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RESEARCH

Factors influencing haulout behaviour of non-breeding weddell seals (*Leptonychotes weddellii*) at Cape Royds, Antarctica

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Abstract

The Weddell seal (*Leptonychotes weddellii*) is a fast-ice obligate species that plays an important role as both predator and prey within the high-latitude, coastal Southern Ocean. Weddell seals are affected by pressures of marine resource extraction and variation in sea-ice extent and characteristics that are affected by climate. Thus, monitoring their population dynamics provides an indicator of the effectiveness of fisheries management, and impacts of changing climate in the high latitude Southern Ocean ecosystem. Satellite imagery is increasingly being used to monitor the populations of this species, but assessment techniques require a better understanding of the environmental factors influencing the likelihood that individuals will be on the sea-ice and therefore visible in a satellite image. Addressing that goal, we captured 5054 trail camera photos during spring 2017 in the 24-h light at Cape Royds, Antarctica, and then counted seals on the fast ice every 30 min over 59 days. Using a generalised additive model (63% deviance explained) we described the haulout behaviour of non-breeding Weddell seals according to time of day, date, air temperature, pressure, solar radiation, and wind speed. We found that the seals' haulout cycle is driven to a significant degree by weather variables, primarily temperature and wind speed. Quantifying these haulout patterns can be used to determine the time of day, and under what conditions, that most seals are hauled out. Integrating environmental parameters to correct time-of-day patterns would allow better cross-site abundance comparisons, leading to better Weddell seal population estimates for the Ross Sea region and the wider coastal Antarctica.

Keywords Southern Ocean · Marine mammals · Pinnipeds · Antarctica · Ecosystem monitoring · Remote sensing

Introduction

Weddell seals (*Leptonychotes weddellii*; WESE) are the southern-most of all seal species and are endemic to the high-latitude Antarctic, using fast ice as a haulout substrate (Garrott et al. 2012; Rotella et al. 2012). Based on recent modelling involving satellite imagery, an estimated ~ 84,000 reproductive female WESE were found along Ross Sea coasts in 2011 (LaRue et al. 2021). The females haul out to give birth and suckle young, whilst the males remain in the water to defend their 'harem' and, thus, assessments of breeding populations are based around counting females. Due to their key role as mesopredator (Abrams et al. 2016; Ainley et al. 2021), quantifying their population size and distribution is of great importance to better understand the Ross-Sea region food web. Indeed, this seal has been deemed a key indicator of food web dynamics in the recently designated Ross Sea Region Marine Protected Area (CCAMLR 2018a, b). Moreover, WESE are also sensitive to the presence and type of fast ice, upon which they form haulouts, that ice in turn being sensitive to climate factors, such as wind (Siniff et al. 2008; Kim et al. 2018). Our ability to understand the population dynamics of WESE hinges on our capacity to accurately estimate populations and their changes over time.

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Satellite imaging is proving an indispensable tool for understanding WESE ecology in coastal Antarctica (LaRue et al. 2019, 2021; Koerich et al. 2022). Prior to the availability of high-resolution satellite imagery, the best-studied seal haulout assemblages are near established research stations with observations biased toward the Austral summer (Siniff et al. 1977). This state of affairs poses a challenge to researchers seeking to understand the behaviour of WESEs away from logistical centres (Testa & Siniff 1987; Kennicutt et al. 2019). The challenge was solved by application of various emerging remote sensing technologies, such as satellite imaging (Andrews et al. 2008; LaRue et al. 2011; Marvin et al. 2016; Moxley et al. 2017). The WESE has proven to be an excellent study species for satellite sensing due to their propensity to haul out for long periods on the sea ice, the contrast between their dark coat and the white ice, and their predisposition to be spaced a body or more apart during haulout, rather than lying atop one another which characterizes most other pinnipeds (LaRue et al. 2020).

A principal problem in using satellite imagery to estimate WESE numbers is that image availability is limited by cloud cover (which in summer is pervasive in the coastal Southern Ocean), and the timing of satellite orbits (Banner 2012). These orbits were not placed nor timed with counting seals in mind (LaRue et al. 2021)! The most accurate counts are ones undertaken 'in person' over a series of days based on individually marked individuals (Rotella et al. 2012). Even that effort is compounded by the WESE haulout cycle (Stirling 1969a; Testa & Siniff 1987), a cyclical variation leading to a systematic under-sampling at specific times of day (LaRue et al. 2011)—at different times of day, a different proportion of the seal population is hauled-out. Thus, in the case of breeding individuals, in which the cycle has been studied, images taken in the early afternoon local time contain a larger proportion of the population than at other times (Smith 1965; Siniff et al. 1971). Consequently, the diurnal nature of WESE haulout needs to be quantified to design an effective field effort especially to compare numbers counted at different locations that had been counted at different times of day.

Although the diurnal patterns of haulout have been quantified for breeding/pupping assemblages (e.g., Smith 1965; Stirling 1969a; Testa and Siniff 1987), it has not been done for non-breeders which tend to haul out at the periphery of where breeders concentrate. We set out to determine factors that influence haulout patterns of these non-breeding seals, and chose to conduct our study at Cape Royds, approximately two kilometres north of the largest known pupping haulout for the species (Erebus Bay, McMurdo Sound; LaRue et al. 2019; Fig. 1). By combining camera count data with concurrent weather data, we aimed to develop an understanding of the proportion of non-breeding WESEs hauled out at a specific point in time as affected by a specific set of environmental conditions. Our initial hypotheses follow that of previous research observing WESE breeding populations (Stirling 1969b; Siniff 1991; Lake et al. 1997). We expected the Cape Royds non-breeding WESE population

