criteria (AICc) using the R package "MuMIn" (Barton 2009). Models with a delta AICc > 6.0 were considered significantly different (Harrison et al., 2018). All statistical analyses were performed using "R version 3.3.3" statistical software (R Core Team 2017).

Results

During the 4 sampling seasons (8 November 2004 to 30 March 2005; 10 December 2005 to 20 March 2006; 26 December 2006 to 20 March 2007; and 14 December 2016 to 4 March 2017), we performed a total of 784 h of observation, recording 213 events of SASLs entering the SAFS breeding colony with 0.27 SALSs intromission per observation hour.

A total of 205 agonistic interactions were recorded between SASL and SAFS. Of the 205 agonistic interactions, 43.4% were stampedes (n = 89), 38.5% corresponded to threats (n = 79), 17.1% were bites (n = 35), and 1% were abductions (n = 2) (Figure 1). Abductions were reported only for the 2016–2017 study season (Video 1). A mean (± SD) of 0.38 ± 0.17 agonistic interactions per hour of observation were recorded during the study, with no differences in the proportion of aggression between seasons (Pearson's chi-square test, $\chi^2 = 0.01$, $P = 0.9$) (Table 1).

Adult males represented 65% (n = 44) of SASL individuals that entered the SAFS colony in 2004–2005; 54% (n = 33) in 2005–2006; 64% (n = 45) in 2006–2007; and 56% in 2016–2017 (Figure 2). The receptor of aggressive behaviors in all cases were SAFSs, and in 68% of interactions all SAFS age groups in the colony

Figure 1. Impact of the intromission of SASLs into the SAFS colony at Guafo Island, Northern Chielan Patagonia. Note the SASL subadult male (white arrow) entering the SAFS colony through a rocky platform. This intromission generated a stampede that forced SAFS adult females (white arrowhead) to the edge of a small cleft.

Video 1. Abduction of a SAFS pup by a subadult male SASL. The SASL grabs the SAFS pup by the neck and takes it into the sea. Not shown in the video is the posterior consumption in the water of the drowned SAFS pup by the SASL.

were affected, and in 16% and 15% of times, the age class receptor of the aggression was pups and adult females, respectively.

SAFS abundance was positively correlated to SAFS adult male density, and positively correlated to SASL abundance and mSASL density (Spearman ρ, $r = 0.75$, $P < 0.001$). However, out of all otariid populations numbers, only total SAFS abundance (Spearman ρ, $r = -0.37$, $P = 0.003$) and number of adult mSAFS in the colony (Spearman ρ, $r = -0.36$, $P = 0.0175$) were negatively correlated to agonistic interactions (Figure 3; Supplementary Table S1). For proxies of marine productivity, agonistic interactions were positively correlated to SST (Spearman ρ, $r = 0.45$, $P < 0.001$), a negative proxy for marine productivity. Slender tuna landings were positively correlated to the number of agonistic interactions (Spearman ρ, $r = 0.12$, $P = 0.004$). Air temperature was positively correlated with agonistic interactions (Spearman $\rho = 0.41$, $P < 0.001$), whereas wind speed was negatively correlated with agonistic interactions (Spearman $\rho = -0.41$, $P < 0.001$).

Table 1 Agonistic interactions between SAFSs and SASLs per hour during 4 reproductive seasons at Guafo Island, Northern Chilean Patagonia

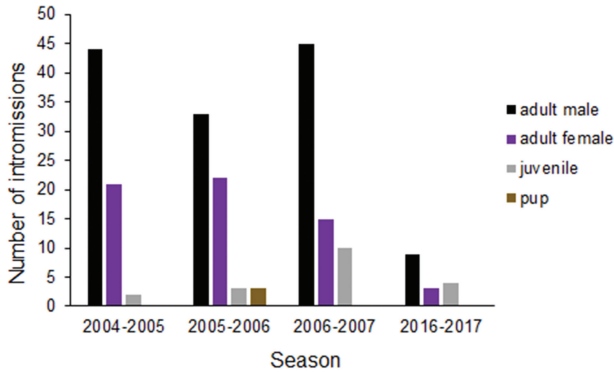| Season	Hours of observation	Interactions per hour					
		Threat	Bite	Stampede	Abduction	Total	Proportion of aggression
2004–2005	480	0.07	0.02	0.05	0.0	0.15	0.85
2005–2006	89	0.22	0.04	0.28	0.0	0.55	0.82
2006–2007	186	0.11	0.10	0.18	0.0	0.39	0.92
2016–2017	29	0.10	0.10	0.17	0.7	0.45	0.85