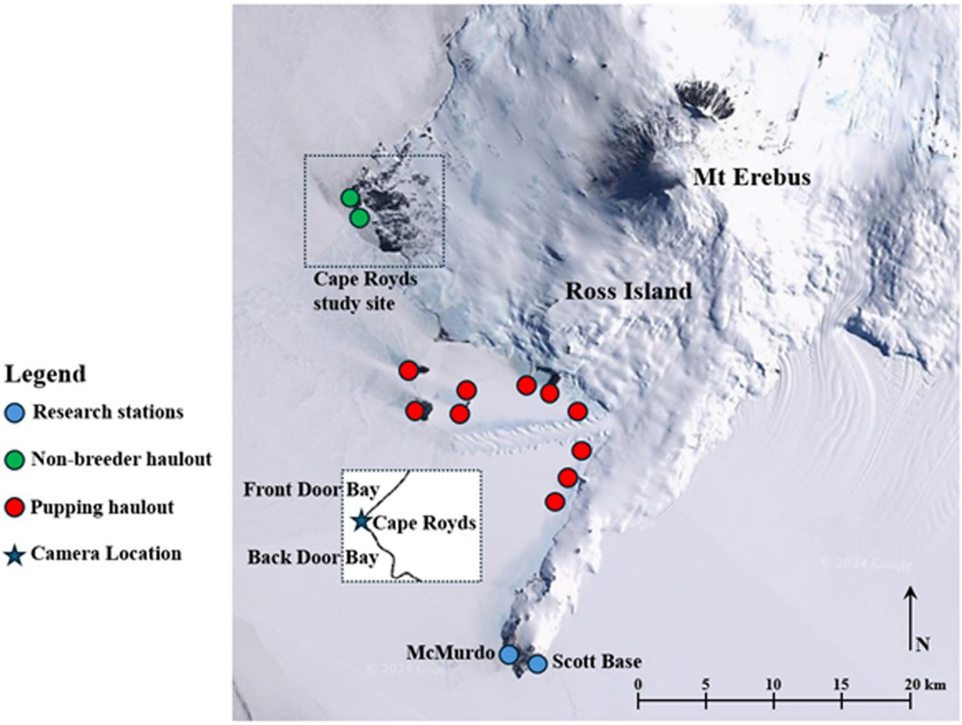

Fig. 1 Map of Ross Island identifying the location of the study site at Cape Royds in relation to Erebus Bay pupping concentration. Map courtesy of publicly available data provided by https://earth.google.com/web

to behave similar to breeders and we hypothesized that: (1) time of day affects the number of WESE hauled out on the fast-ice, with fewer in the morning and more in the afternoon (Smith 1965; Siniff et al. 1971); (2) more WESEs haul out when it is warmer; and (3) more WESEs haul out when the winds are calmer (Smith 1965). The greater understanding of haulout cycles we generate will help the accuracy of future satellite population counts by enabling adjustments to be made depending on the time of day or date at which satellite imagery is acquired.

Methods

Study area

The study was conducted in 2017 at Cape Royds (77°33′33.8"S, 166°09′46.1"E, Fig. 1), where the Shackleton party erected a hut in 1907–09. situated ~ 35 km due north of Scott Base and McMurdo Station, on the eastern McMurdo Sound shoreline of Ross Island. They loaded supplies from the ship anchored in Back Door or Front Door bays. This region experiences a large seasonal variability in sea-ice cover, with complete ice coverage during austral winter, sea-ice breakout between November and January, with the fast ice edge residing at Cape Royds across to Marble Point, eventually leading to open water by February (Kim et al. 2018). The ocean floor along the coast initially slopes gently to around 100-m deep, before dropping off rapidly to over 800 m (Robinson 1963). Temperatures at Cape Royds tend to vary between a monthly mean of − 30 °C in the austral winter and 0 °C in the summer (Stearns 1988). In general Cape Royds experiences relatively warmer and calmer weather than the nearby Ross Ice Shelf (RIS) as the cold southerly winds coming off the RIS are diverted eastward by the topography of Ross Island (Monaghan et al. 2005).

Seal data

Three Cuddeback trail cameras (20MP, model-E) were set up along the rocky shore of Cape Royds viewing Back Door and Front Door bays (Fig. 1). The cameras were pointed at a series of tidal pressure ridges and ice cracks where seals typically haul out. Cameras were set up at varying heights above the fast ice (highest ~ 50 m) and, consequently, the scope of the area captured varied from camera to camera. These cameras took one photograph every 30 min between the 30th of October and the 31st of December 2017.

We first counted the number of observable seals in every photograph taken by the three trail cameras, also recording the date and time of the photograph, the camera the photograph set belonged to, and the associated metadata of photograph quality and sea-ice cover. In some cases, due to either a white-out event or overexposure of the camera from sunlight reflected into the lens, we excluded the image from the dataset. In general, photographs were rated as anywhere between low (low confidence in recording all seals) through medium, to high (high confidence in observing all seals in a photograph) (Supplementary Table 1).

Environmental data

We used weather data from the Cape Royds Adélie penguin colony provided by the “PenguinCam,” which included meteorological instruments (http://penguinscience.com, and https://www.polar66.org/pcam/images.shtml). The environmental variables recorded were temperature (°C), pressure (hPa), wind speed (ms^{-1}), wind direction (°), humidity (%), and solar radiation (V). The data were recorded at hourly intervals across the length of the study period.

Statistical modelling

All data processing was conducted in R v4.0.3 (R Core Team, 2021) with the tidyverse package (Wickham et al. 2019). Weather and seal dates were adjusted to match the time zone for austral summer 2017 (NZDT). At the beginning of the dataset, camera #1 only took one photograph per hour, before being recalibrated to take half-hourly images. Consequently, to maintain consistent time intervals, we interpolated half-hourly seal numbers for a subset of 156 data points by averaging the number of seals at the adjacent hourly time stamps.

To overcome the complexities of the dataset (such as the nonlinear relationship between environmental covariates and WESE haulout behaviour or temporal autocorrelation), we chose to use Generalised Additive Models (GAMs) provided by the R package ‘mgcv’ (Wood 2008). One of the biggest strengths of GAMs is that their additive nature facilitates decomposing complex temporal structures into their constituent components (Ciannelli et al. 2008). This allowed us to specifically target temporal autocorrelation as our model breaks down the observed variation in seal numbers into its constituent components making all the variables conditionally independent from each other. Thus, we could separately address the effect of date and time on seal variation from our other variables, such as temperature or pressure.

We constructed the following GAM to reveal haulout patterns using date, time, camera metadata, and environmental variables from Cape Royds:

$$\begin{aligned}\log(\mu_i) &= 1 + f_1(\text{Datetime}) + f_2(\text{time of day}) \\ &+ f_3(\text{temperature}) + f_4(\text{pressure}) \\ &+ f_5(\text{wind speed}) + f_6(\text{solar radiation}) \\ &+ f_7(\text{photograph quality}) + Camera_k\end{aligned}$$

where: $y_i \sim \text{Poisson}(\mu_i;\phi)$

where k is a categorical predictor for three unranked camera angles (1, 2, 3), f_n is the smoothing term associated with each variable (Table 1), and μ is the mean, ϕ the overdispersion parameter.

We set the date as a cubic smooth function ("cs") as cubic functions can handle temporal autocorrelation structures well (Ciannelli et al. 2008; Wood 2008). All environmental covariates in our models were fitted as penalised thin-plate smooths ("ts") to account for their correlation structures and optimised by restricted maximum likelihood (REML) method (Blanchet et al. 2015; McIntosh et al. 2015). The penalization of these smooths automatically accounts for collinearly present variables (Wood 2008; Marra and Radice 2010), reducing the effective size of the smooth and accounting for overfitting. We selected variables in accordance with these hypotheses and selected the final model by comparing AIC, deviance explained, and a bias for simplicity.

Results

We processed 5311 photographs from three separate cameras during the spring of 2017. In total 8153 WESE observations were recorded, with at least one seal present in 2662 (50%) of the photographs. The mean number of WESEs observed per photograph was 1.72 (SE ± 0.03), and the largest number of WESEs counted within one photograph was 14 individuals. The time of day in which the fewest WESEs were hauled out was 0330 NZT with a mean of 1.07 (SE ± 0.16) seals, whilst the time with the most WESEs was 1330 NZST, with a mean of 2.45 (SE ± 0.28) WESE (Fig. 2). The highest daily mean was 5.32 (SE ± 0.41) on 30 November. The most WESE observed simultaneously across three cameras at the same point in time was 20 individuals. Across the 2507 half-hourly time points between 31 October and 28 December 2017, 895 (36%) were captured in all three cameras; 601 (24%) were captured by two cameras; and 1011 (40%) by only one camera.

Time of year was overall the largest contributing factor to the number of WESEs hauled out at Royds. The mean number hauled out per image was 2.5 individuals fewer at the end of December compared to the beginning of November (Fig. 3). We found that haulout behaviour was cyclical, although once controlled for meteorological variables, the effect of time of day itself on haulout is much reduced (Fig. 4), with the model only attributing a variation of 0.3 seals between early morning and early afternoon. Whilst all environmental variables contributed to explaining WESE haulout behaviour, our model identified wind speed and temperature as the primary environmental drivers of haulout. The final model explains 63% of the variation in WESE haulout observed in photograph counts at Cape Royds (Table 1).

Discussion

Through trail camera observations at Cape Royds, McMurdo Sound, Antarctica during the WESE pup-rearing season (austral spring), we found that variation in environmental

Table 1 Results of the GAM used to explain non-breeding Weddell seal haulout behaviour at Cape Royds, Antarctica between 31 October and 28 December 2017

Variable	Smoothing terms	Estimated degrees of freedom	Chi-squard	*P*-value
Datetime	Cubic regression (cr)	3.975	1890.83	< 0.0001
Time of day	Cyclic cubic (cc)	4.230	40.12	< 0.0001
Temperature	thin-plate shrinkage (ts)	6.972	469.11	< 0.0001
Pressure	thin-plate shrinkage (ts)	3.283	62.99	< 0.0001
Wind speed	thin-plate shrinkage (ts)	7.144	543.52	< 0.0001
Solar radiation	thin-plate shrinkage (ts)	4.612	200.37	< 0.0001
Photograph quality	random effect (re)	1.945	417.51	< 0.0001
Camera number	random effect (re)	1.998	3355.86	< 0.0001

The model explains 62.5% of the deviance observed

Estimated degrees of freedom are a representation of the 'wiggliness' of a relationship between covariate and response variable, an estimated degree of freedom of 1 implies a linear relationship and larger numbers imply progressively more wiggliness

Chi-squared describes the relative contribution of a variable to the observed deviation in seal numbers, with a higher Chi-squared implying a higher contribution