Figure 2. Number of SASL intromissions to the SAFS colony according to age group per season.
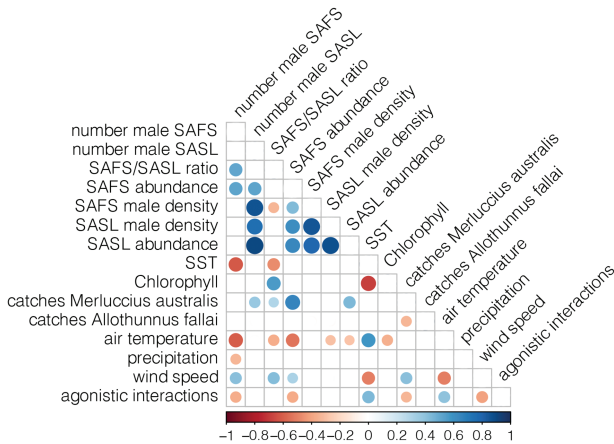

Figure 3. Correlations between number of agonistic interactions and several population structure, marine productivity, and weather indicators. The number of agonistic interactions between SASLs and SAFSs was negatively correlated to the density of mSAFS SAFS abundance and wind speed. There was a positive correlation between agonistic interactions and SST and air temperature (significant correlations after Bonferroni's correction indicated in circle and circle color intensity indicates Spearman ρ r coefficient in the horizontal bar).

Multi-model inference results are presented in Table 2. Out of the 15 assessed predictors, only 2; SST and total demersal-pelagic catches, had statistically significant effects in their respective top-ranked models. These effects remained significant after calculating the conditional estimates averages of all top-ranked models (Table 3). These models indicated that warmer SST (GLMM $\beta = 1.29 \pm 0.43$, $Z = 2.89$, $P = 0.004$) and low levels of demersal catches (GLMM $\beta = 4.71 \pm 2.0$, $Z = 2.19$, $P = 0.04$) increased the number of agonistic interactions (Figure 4).

Discussion

Biotic and abiotic environmental factors can impact the behavior and ecology of animal populations; however, the specific environmental factors that modulate the interactions between species are relatively unknown (Kordas et al. 2011; Imperio et al. 2012; Cherry and Barton 2017). Under the current scenario of global environmental change, understanding the size and direction of environmental effects on animal behavior is critical to know how species will interact in the ecosystems of the future. We found that agonistic interactions between SAFS and SASL were common, and in 16% of occasions resulted in adverse outcomes for the smaller SAFS. More importantly, we found that indirect indicators of lower marine productivity (higher SST and lower fish catches) increased the number of agonistic interactions between SASL and SAFS, suggesting that decline in marine biomass could increase aggression from SASL toward SAFS.