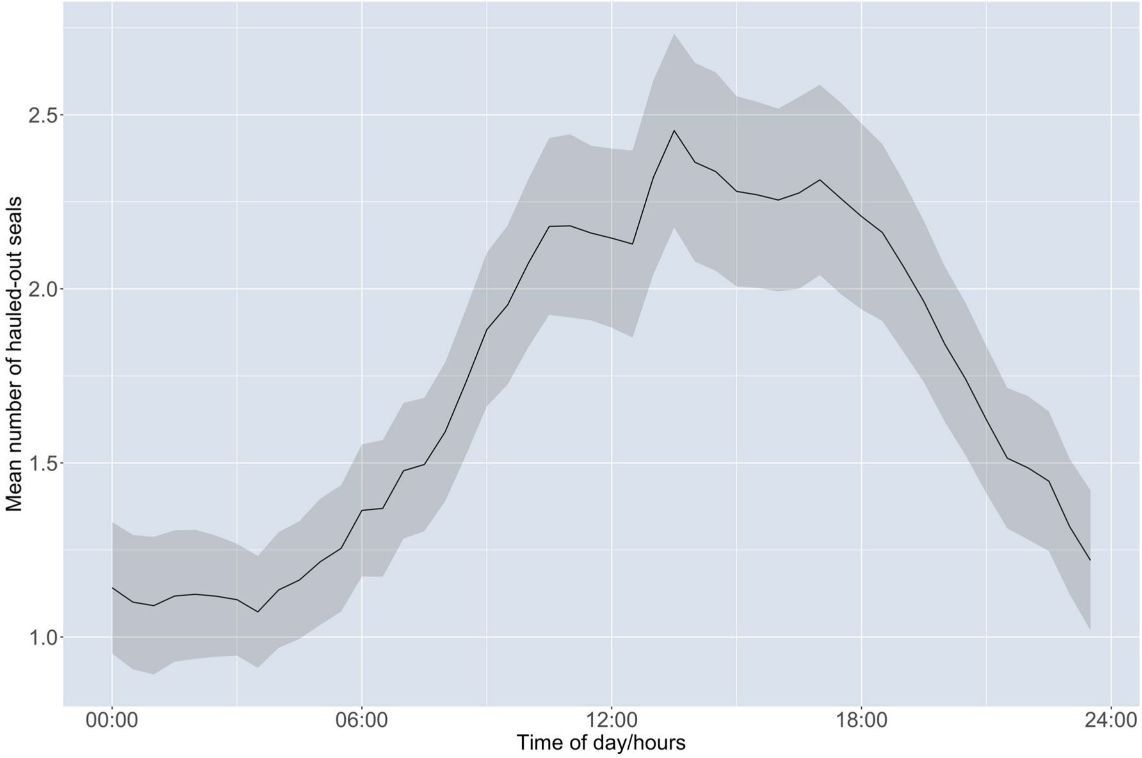

Fig. 2 Mean number of Weddell seals per photograph per 30-min-time period hauled out on the sea ice at Cape Royds over a 24-h period between 31 October and 28 December 2017 as observed by three separate Cuddeback trail cameras. Shading represents 1 standard error on either side of the mean

covariates, such as temperature and wind speed, are the primary factors affecting the diurnal cycle in number of non-breeders hauled out at Cape Royds. Our work builds upon and explains previous work that demonstrates the general principle that more WESEs haul out in the afternoon than in the morning, local time (Smith 1965; Stirling 1969a; Siniff et al. 1971; Thomas and DeMaster 1983; Lake et al. 1997; Banner 2012). We suggest that whilst population estimates acquired from satellite imagery may be able to correct for time-of-day and day-of-year (LaRue et al. 2021), including local environmental covariates may increase the precision of population estimates.

Seasonal variation

The number of individual WESEs hauled out per photograph declined between 31 October and 28 December, which is in line with other work in the Vestfold Hills, East Antarctica, which found a decrease of ~ 10%–an order of magnitude less than in our model (c.f. Lake et al. 1997). The decrease in seal presence in our case is unlikely to be caused solely by individuals spending less time hauled out in December compared to November and is more likely explained by WESEs leaving the study area to haul out elsewhere, such as southern McMurdo Sound. There, fast ice persists longer and that is where large numbers undergo their annual moult (Ainley et al. 2015). We hypothesize two reasons why this pattern shows up at Cape Royds. First, WESEs at Cape Royds tend to be non-breeding and are not tied to a location by the presence of a pup (Stirling 1969b). In other words, subadults and skip-breeders are mobile. Second, distance to the fast-ice edge is a significant predictor of WESE distribution, where there exists a certain 'ideal' distance away that WESEs are more likely to be located (Larue et al. 2019). At the fast-ice edge at Cape Royds, the seals are risking predation by mammal-eating, type-B killer whales (*Orcinus orca*), which arrive in mid-November (Ainley et al. 2017). It appears that the break-out of fast-ice at Cape Royds and the associated increase in predation risk from killer whales may contribute to the decreasing trend of WESE hauling out through the season. Indeed, upon the arrival of killer whales no longer do WESE remain at the ice edge, heading to the interior of the McMurdo Sound fast ice (Saenz et al. 2020).

Therefore, we suggest that the apparent seasonal decrease of animals at Cape Royds is due to regional movements of WESE (Smith 1965; Ainley et al. 2015). This is an important caveat for our model, as it implies that the effect of date is unique and specific to the Cape Royds population, although analogous patterns should be found elsewhere. Fast-ice will

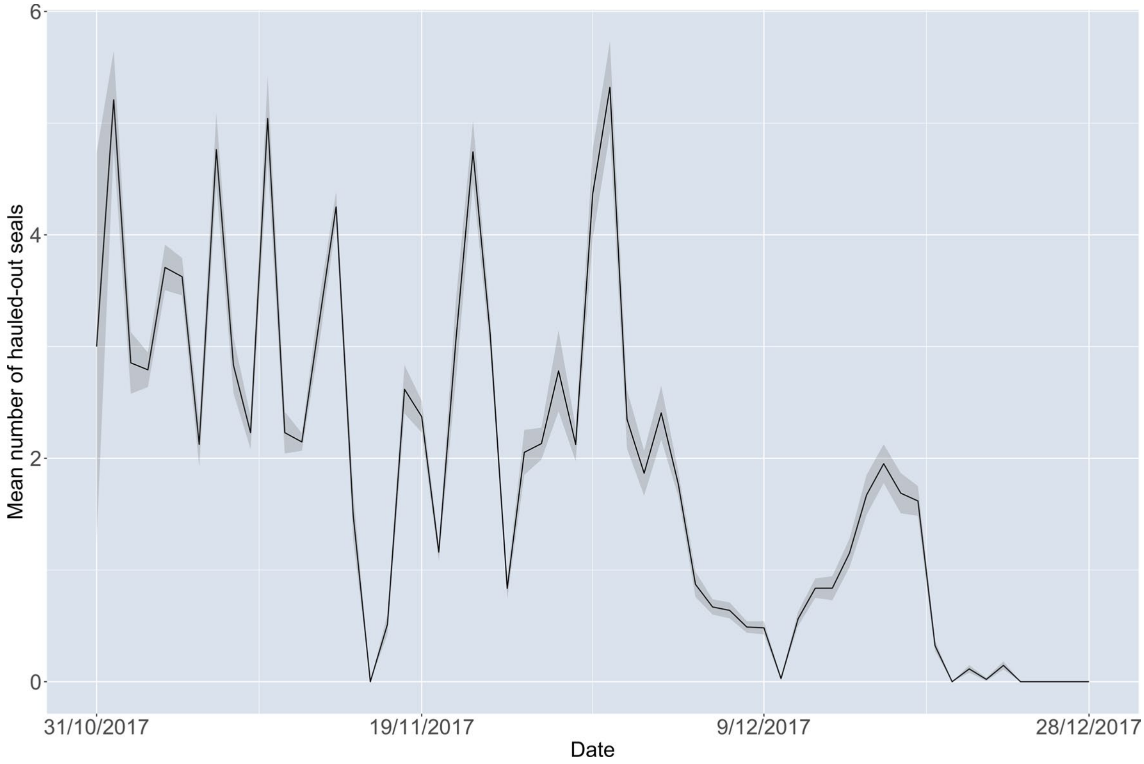

Fig. 3 Mean number of Weddell seals per photograph per day hauled out on the fast ice at Cape Royds, Antarctica between 31 October and 28 December 2017. Photographs were taken by three separate Cuddeback trail cameras at 30-min time intervals. Shading represents 1 standard error on either side of the mean

break out at different points in time around the continent, possibly exposing WESE populations to different predation pressures and their timing.

Haulout cycle

The presence of a haulout cycle was not surprising considering several other studies documented this phenomenon (Smith 1965; Siniff et al. 1971). Our model indicates that fewer WESEs haul out when it is colder, and windier, likely a function of thermoregulation, as wind speed is a significant contributor to heat loss in hauled-out WESEs (Mellish et al. 2015). These findings are in line with research conducted at Syowa station in East Antarctica, where it was found that fewer WESE hauled out when windspeeds exceeded 5.3 m/s or temperatures were below − 8.3 °C, in a behavioural attempt to manage thermoregulation and prevent heat-loss (Sato et al. 2003).

Part of the haulout cycle exhibited at Cape Royds may also be due to the diurnal pattern of prey availability (Stirling 1969b). The depth of Antarctic silverfish (*Pleuragramma antarcticum*) and Antarctic toothfish (*Dissostichus mawsoni*) correlates with surface light intensity, and they are both highest in the water column and thus more available when light intensity is at its lowest (Fuiman et al. 2002; Ainley et al. 2016)—the shadow of Mt Erebus (height 3800 m) spreads across southeastern McMurdo Sound during the ‘morning’ (2300–0600 local time). Indeed, unlike (Sato et al. 2003), we also observed that more seals were in the water when solar radiation was at its lowest amplitude. This pattern likely reflects observations being limited to early afternoon and therefore not capturing the diurnal variation in solar radiation that we observed, that can drive prey availability and seal haulout. In Arctic ringed seals (*Pusa hispida*) there is a diurnal haulout cycle associated with zooplankton movements (Von Duyke et al. 2020), and grey seals (*Halichoerus grypus*) show a cycle in foraging behaviour linked to diurnal movements of sand eels (Photopoulou et al. 2014). Time-depth recordings of eight adult WESEs from the eastern Weddell Sea (Plötz et al. 2001) found that foraging dives increased in depth between 0800 and 1000 local time. Thus, our observation of a diurnal WESE haulout cycle may be partially a consequence of a foraging pattern driven by diurnal variation in prey availability (see also Beltran et al. 2021).

Our model suggests that this study did not capture all the drivers of diurnal variation in non-breeding WESEs at Cape Royds. Due to higher daily counts of seals at Big Razorback (around 20 per day), one of the pupping sites south of Cape Royds (Fig. 1), Banner (2012) was able to