Fur seal and sea lion species are generalist predators but require unique coastal environments for reproduction. These coastal areas can become precious resources for these marine mammals, eliciting competition within and between species. Therefore, in different regions, competition for reproductive areas between sea lions and fur seals is common (Campagna et al. 1988; Meise et al. 2013; Villegas-Amtmann et al. 2013), with agonistic interactions ranging from minor threats to predation (Harcourt 1992; Páez-Rosas et al. 2021). We found that most intromissions of SASL into the SAFS colony resulted in aggressive behaviors from SASL toward SAFS (i.e., threats), although most of these interactions did not result in direct killing of SAFS by SASL beside the 2 recorded cases of abduction and predation. Predation of SASL toward SAFS has been previously recorded in colonies with high SAFS and SASL densities, and it is considered a consequence of competition between these 2 species (Harcourt 1991, 1992). The other agonistic interactions observed; bites and stampedes, do not portend an immediate mortality effect but they can be associated with adverse outcomes for SAFS pups and adults within the colony. During stampedes in otariid colonies, there can be crushing, falling off a cliff, or drowning of pups in tide pools (Seguel et al. 2011, 2013). However, mortality due to stampedes can be difficult to document since death can occur after a falling incident from trauma complications and drowning in hidden tide pools (Seguel et al. 2011, 2013). Similarly, bite wounds on adult males or females usually do not portend immediate mortality risk although they can become infected and cause death due to sepsis (M. Seguel, personal observation). Additionally, SASL intromissions are associated with disruption of the social equilibrium within SAFS colonies, which is important for the normal timing of births, mother-pup early bond, nursing, and reunion between mother and pup after maternal foraging trips (Doidge and Croxall 1989; Harcourt 1992; Sauvé et al. 2015; Seguel et al. 2018; Montalva et al. 2019).

Table 2 Log likelihood (LogLik) and corrected AICc for top-ranked GLMMs with negative binomial distribution for the number of agonistic interactions between SASLs and SAFSs

Model	Predictors	AICc	Delta AICc	LogLik	df	P-value
1	mSAFS/mSASL + SST + (1|season)[a]	73.79	0	−74.60	7	0.001
2	mSAFS/mSASL + chl + mSAFS/mSASL * chl + (1|season)[a]	75.11	1.32	−72.17	9	0.009
3	mSAFS/mSASL + SST+ substrate + (1|season)[a]	76.24	2.45	−74.33	8	0.002
4	mSAFS/mSASL + demersal landings + mSAFS/mSASL * demersal landings + (1|season)[a]	77.85	4.06	−74.59	8	0.003
5	mSAFS+mSASL + SST + (1|season)[a]	78.14	4.35	−72.05	10	0.003

[a] Refers to the season as a random effect.
 Ratio between mSAFS/mSASL, chlorophyll-a (chl), SST, fish landings (demerso-pelagic), winds, and rookery substrate were the predictors.

Table 3 Output from conditional model averaging of standardized parameters with number of agonistic interactions between SAFSs and SASL as response

Predictor	Estimate	SE	Z	P-value
Intercept	−13.336	10.531	1.26	0.208
Males SAFS to males SASL ratio	−0.034	0.126	0.27	0.789
SST	**1.297**	**0.438**	**2.89**	**0.004**
Chlorophyll	−0.595	0.364	1.60	0.110
SAFS to SASL proportion * chlorophyll	0.019	0.028	0.66	0.508
Substrate (rocky)	0.164	0.755	0.21	0.832
Demerso-pelagic fish landings (low)	**4.061**	**2.005**	**2.19**	**0.040**
SAFS to SASL proportion * demersal fish landings catches	−0.099	0.056	1.74	0.082
mSASL abundance	0.013	0.045	0.30	0.765
mSAFS abundance	−0.006	0.004	−1.53	0.125

Ratio between SAFS and SASL males, SST, demersal fish landings, sea surface chlorophyll-a, rookery substrate, and total number of male SAFSs and SASLs are the predictors. Significant predictors are highlighted in bold.
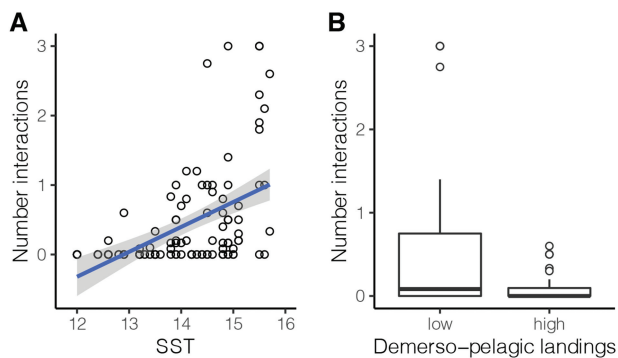

Figure 4. Lower marine productivity increases agonistic interactions between SASLs and SAFSs. (**A**) Higher SST, a negative proxy for marine productivity, was associated with higher number of agonistic interactions (GLMM $\beta = 1.29 \pm 0.43$, $Z = 2.89$, $P = 0.004$). (**B**) Similarly, lower levels of landings of demerso-pelagic fishes, a positive proxy for marine productivity, was associated with higher number of agonistic interactions (GLMM $\beta = 4.71 \pm 2.0$, $Z = 2.19$, $P = 0.04$).

In this study, the population structure of SAFS and SASL populations and climate indicators were correlated to the number of agonistic interactions, as we hypothesized. It is well-known that colony interactions between sea lion and fur seal species, as well as aggression, are positively linked to population density (Harcourt 1991,

1992; Jeglinski et al. 2013). In our case, we found that SAFS density had a negative correlation to agonistic interactions, suggesting that higher numbers of SAFS could offer protection for the intromission of SASL into the SAFS colony, as it has been observed in other fur seal colonies (Szteren et al. 2018). Alternatively, this correlation could result from the seasonal variation in aggressiveness by SAFS reproductive males during the reproductive season, when there is a higher density of SAFS in the colony. Higher wind speed was correlated to lower number of interactions while air temperature had the opposite relationship with interactions. These correlations suggest that when the weather is mild at Guafo Island, which is defined by higher air temperature and milder winds, interactions between SASL and SAFS are more commonly observed. These associations could be due to complications imposed by strong winds and higher surf on the entering strategy of SASL into the SAFS colony. SASL is heavier and slower on land than SAFS, struggling to land on rocky shores with irregular surface, especially under high surf (Vila et al. 2008; Cappozzo and Perrin 2009; Sepulveda et al. 2020); therefore, climatic conditions associated to warmer air temperature and mild winds could favor their intrusion into fur seal colonies. Alternatively, these correlations could be associated to observation bias since adverse climatic conditions can complicate recording of interactions (Montalva et al. 2019). However, in our study site, this option is less likely given that during bad weather days at Guafo Island, SAFS is usually easier to see on land (darker, wet coat) and located closer to observation points (Pavés et al. 2005).

Proxies for marine productivity and biomass such as SST and landings of demersal fishes were found to have a strong influence on the number of agonistic interactions between SASL and SAFS. SST drives the mixing regimes of the Pacific Ocean and with those, significant changes in the concentrations and distribution of nutrients and plankton, the base component of oceanic food webs (Laidre et al. 2008; Doney et al. 2012; Pelayo-González et al. 2021). Therefore, there are significant correlations between the thermal regime of the ocean and the distribution of plankton determined through measurement of chlorophyll concentrations by satellites (Bouffard et al. 2018; Hao et al. 2019). These correlations can result from a direct biological response to temperature, or more commonly from a direct interaction with mixing processes and/or indirect interaction through trophic relationships. Marine ecosystems are maintained by the flow of energy from primary producers at the base of food webs to intermediate consumers and main predators (Doney et al. 2012; Wisz et al. 2013), where changes in the conditions of the ocean and key biological interactions can alter the underlying dynamics that govern the structure and function of these habitats (Wege et al. 2016). Since marine mammals such as otariids act as top predators in marine food webs, an increase in the temperature of the ocean implies a reduction of plankton biomass and, therefore,

the decrease in the prey biomass for the top predators, such as SAFS and SASL (Morissette et al. 2006; Jeglinski et al. 2013; Kiszka et al. 2015). This decline in prey biomass could be an important factor motivating more agonistic interactions between sea lions and fur seals through different mechanisms. For instance, trophic stress could motivate SASL to enter the SAFS colony more often in search for new prey items (e.g., SAFS pups). Additionally, a decline in marine biomass could decrease SAFS density in the colony by driving mortality and/or early migration of reproductive males. Although otariid reproductive males do not forage during the reproductive season, they require sufficient accumulation of fat stores before the season to energetically sustain this stressful period (Campagna et al. 1988; Pavés et al. 2005). Therefore, adverse environmental conditions associated with higher SST and decline in prey items could lead to poor storage of fat reserves and early departure of males from reproductive colonies (Sydeman and Allen 1999; Adame et al. 2020). This reduction in reproductive male density could potentially facilitate intromission of SASL into the fur seal colony, increasing the number of agonistic interactions. However, given the temporal scale of our environmental data, which was recorded during the reproductive season and not during the foraging phase of mSAFS, we could not confirm this hypothesis.