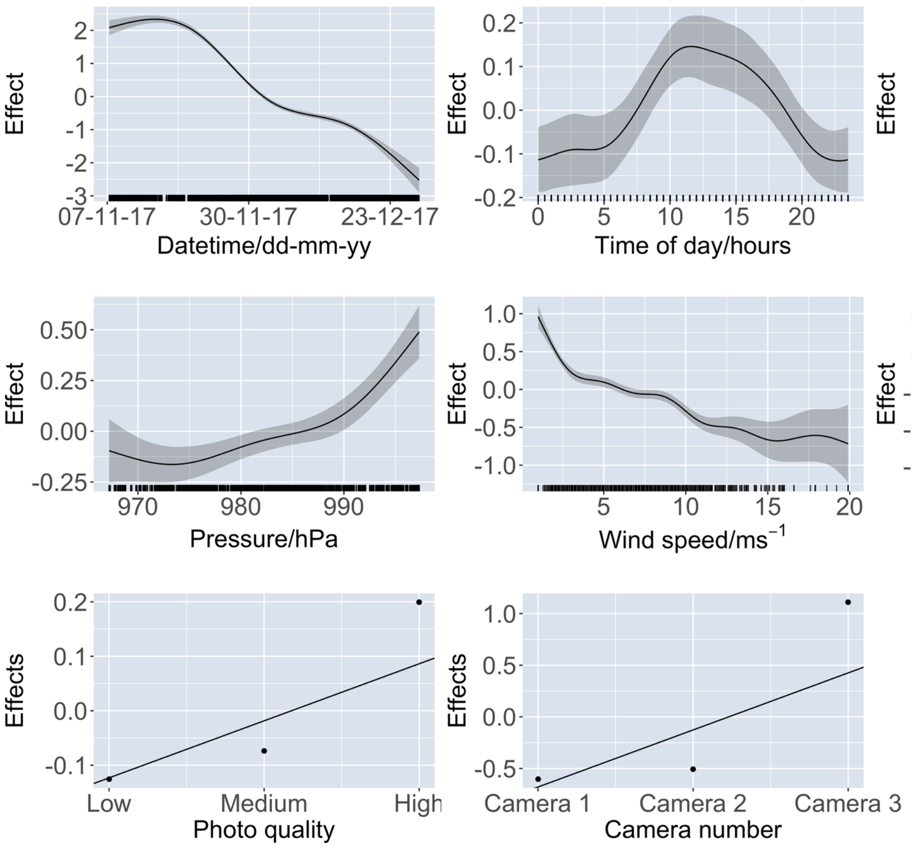

Fig. 4 Estimated smoothing plots for covariates of the Generalised Additive Model (GAM) used to explain non-breeding Weddell seal haulout behaviour at Cape Royds, Antarctica between 31 October and 28 December 2017. Shading represents two standard errors around the respective smoothing function, whilst lugs on the x-axis show distribution of data points informing the smoothing function. The units of the Y-axis are in number of seals, identifying what effect each covariate has on the mean number of seals, all else being equal. Date and time of day refer to the date and time that photographs at Cape Royds were taken with Cuddeback trail cameras, from which the number of Weddell seals hauled out was counted. All environmental variables are collected for those exact dates and times from an automated weather station associated with the PenguinCam at Cape Royds, Antarctica

generate a separate haulout cycle for each day of the study. Haulout patterns observed in both studies demonstrated peak haulout between 1200 and 2000 NZST (Fig. 4). A key point of distinction between the research of Banner (2012) and our study is that we looked at non-breeding WESE, in contrast to pup-suckling female adults. The fact that this haulout cycle persists between both demographics drives home the point that it is not present purely as a result of females needing to balance the acts of foraging and weaning their pups (e.g., Beltran et al. 2017).

Concluding remarks

Better census data are critical in understanding and monitoring the broad-scale ecology of the WESE in both the Ross Sea region and coastal Antarctica as a whole. Given the species' circumpolar distribution (LaRue et al. 2021), they will experience a range of environmental conditions, changing at different rates, from climatic changes and less sea ice to altered fish availability (Vaughan et al. 2003; Joughin et al. 2014; Ainley et al. 2015; Salas et al. 2017). Monitoring how the WESE reacts to these changes will improve our understanding of the impacts that environmental change will have on Antarctic ecosystems, and especially the Ross Sea Region MPA, the WESE being an "indicator species" (Koerich et al. 2022; CCAMLR 2018a, b). The need to adjust census-based data is paramount to establishing regional population estimates. In a field increasingly relying on remote sensing, between-site calibration of haulout cycles will remain important.

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Author contributions AA wrote the main manuscript text, conducted statistical analysis, and prepared figures. JT provided supervisory guidance throughout the research process. JP and DA collected the original data on which this analysis was built. DG provided guidance with statistics. MLR provided guidance throughout the entire research process and contributed significantly to manuscript text. All authors reviewed and provided feedback on the manuscript.

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Declarations

Competing interests The authors declare no competing interests.

References

Abrams PA, Ainley DG, Blight LK, Dayton PK, Eastman JT, Jacquet JL (2016) Necessary elements of precautionary management: implications for the Antarctic toothfish. Fish Fish 17:1152–1174. https://doi.org/10.1111/faf.12162

Ainley DG, Larue MA, Stirling I, Stammerjohn S, Siniff DB (2015) An apparent population decrease, or change in distribution, of Weddell seals along the Victoria land coast. Mar Mamm Sci 31(4):1338–1361. https://doi.org/10.1111/mms.12220

Ainley DG, Ballard G, Eastman JT, Evans CW, Nur N, Parkinson CL (2016) Changed prevalence, not absence, explains toothfish status in McMurdo sound. Antarct Sci 29(2):165–171. https://doi.org/10.1017/S0954102016000584

Ainley DG, Lindke K, Ballard G, Lyver POB, Jennings S, Toniolo V, Pennycook J, Massaro M, Santora JA (2017) Spatio-temporal occurrence patterns of cetaceans near Ross island, Antarctica, 2002–2015: implications for food web dynamics. Polar Biol 40(9):1761–1775. https://doi.org/10.1007/s00300-017-2100-9

Ainley DG, Cziko PA, Nur N, Rotella JJ, Eastman JT, LaRue M, Stirling I, Abrams PA (2021) Further evidence that Antarctic toothfish are important in Weddell seal diet. Antarct Sci 33:17–29. https://doi.org/10.1017/S0954102020000437

Andrews RD, Pitman RL, Ballance LT (2008) Satellite tracking reveals distinct movement patterns for Type B and Type C killer whales in the southern Ross Sea. Antarct Polar Biol 31(12):1461–1468. https://doi.org/10.1007/s00300-008-0487-z

Banner KM (2012). Correcting for time-of-day to compare satellite images and ground counts of Weddell seals in big Razorback Haulout (Erebus Bay, Antarctica). University of Montana. http://www.math.montana.edu/grad/writing-projects/12banner.pdf

Beltran RS, Testa JW, Burns JM (2017) An agent-based bioenergetics model for predicting impacts of environmental change on a top marine predator, the Weddell seal. Ecol Modelling 351:36–50. https://doi.org/10.1016/j.ecolmodel.2017.02.002

Beltran RS, Kilpatrick AM, Breed GA, Adachi T, Takahashi A, Naito Y, Robinson PW, Smith WO Jr, Kirkham AL, Burns JM (2021) Seasonal resource pulses and the foraging of depth of a Southern ocean top predator. Proc R Soc B 288:20202817. https://doi.org/10.1098/rspb.2020.2817

Blanchet MA, Lydersen C, Ims RA, Kovacs KM (2015) Seasonal, oceanographic and atmospheric drivers of diving behaviour in a temperate seal species living in the high arctic. PLoS ONE 10(7):1–28. https://doi.org/10.1371/journal.pone.0132686

Ciannelli L, Fauchald P, Chan KS, Agostini VN, Dingsør GE (2008) Spatial fisheries ecology: recent progress and future prospects. J Mar Syst 71(3–4):223–236. https://doi.org/10.1016/j.jmarsys.2007.02.031

Fuiman LA, Davis RW, Williams TM (2002) Behavior of midwater fishes under the Antarctic ice: observations by a predator. Mar Biol 140:815–822

Garrott RA, Rotella JJ, Siniff DB, Parkinson CL, Stauffer GE (2012) Environmental variation and cohort effects in an Antarctic predator. Oikos 121(7):1027–1040. https://doi.org/10.1111/j.1600-0706.2011.19673.x

Joughin I, Smith BE, Medley B (2014) Marine ice sheet collapse potentially under way for the Thwaites glacier basin, west Antarctica. Science. https://doi.org/10.1126/science.1249055

Kennicutt MC, Bromwich D, Liggett D, Njåstad B, Peck L, Rintoul SR, Ritz C, Siegert MJ, Aitken A, Brooks CM, Cassano J, Chaturvedi S, Chen D, Dodds K, Golledge NR, Le Bohec C, Leppe M, Murray A, Nath PC, Chown SL (2019) Sustained Antarctic research: a 21st century imperative. One Earth 1(1):95–113. https://doi.org/10.1016/j.oneear.2019.08.014

Kim S, Saenz B, Scanniello J, Daly K, Ainley D (2018) Local climatology of fast ice in McMurdo sound. Antarct Antarct Sci 30(2):125–142. https://doi.org/10.1017/S0954102017000578

Koerich G, Fraser CI, Lee CK, Morgan FJ, Tonkin JD (2022) Forecasting the future of life in Antarctica. Trends Ecol Evol. https://doi.org/10.1016/j.tree.2022.07.009

Lake SE, Burton HR, Hindell MA (1997) Influence of time of day and month on Weddell seal haulout patterns at the Vestfold hills. Antarct Polar Biol 18(5):319–324. https://doi.org/10.1007/s003000050194

LaRue MA, Rotella JJ, Garrott RA, Siniff DB, Ainley DG, Stauffer GE, Porter CC, Morin PJ (2011) Satellite imagery can be used to detect variation in abundance of Weddell seals (*Leptonychotes weddellii*) in Erebus Bay. Antarct Polar Biol 34(11):1727–1737. https://doi.org/10.1007/s00300-011-1023-0

Larue MA, Salas L, Nur N, Ainley DG, Stammerjohn S, Barrington L, Stamatiou K, Pennycook J, Dozier M, Saints J, Nakamura H (2019) Physical and ecological factors explain the distribution of Ross sea Weddell seals during the breeding season. Mar Ecol Prog Ser 612:193–208. https://doi.org/10.3354/meps12877

LaRue MA, Ainley DG, Pennycook J, Stamatiou K, Salas L, Nur N, Stammerjohn S, Barrington L (2020) Engaging "the crowd" in remote sensing to learn about habitat affinity of the Weddell seal in Antarctica. Remote Sens Ecol Conserv 6(1):70–78. https://doi.org/10.1002/rse2.124

LaRue M, Salas L, Nur N, Ainley D, Stammerjohn S, Pennycook J, Dozier M, Saints J, Stamatiou K, Barrington L, Rotella J (2021) Insights from the first global population estimate of Weddell seals in Antarctica. Sci Adv. https://doi.org/10.1126/sciadv.abh36743655208

Marra G, Radice R (2010) Penalised regression splines: theory and application to medical research. Stat Methods Med Res 19(2):107–125. https://doi.org/10.1177/0962280208096688

Marvin DC, Koh LP, Lynam AJ, Wich S, Davies AB, Krishnamurthy R, Stokes E, Starkey R, Asner GP (2016) Integrating technologies for scalable ecology and conservation. Glob Ecol Conserv 7:262–275. https://doi.org/10.1016/j.gecco.2016.07.002

McIntosh RR, Kirkwood R, Sutherland DR, Dann P (2015) Drivers and annual estimates of marine wildlife entanglement rates: a long-term case study with Australian fur seals. Mar Pollut Bull 101(2):716–725. https://doi.org/10.1016/j.marpolbul.2015.10.007