In line with our initial hypothesis and with the results from SST, we found that lower landings of demerso-pelagic fish species increased the number of agonistic interactions. In the Northern Pacific Patagonia, fishing activity is intense, and fishing quotas are regulated through the agreement of several invested parties and with little input from scientific data on the conditions of fish stocks (Seguel et al. 2018; Porobic et al. 2018; Estévez et al. 2020). Therefore, landings usually reflect changing in stocks abundance rather than changes in fishing effort, which has remained relatively stable over the last 10 years in Chile (Estévez et al. 2020; OECD 2021). SAFS at Guafo Island prey preferentially on demersal and energy-dense fish species such as the southern hake (Seguel et al. 2013; Cardenas and Oliveira 2015), but for SASL their diet preferences in this region are unknown. Therefore, a reduction in energy-dense demersal species could portend an energetic constraint on SAFS and potentially to SASL, facilitating negative interactions if the decline in high-quality prey items disrupts migration patterns or motivates searching for new prey from SASLs.

Global climate impacts SST regimes, marine productivity, local weather, and the abundance and health of marine top predators, creating an interconnected network of biotic and abiotic changes in marine ecosystems (Constable et al. 2014; Hazen et al. 2019). Although we found that most of these elements were correlated to agonistic interactions between fur seals and sea lions, only marine productivity proxies remained as strong predictors of agonistic interactions. This suggests that despite the likely impact of local weather and population structure on interactions, marine productivity is probably one of the most important drivers of agonistic interactions between otariid species. Given the direct link between climate and marine productivity (Frey et al. 2020; Moore et al. 2018; Sakshaug and Walsh 2000), these findings portend significant implications for future studies. There is a growing concern about the potential negative effects of climate change on behavior and ecology of animal populations (Hazen et al. 2019; Fuller et al. 2021). Furthermore, changes in community structure and ecosystem function may result from disruptions in biological interactions (Fuller et al. 2021). In this way, it would be interesting to evaluate the evolution of this type of behavior in times of macro-scale climatic fluctuations, such as the El Niño-Southern Oscillation (ENSO) phenomenon, which

can significantly impact primary productivity and food availability in marine ecosystems. Habitat change or loss particularly affect highly specialized species that depend on certain ecological conditions at specific times of the year (Mantyka-Pringle et al. 2012), so it is possible that, in the context of climate change, these types of interactions become more recurrent. Future investigations could focus on quantifying the magnitude of the impact of changing ecological conditions, both biotic and abiotic, on ecological dynamics through behavioral shifts in marine mammals.

In this work, we identified that proxies of lower marine productivity such as higher SST and lower landing of demerso-pelagic fishes predicted an increase in the number of agonistic interactions between SAFS and SASL. Under the predicted scenario of decline in marine biomass due to climate change and overfishing, there could be an increase in agonistic interactions between competing marine predators.

Ethical Statement

Field work conducted under several permits issued by the Chilean Subsecretary of fisheries ("Resolución exenta No 88/SSP 2014" and "Resolución exenta No 976/SSP 2016").

Authors' Contributions

F.M., H.P., and M.S. conceived the study and drafted the manuscript. F.M. and M.S. carried out the statistical analyses. F.M., H.P., D.P.V., K.B., C.V., D.M., and M.S. collected data and critically revised the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Availability of Data and Material

All relevant data are within the paper and its Supporting Information files.

Conflict of Interest

The authors declare that there is no conflict of interest regarding the publication of this article.

Supplementary Material

"Supplementary material can be found at https://academic.oup.com/cz." Dataset available in supplementary table 3.

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