Mellish JAE, Hindle AG, Horning M (2015) Heat loss in air of an Antarctic marine mammal, the Weddell seal. J Comp Physiol b: Biochem, Syst Environ Phys 185(1):143–152. https://doi.org/10.1007/s00360-014-0868-2

Monaghan AJ, Bromwich DH, Powers JG, Manning KW (2005) The climate of the McMurdo, Antarctica, region as represented by one year of forecasts from the Antarctic mesoscale prediction system. J Clim 18(8):1174–1189. https://doi.org/10.1175/JCLI3336.1

Moxley JH, Bogomolni A, Hammill MO, Moore KMT, Polito MJ, Sette L, Sharp WB, Waring GT, Gilbert JR, Halpin PN, Johnston DW (2017) Google haulout: earth observation imagery and digital aerial surveys in coastal wildlife management and abundance estimation. Bioscience 67(8):760–768. https://doi.org/10.1093/biosci/bix059

Photopoulou T, Fedak MA, Thomas L, Matthiopoulos J (2014) Spatial variation in maximum dive depth in gray seals in relation to foraging. Mar Mamm Sci 30(3):923–938. https://doi.org/10.1111/mms.12092

Plötz J, Bornemann H, Knust R, Schröder A, Bester M (2001) Foraging behaviour of Weddell seals, and its ecological implications. Polar Biol 24(12):901–909. https://doi.org/10.1007/s003000100297

Robinson ES (1963) Geophysical investigations in McMurdo sound. Antarct J Geophys Res 68(1):257–262. https://doi.org/10.1029/jz068i001p00257

Rotella JJ, Link WA, Chambert T, Stauffer GE, Garrott RA (2012) Evaluating the demographic buffering hypothesis with vital rates estimated for Weddell seals from 30 years of mark-recapture data. J Anim Ecol 81(1):162–173. https://doi.org/10.1111/j.1365-2656.2011.01902.x

Saenz BT, Ainley DG, Daly KL, Ballard G, Conlisk E, Elrod ML, Kim SL (2020) Drivers of concentrated predation in an Antarctic marginal-ice-zone food web. Sci Rep 10:7282. https://doi.org/10.1038/s41598-020-63875-y

Salas L, Nur N, Ainley D, Burns J, Rotella J, Ballard G (2017) Coping with the loss of a large, energy-dense prey: a potential bottleneck for Weddell seals in the Ross sea. Ecol Appl 27(1):10–25. https://doi.org/10.1002/eap.1435

Sato K, Tsuchiya Y, Kudoh S, Naito Y (2003) Meteorological factors affecting the number of Weddell seals hauling-out on the ice during the molting season at Syowa station, east Antarctica. Polar Biosci 16:98–103

Siniff DB (1991) An overview of the ecology of Antarctic seals. Integr Comp Biol 31(1):143–149. https://doi.org/10.1093/icb/31.1.143

Siniff DB, Tester JR, Kuechle VB (1971) Some observations on the activity patterns of Weddell seals as recorded by telemetry. Antarct Pinnipedia. https://doi.org/10.1029/ar018p0173

Siniff DB, DeMaster DP, Hofman RJ, Eberhardt LL (1977) An analysis of the dynamics of a Weddell seal population. Ecol Soc Am 31(4):337–367

Siniff DB, Garrott RA, Rotella JJ, Fraser WR, Ainley DG (2008) Opinion: projecting the effects of environmental change on Antarctic seals. Antarct Sci 20(5):425–435. https://doi.org/10.1017/S0954102008001351

Smith MSR (1965) Seasonal movements of the Weddell seal in McMurdo sound. Antarctica 29(3):464–470

Stearns CR (1988) Research results from Antarctic automatic weather stations. Dep Meteorol Univers Wis Madison 26(1):45–61

Stirling I (1969a) Distribution and abundance of the Weddell seal in the western Ross Sea, Antarctica. NZ J Marine Freshw Res 3(2):191–200. https://doi.org/10.1080/00288330.1969.9515288

Stirling I (1969b) Ecology of the Weddell Seal in McMurdo Sound Antarctica. Ecology 50(4):573–586. https://doi.org/10.2307/1936247

Testa JW, Siniff DB (1987) Population dynamics of Weddell seals (*Leptonychotes weddellii*) in McMurdo sound. Antarct Ecol Monogr 57(2):149–165

Thomas JA, DeMaster DP (1983) Diel haulout patterns of Weddell seal (*Leptonychotes weddelli*) females and their pups. Can J Zool 61(9):2084–2086. https://doi.org/10.1139/z83-273

Vaughan DG, Marshall GJ, Connolley WM, Parkinson C, Mulvaney R, Hodgson DA, King JC, Pudsey CJ, Turner J (2003) Recent rapid regional climate warming on the Antarctic Peninsula. Clim Change 60:243–274. https://doi.org/10.1017/S0016756800021464

Von Duyke AL, Douglas DC, Herreman JK, Crawford JA (2020) Ringed seal (*Pusa hispida*) seasonal movements, diving, and haulout behavior in the Beaufort, Chukchi, and Bering seas (2011–2017). Ecol Evol 10(12):5595–5616. https://doi.org/10.1002/ece3.6302

Wickham et al (2019) Welcome to the tidyverse. J Open Sour Softw 4(43):1686. https://doi.org/10.21105/joss.01686

Wood SN (2008) Fast stable direct fitting and smoothness selection for generalized additive models. J R Stat Soc Ser b: Stat Methodol 70(3):495–518. https://doi.org/10.1111/j.1467-9868.2007.00646.x